PROJECT REPORT
2001-14
FINAL PROJECT REPORT

sustainable forest management network

réseau sur la gestion durable des forêts

Pattern and Process in the Boreal Forest Understory

S. Ellen Macdonald, Lisa Cuthbertson, Brent Frey, Treena Fenniak,
Lance Lazaruk, Steve Kembell, Suzanne Mills, Vic Lieffers,
Mark Dale, K.I. Mallett, Alison Munson, Dale Vitt

A Network of Centres of Excellence
Un réseau de centres d'excellence

For copies of this or other SFM publications contact:

Sustainable Forest Management Network
G208 Biological Sciences Building
University of Alberta
Edmonton, Alberta, T6G 2E9
Ph: (780) 492 6659
Fax: (780) 492 8160
http://www.ualberta.ca/sfm

ISBN 1-55261-124-8

Pattern and Process
in the Boreal Forest Understory

SFM Network Project: Patterns and processes of the boreal forest understory: a comparison of post-fire and post-harvest dynamics

by

S. Ellen Macdonald[1], Lisa Cuthbertson[1], Brent Frey[1], Treena Fenniak[1], Lance Lazaruk[1], Steve Kembell[2], Suzanne Mills[1], Vic Lieffers[1], Mark Dale[2], K.I. Mallett[3], Alison Munson[4], Dale Vitt[5]

[1] Department of Renewable Resources, University of Alberta, Edmonton, AB T6G 2E3

[2] Department of Biological Sciences, University of Alberta, Edmonton, AB Y6G 2E9

[3] Canadian Forest Service, Northern Forestry Centre, Edmonton, AB

[4] Dép. Sciences du bois et de la forêt, Université Laval, Sainte-Foy,Québec

[5] Dept of Plant Biology, Southern Illinois University, Carbondale, Illinois

Authorship Note: The principle author of the report is listed first followed by the names of the six graduate student authors (in alphabetical order) followed by the remaining graduate supervisors (in alphabetical order)

May 2001

ABSTRACT

We report on the results of six different graduate student projects, each of which examined different aspects of pattern and process in the boreal forest understory as part of the EMEND (Ecosystem Management Emulating Natural Disturbance) experiment conducted in northwestern Alberta. Vascular and non-vascular understory plants were examined, as were wood-decay and ectomycorrhizal fungi.

The wood decay fungi *Armillaria sinapina* was found to be infecting 90% of healthy hardwood trees in pure hardwood-dominated forest stands. As the number of hardwood trees present in a stand increased, the presence of *A. sinapina* infecting both hardwoods and softwoods increased. *A. sinapina* was more likely to be present in larger diameter, deciduous logs, which were in contact with the ground. *A. sinapina* occurred in the forest floor in the form of rhizomorphs and its presence was not dependent on basic soil nutrients or moisture. It is unknown if *A. sinapina* could be a problem in regenerating mixed-wood stands but our finding of its widespread occurrence in healthy stands suggests the need for awareness of the potential for outbreaks.

The interactive effects of various partial-cut harvest types and forest floor disturbance [burn, mix (organic matter mixed with mineral soil), scalp (forest floor removed), mound (inverted mineral-cap) and control] on vegetation and nutrient dynamics were evaluated. Forest floor treatments substantially altered nutrient availability; burns had the highest nutrient availability while controls had the lowest. Burning promoted higher cover of *E. angustifolium,* while scalping promoted root suckering by *Populus spp.* Mixing and mounding provided the best control of competing vegetation. Short-term nutrient availability can be increased or diminished by forest floor treatments. Higher nutrient availability may be more of a benefit to competing vegetation rather than planted seedlings, or if vegetation establishment is poor nutrients may be subject to leaching. Mixing decreased mineralization in the short-term, and this may contribute to greater control of vegetation and less nutrient leaching. Forest floor treatments can be used to promote different types of vegetation development following harvesting.

Canopy - understory relationships were examined in hardwood-dominated and mixedwood forests. Canopy trees, understory trees and understory vegetation were found to be very patchy in their distribution. Spruce seedlings tended to occur in canopy gaps while aspen saplings often occurred under both canopy gaps and closed canopy. Understory species richness, diversity and total cover were all highest under canopy gaps. Trends were more pronounced in Conifer-dominated and Mixed stands than in Aspen-dominated stands. These results suggest that partial-cutting may have less effect on understory plants in hardwood-dominated stands than in mixedwood or conifer-dominated forest.

Occurrence of active white spruce root tips and the richness and composition of the white spruce ectomycorrhizal (ECM) community was examined in response to various partial-cut harvesting treatments and burns in conifer-dominated forest. The total number white spruce fine root tips, the percentage of active white spruce fine root tips, the richness and diversity of white spruce ectomycorrhizae all decreased with increasing harvesting intensity. Within partial-cut compartments the magnitude of this decrease was greater in the machine corridors compared to the residual strips. Furthermore, the density of fine root tips and ECM diversity was the lowest in the burned portion of the burned site. There were considerably differences in the composition of the ECM community among treatments with clearcuts and burns being most different than the uncut control, although these two treatments also differed from one another. Both the removal of the ECM fungi's host (ie. white spruce trees) and the compaction associated with the harvesting equipment are thought to have contributed to the results of this study.

Richness, diversity and composition of nonvascular plants (bryophytes) were examined at a variety of spatial scales in conifer-dominated forest. The number of bryophyte species present was first and foremost related to the type of microsite. Large deciduous and coniferous logs in different stages of decay are very important for bryophyte species diversity. Species and decay class of logs and stumps were important in controlling bryophyte richness and composition. At intermediate spatial scales bryophyte species diversity was fairly homogenous and only loosely linked to microclimate and substrate availability. At the mesosite scale decreasing tree abundance increased bryophyte species richness. The results imply that the presence of large woody debris in different stages of decay (both coniferous and deciduous) and disturbed patches of forest floor, are the most important indicators of bryophyte species diversity. Tree fall disturbances, deciduous and coniferous large sized dead woody debris in a variety of decay classes, and a moist understory are essential for the maintenance of bryophyte species diversity. Since many bryophyte species are dependent on large live and dead aspen within the favourable moisture regime of a conifer dominated canopy mixed wood management will likely also be important for maintenance of bryophyte species diversity in the boreal forest.

Understory species composition and the associated microenvironment were examined in conifer-dominated, mixedwood, and deciduous-dominated forest stands under four treatments: clearcut, 20% retention partial-cut, 75% retention partial-cut, uncut controls. Partial-cut harvesting resulted in similar changes in understory environment, regardless of forest canopy composition. Species diversity and richness were lower in clearcut and 20% retention partial-cuts than in the 75% retention and uncut controls. Understory species composition became less similar among treatments over time following harvesting. Clearcut and 20% treatment stands diverged from 75 % retention and uncut controls. Understory species composition became more similar among forest types (conifer-dominated, mixedwood, deciduous-dominated) over time following partia-cut harvesting. Results also suggest that the establishment and success of understory species after partial and total canopy harvesting may be different in different community types; partial-cut harvesting may have less impact on deciduous dominated forests than on those with a significant component of conifer in the canopy.

ACKNOWLEDGEMENTS

In addition to the funding provided by the Sustainable Forest Management Network of Centres of Excellence we are grateful to the following for their generous financial support: Daishowa-Marubeni International Ltd., Canadian Forest Products Ltd., Canadian Circumpolar Institute and Dept. of Indian and Northern Affairs, Natural Sciences and Engineering Research Council (Canada), Canadian Forest Service, Biodiversity Challenge Grants Program funded by Alberta Conservation Association, and from the University of Alberta: the Department of Biological Sciences, Faculty of Science, Department of Renewable Resources, and Faculty of Graduate Studies and Research.

Field assistance was provided by: John Dale, Erin Flynn, Carmen Gibbs, Christopher Guest, Charlene Hahn, Jeff Heinlen, Jyrchi Jalonen, Athena McKown, Johanna Murdoch, Jacqueline Pollard, and Pete Present as well as the EMEND core crew in 1999 and 2000.

In addition, we thank the following for their contributions to various aspects of the research described herein: Peter Blenis, David Board, John Brzustowski, Hannah Buckley, Natalie Cleavitt, Joe Crumbaugh, Bill deGroot, Jennifer Doubt, Lars Hedenas, Robert Ireland, Norton Miller, Derek Sidders, Lars Soderstrom, and Rob Taylor.

INTRODUCTION

Many scale-dependent variables affect the distribution of plants, and thus the composition of plant communities. Mechanisms that operate at small scales, such as germination micro-sites, litter depth, and neighbourhood effects, relate directly to the abundance and fitness of individuals within a population (Harper 1977). Local climate, soils, and frequency and intensity of disturbance, operate at larger geographic scales, affecting the distribution of populations at the landscape level (Spurr and Barnes 1980). Species coexistence in communities may be explained through differences in resource use (Whittaker 1975). However, models have also highlighted the key roles of environmental variability, establishment processes, and/or limiting resources in plant community dynamics (Grubb 1977, Grime 1979, Tilman 1988). A common theme of models that predict plant community composition (Grubb 1977, Grime 1979, Tilman 1988) is that disturbance and the availability of resources interact with the species' competitive ability.

An increasing focus on the ecological sustainability of forest harvesting has driven interest in alternative forest management practices, which attempt to more closely mimic the process, and resulting pattern, of natural disturbance. At the stand scale partial-cut harvesting is one such practice. A major difference between fire (the predominant natural disturbance in the western boreal forest) and forest harvesting is the within-stand heterogeneity and the amount of residual material left on-site following disturbance. By leaving more residual live and dead material on-site managers hope to achieve a result more similar to natural disturbance than would clearcutting; in turn, the assumption is that ecosystem function will be better preserved and natural levels of biodiversity will be maintained. A key pre-requisite to the adoption of natural disturbance based management is a clear understanding of patterns and processes driving biodiversity in undisturbed forests, as well as their response to disturbance. The research program described herein included six different projects, each of which examined different aspects of pattern and process in the boreal forest understory. Our objective was to develop a better understanding of patterns and processes in vascular and non-vascular plants as well as mycorrhizal and wood-decay fungi in undisturbed western boreal forest. In addition we examined the impact of disturbance on vascular plants and on mycorrhizal fungi. In this report each project is summarized separately.

Spatial Pattern of *Armillaria sinapina* in Stands of Boreal Mixed-wood Forest in North-Western Alberta

Lisa Cuthbertson, S. Ellen Macdonald, and K.I. Mallett

Introduction

Armillaria root disease is an important disease of trees in Canada (Mallett 1990). The disease is caused by several species of the soil inhabiting fungus *Armillaria*. They are a common group of root-infecting fungi with a wide host range, including angiosperm and gymnosperm trees, shrubs, and herbs (Rayner and Boddy 1988). *Armillaria* species also behave saprophytically by causing wood-decay in the form of 'white rot' in woody substrates, which plays a role in decomposition of wood (to release the nutrients that are locked within) (Rayner and Boddy 1988). They are able to disperse vegetatively by rhizomorphs through the forest floor, subcortically by mycelia in woody substrates, by contact between healthy and diseased roots (root to root contact) and through the air by basidiospores (sexually produced, haploid spores) (Rayner and Boddy 1988).

Armillaria species are root and butt rot pathogens of trees in the boreal forest of Canada. In addition to rotting roots and butts of trees, these fungi also function in decomposing logs on the forest floor. In Alberta, the root and butt rot pathogen, *Armillaria sinapina*, has mainly been found associated with declining or dead hardwood trees.

Armillaria sinapina Bérubé & Dessureault is a known biological species in the Canadian boreal forest (Bérubé and Dessureault 1988, Mallett 1990). To date, there are few studies that have focused on identifying the important environmental predictors of the occurrence of *A. sinapina* in these forests. So far, all that has been established is that the species is readily baited from the soil with trap logs and it has been suggested that it prefers deciduous over coniferous hosts (Mallett 1990, Blenis et al. 1995).

The objectives of this research were to:

1) describe the pattern of occurrence of Armillaria sinapina, in forest stands, by mapping its presence on living and dead trees, downed woody material (DWM) and in the soil;

2) better understand this pattern by relating it to measured environmental variables in mixed-wood stands in the boreal forest of north-western Alberta.

Methods

The research took place north-west of Peace River, Alberta, at the EMEND field site. I worked in three forest types, softwood dominant, hardwood dominant and mixedwood ranging in age from 90 to 120 years old. The spatial pattern of occurrence of *Armillaria sinapina* was documented in forest stands by mapping its presence in live and dead trees, in the soil, and in logs, for nine 40 × 40 meter plots. Species identifications were made by DNA analysis (RFLPs) on selected sub-samples.

Summary of data analysis

To determine the best predictors of the presence of *Armillaria sinapina* within samples (trees, snags, stumps, downed woody material, forest floor cores, and trap logs) in plots, forward selection stepwise multiple logistic regressions were performed using generalised linear models assuming a binomial error distribution (Legendre and Legendre 1998). These regressions related the presence of *A. sinapina* to the measured environmental and spatial variables associated with each type of sample. Ripley's K-function was used to analyze spatial point patterns within the nine plots.

Results

Some of our major findings were:

1) the pattern of infection, under a distance of 10 meters, appears to be no different than a random pattern;

2) in pure hardwood stands greater than 90% of healthy hardwoods were infected by *A. sinapina*. This is an exciting result because we were not aware of the extent of healthy trees being infected by this fungus;

3) As the number of hardwood trees present in the canopy increased, the presence of *A. sinapina* infecting trees increased; and

4) *A. sinapina* was more likely to be present in larger diameter, deciduous logs, which were in contact with the ground.

Management applications

There may be some significant forest management implications if the goal is to regenerate hardwoods following harvest in sites where *A. sinapina* is prevalent. To date, it is unknown if *A. sinapina* could be a problem in regenerating mixed-wood stands. This research is one small step in understanding the ecology of *A. sinapina* in mixed-wood forests of Alberta.

Conclusions

This research is unique in that this is the first time that the occurrence of *A. sinapina* in particular has been studied. The most important result was that in the purely deciduous plots, greater than 90% of asymptomatic deciduous trees were infected by *A. sinapina*. *A. sinapina* was more likely to be found on DWM of larger diameter, that were laying on the ground, and were at later stages of decay. *A. sinapina* occurred in the forest floor in the form of rhizomorphs and its presence was not dependent on basic soil nutrients or moisture. The fungus was easily baited from the soil using trap logs. On a small scale (less than 10 m) the pattern of infection by *A. sinapina* appeared to be no different than random.

More detailed information for this study may be found in:

Cuthbertson, L. (in progress). Spatial Pattern of *Armillaria sinapina* in Stands of Boreal Mixed-wood Forest in North-Western Alberta. M.Sc. Thesis, Department of Renewable Resources, University of Alberta, Edmonton, Alberta.

Impacts of Forest Floor Disturbance on Vegetation and Nutrient Dynamics in Clearcut and Partial-Cut Stands

Brent R. Frey, Victor J. Lieffers, Alison D. Munson

Abstract

The interactive effects of harvest type and forest floor disturbance on vegetation and nutrient dynamics were evaluated in the boreal mixedwood of Alberta. The experiment used a split-plot design with harvest types of clearcut and partial-cut, and forest floor disturbances of burn, mix (organic matter mixed with mineral soil), scalp (forest floor removed), mound (inverted mineral-cap) and control. Ion exchange resins were used to assess availability of NO_3-N, NH_4-N, P, Ca, Mg and K in all disturbances, and incubated soil cores were used to assess N mineralization. There tended to be higher Mg and Ca in the clearcut, however there was otherwise no clear impact of harvest intensity on nutrient availability or mineralization rates. Forest floor treatments substantially altered nutrient availability between the different disturbances. Within forest floor disturbances, burns had the highest availability of NH_4-N, NO_3-N, and P, while controls had the lowest NO_3-N availability. Ca and Mg were highest, but K lowest, in the scalps in both harvest types. Vegetation response was evaluated by species, percent cover and height for all shrubs, *Populus spp*. and *Epilobium angustifolium*. Burning promoted higher cover of *E. angustifolium,* while scalping promoted root suckering by *Populus spp.* Mixing and mounding provided the best control of competing vegetation.

These findings have several implications. First, they suggest that short-term nutrient availability can be increased or diminished depending on the type of disturbance. Higher nutrient availability may be more of a benefit to competing vegetation rather than planted seedlings, or alternatively if vegetation establishment is poor, nutrients may be subject to leaching. Therefore the treatments with higher nutrient availability such as burns, mounds or scalps may promote more vigorous vegetation development and or be subject to nutrient leaching. In contrast, mixing decreased mineralization in the short-term, and this may contribute to greater control of vegetation and less nutrient leaching. Second, these finding suggest that certain forest floor treatments control the establishment of competing vegetation. Clearly mixing reduced vegetation competition and improved light transmission, whereas burning and scalping produced high levels of cover and reduced light transmission. Third, it was evident that different treatments could promote different types of vegetation. Understanding the response that a certain treatment induces could be useful if by establishing a certain type of vegetation, another more aggressive competitor could be controlled. Last, although aspen regeneration was not a focus of this study, it did appear that a light scalp that removed much of the forest floor stimulated aspen suckering, and thus may be a suitable site preparation treatment for aspen regeneration.

Introduction

In the mixed-wood boreal forest of Alberta, establishment of white spruce in harvested stands is an important, yet challenging silvicultural objective. Regeneration of white spruce is highly affected by microsite conditions; vegetation competition, soil temperature and nutrient availability all significantly affect white spruce growth (Brand and Janas 1987, Delong et al. 1997). Vegetation competition is probably the most important determinant of seedling success, as it affects not only light availability but also availability of soil nutrients and moisture (Munson et al. 1993). Such species as *Epilobium angustifolium* or *Calamagrostis canadensis* establish vigorously on boreal sites following disturbances such as clearcutting (Hogg and Lieffers 1991) or fire (Dyrness and Norum 1983) and pose significant competition problems. The growth of spruce will be highly dependent upon the control of such vigorous competitors (Thevathasan et al. 2000). Silvicultural strategies other than use of herbicides are sought to control competing vegetation for the successful establishment of white spruce.

Partial-cut systems have received increasing attention as a means to control competitor vegetation and improve seedling establishment. Silvicultural systems that retain partial canopies will limit light conditions in the understory and may shade out competitors sufficiently to allow establishment of spruce seedlings (Lieffers et al. 1993). For example, both *E. angustifolium* and *C. canadensis* species are adapted to open light conditions of disturbed sites, and tend to be less vigorous and abundant under denser canopies. At 40 percent light, white spruce seedling growth is maintained while cover and height of *C. canadensis* and *E. angustifolium* are significantly diminished (Lieffers and Stadt 1994).

Forest floor treatments provide another silvicultural option for limiting competing vegetation and improving the seedling microsite (Lieffers et al. 1993). In boreal forests, the forest floor represents the principal reservoir of nutrients (Van Cleve et al. 1983) thus silvicultural options that manipulate the forest floor may have significant effects upon nutrient cycling and plant growth. Significant increases in nitrogen availability in clearcuts have been noted (Binkley 1984). Moreover, rates of mineralization may increase under site preparation (Vitousek et al. 1992). However, responses are difficult to generalize and nutrients do not respond uniformly. Noteable changes in soil properties including conductivity, pH, and nutrient concentrations may only occur when substantial amounts of forest floor removal occur (Van Cleve et al. 1983). In boreal forests, fire plays a dominant role in forest floor disturbance. Forest floor consumption by fire may result in increased N (nitrogen) concentrations under moderate burns, but may decrease in heavier burns whereas P (phosphorous) tends to increase with burn intensity (Dyrness and Norum 1983). Soil pH, and cation exchange capacity (CEC) generally increase under burning, although the latter may increase or decrease depending on the extent of forest floor loss (Feller 1982).

Mechanical site preparation or prescribed burning may be used in conjunction with different cutting systems for preparing forest sites for regeneration. There has been little investigation into the use of partial-cut systems with understory site preparation. The application of different site preparation techniques under different canopy levels will alter microsite conditions, reducing insolation in the partial cuts relative to clearcuts which may result in lower soil temperatures, microbial activity and mineralization rates, all possibly affecting plant response. Little is known of the effects of alternative systems on organic matter and nutrient dynamics (Prescott 1997). Anticipating the growth response of seedlings under different levels of overstory competition is important for understanding the effects of alternative silvicultural systems that retain overstory (Palik et al. 1997). In addition, little attention has been given to the relationships between fire intensity and seedling establishment and success (Weber et al. 1995). A number of strategies ranging from deep burns, to soil scalps and mounds or partial canopy retention may be used for promoting successful seedling establishment (Lieffers et al. 1993).

This study examined the impacts of forest floor disturbance on nutrient availability and vegetation development within clearcut and partial cut stands, with the following objectives:

1. To compare the effects of different types of forest floor disturbance on nutrient availability and mineralization under different canopy levels.

2. To assess the response of understory vegetation to forest floor disturbance under different canopy levels.

3. To examine the relationships between measured environmental variables, nutrient availability, and vegetation development in the different disturbances to evaluate their suitability for regenerating white spruce.

Methods

The experiment was initiated in May 1999 at the EMEND (Ecosystem Management Emulating Natural Disturbance) northwest of Dixonville, Alberta. The experiment was a randomized split-plot design replicated 3 times. Canopy level was the main plot treatment. There were 2 canopy levels (clearcut and 50% canopy) created at the EMEND site through selective harvesting. There were 5 forest floor disturbance levels (burn, scalp, mix, mound and a control) replicated 4 times in each canopy treatment replicate. The forest floor disturbance treatments were approximately 2m by 2m subplots with each subplot buffered by at least 1m from any adjacent subplot. Site preparation treatment subplots were located on sites determined to be uniform in microtopography, slope, soil and forest floor depth. Mechanical site preparation subplots were installed in May with an excavator equipped with 2 attachments (a mounding bucket for scalp and mound treatments and a Meri-Crusher high-speed horizontal drum mulcher for the mixing treatments). Burns were carried out during the last week of May and first week of June using a propane torch.

In July 1999, 5 spruce seedlings were planted in each plot. Ion exchange resin bags (mixed bed) were installed in June of 1999 to assess nutrient availability. Resin bags were placed

3 per subplot at a depth of 5 cm in the mineral soil. Soil core incubations were used to assess rates of mineralization. A set of cores (mineral and organic) for each plot was taken in July of 1999 for initial nitrogen concentration analysis, and paired sets of cores were incubated in the field from July until October 1999. Resin bags were extracted in the lab and analysed for nitrogen (ammonium and nitrate), phosphorous, potassium, calcium, and magnesium. Soil moisture cores were sampled in July and August 1999 and processed by oven drying to provide a measure soil moisture variability among forest floor treatments and canopy treatments to assess availability of water for plant growth. Soil temperature was assessed in June, July and August 1999 using thermocouples placed at depths of 5cm and 20cm.

In July 1999 species and percent cover of herbaceous plants were evaluated using 5-50cm diameter quadrats per subplot. In August 1999 and 2000, species, stem length, and percent cover of shrubs and fireweed was evaluated using a 1.5m X 1.5m quadrat centred in the plot.

Treatments were analysed by analysis of variance (ANOVA) for a split-plot design where canopy level (clearcut vs. partial cut) is considered the main plot and forest floor disturbance treatments as the subplot (split-plot).

Results

Soil temperatures were higher in the clearcut than the partial cut, and mounds had higher temperatures than all other forest floor treatments (Figure 1). Soil moisture was lower in the mineral and organic layers of the mounds.

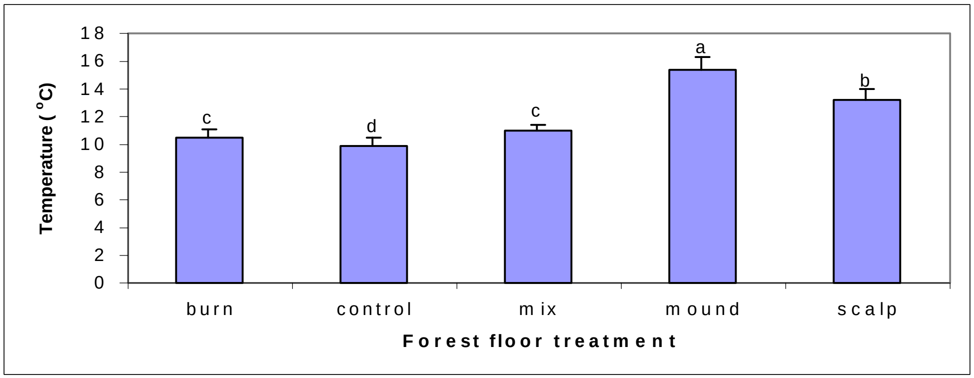

Figure 1. Soil temperature at 20cm depth for forest floor disturbances (mean+SE, n=3).

Overall, nitrogen availability was higher in the burns, both as NH_4 (Figure 2) and NO_3 (Figure 3). Scalps also had higher NO_3. P was highest in burns, lowest in scalps, while Ca and Mg were highest in scalps.

Net N mineralization in the organic horizon was highest in the mounds, and lowest in the mix treatment (Figure 4). Net N mineralization was lower in the mineral horizon compared to the organic, but there were no obvious trends among the treatments.

Light transmission to both ground level and to seedling height was highest in mix treatment, reflecting less vegetation (Figure 5).

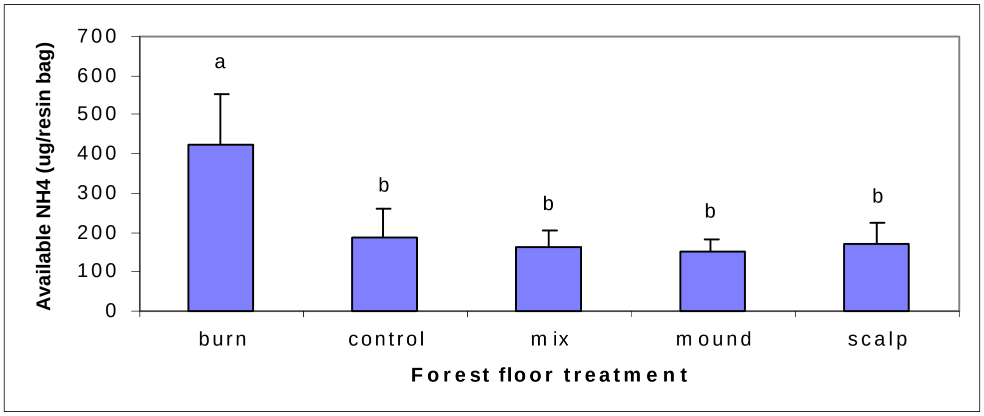

Figure 2. Available NH_4 per resin bag for forest floor disturbances (mean+SE, n=3).

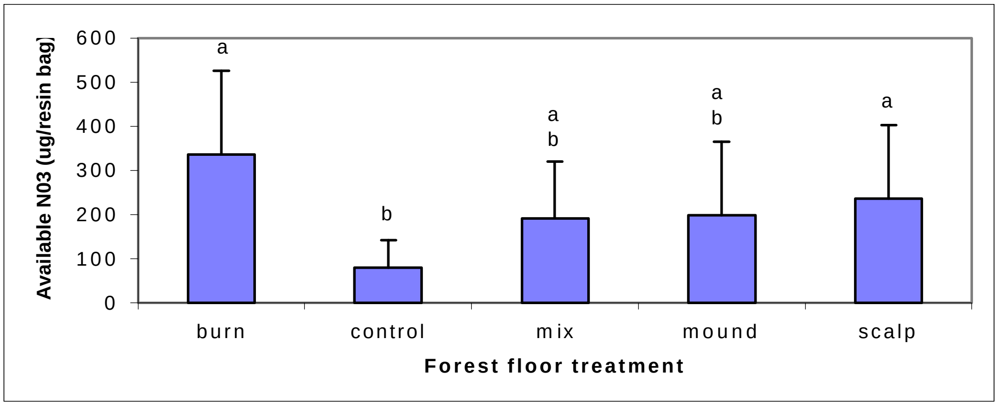

Figure 3. Available NO_3 per resin bag for forest floor disturbances (mean+SE, n=3).

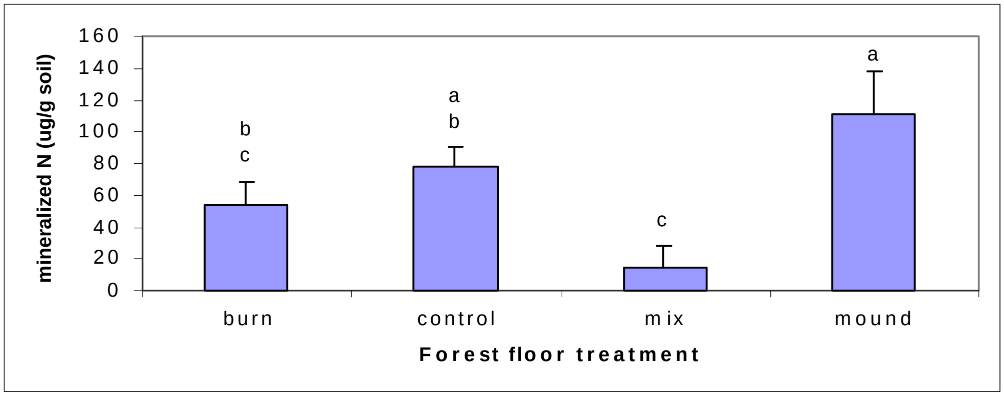

Figure 4. Net N mineralization for forest floor disturbances (mean+SE, n=3).

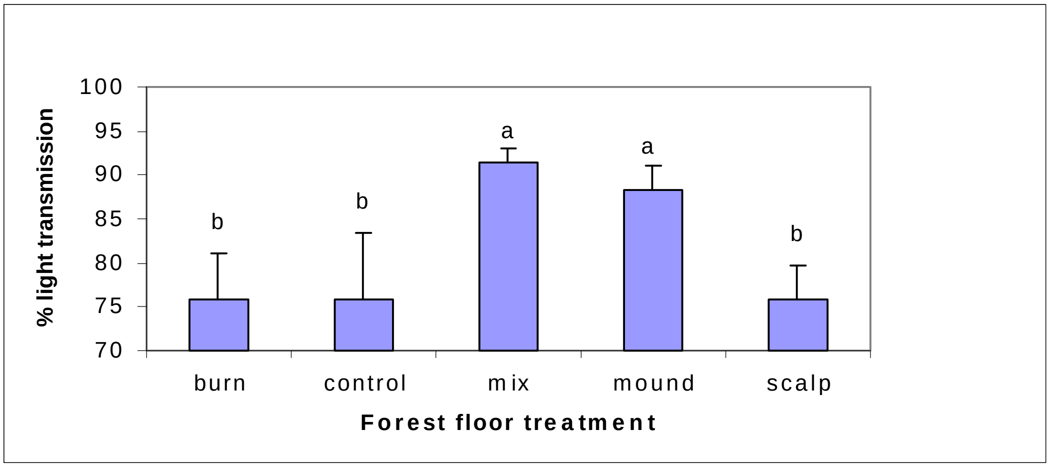

Figure 5. Light transmission to ground level in forest floor disturbances (mean+SE, n=3).

Notable impacts of the treatments on vegetation were evident. Burning significantly increased fireweed cover (Figure 6), while scalping increased aspen cover substantially (Figure 7). Total cover for all shrubs, aspen and fireweed was lowest in the mixing treatment (Figure 8).

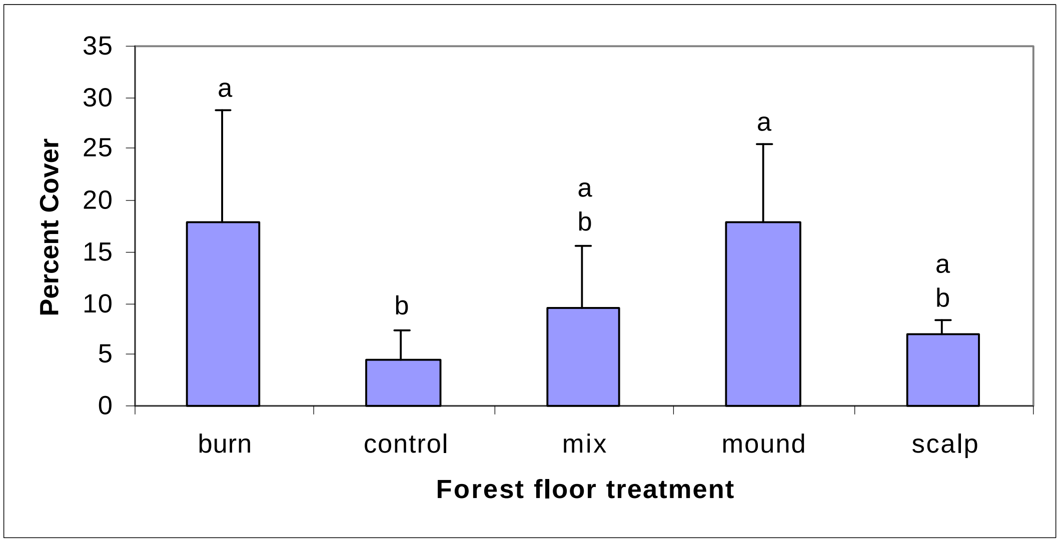

Figure 6. Percent fireweed cover in 2000 in forest floor disturbances (mean+SE, n=3).

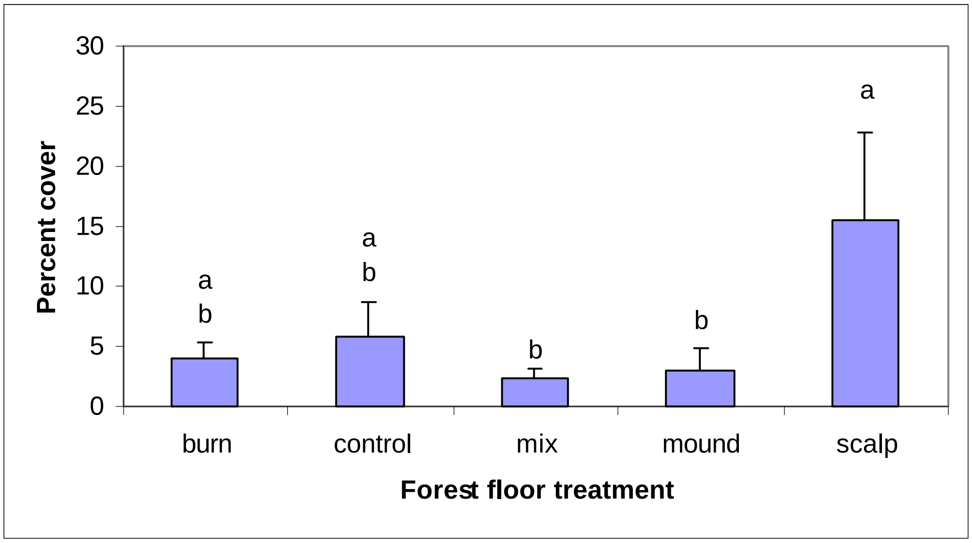

Figure 7. Percent aspen cover in 2000 in forest floor disturbances (mean+SE, n=3).

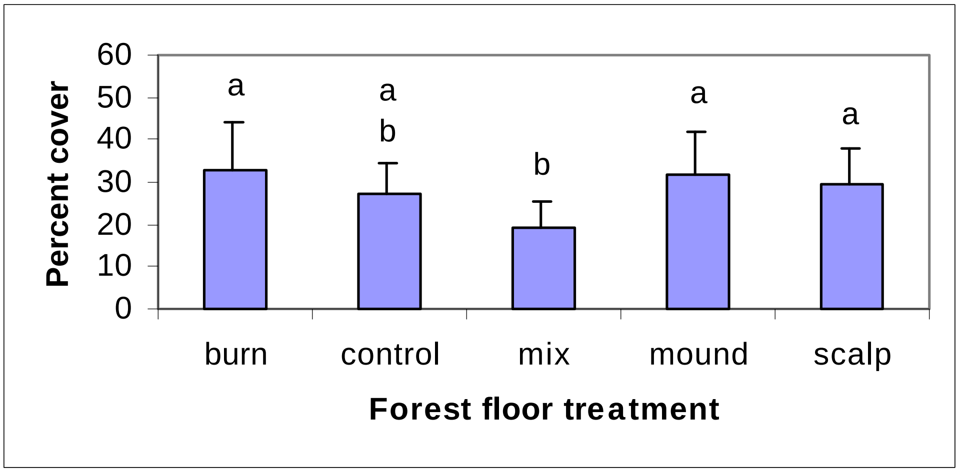

Figure 8. Total vegetation cover in 2000 in forest floor disturbances (mean+SE, n=3).

Management applications

There are a number of implications of this study for the establishment of white spruce seedlings, and these are highlighted below. In general, the results show that different types of disturbance at the forest floor level will have different impacts on nutrient availability and vegetation development. Treatments that control vegetation are recommended for the establishment of white spruce seedlings. Nutrition will also be important, however high nutrient availability following disturbance can be of more benefit to competing vegetation (Thevathasan et al. 2000). Consequently, high nutrient availability induced by the disturbance may not benefit the seedling in the short term, or may even be detrimental if it increases competition, and this should be considered when evaluating the treatments summarized below.

- **Burning** – A low-intensity burn can substantially increase short-term nutrient availability. At the same time, a low-intensity burn can stimulate greater cover of fireweed, which should help the retention and cycling of nutrients. The increased cover of fireweed, while potentially competing with planted white spruce, may be effective in limiting the development of more vigorous competitors (eg. *Calamagrostis canadensis*).

- **Mixing** – Mixing of the organic and upper mineral layer reduces vegetation competition substantially, likely by destroying roots and rhizomes. This results in lower vegetation cover and higher light transmission, and thus should be favourable to seedling establishment. Also, mixing reduces short-term rates of mineralization, which may desirable in the early stages of seedling establishment when greater nutrient availability will be of more benefit to the establishment of competing vegetation.

- **Mounding –** The mounding treatment produces a microsite that is much warmer than any of the other treatments. The high temperatures appear to drive high rates of mineralization in the buried organic horizon of the mound which should be of benefit to seedlings providing competing vegetation does not sprout through the mineral cap. The mounds generally appeared to control vegetation competition, although where vegetation did establish in mounds, it also benefited from the high resource availability. Therefore, where vegetation competition is more severe, a thicker mineral cap may be necessary.

- **Scalping –** A light scalp that removes most of the forest floor results in increased nutrient availability but also very high cover of *Populus spp*. This treatment thus does not appear to be a suitable means for establishing white spruce, however it could be a very effective means for regenerating *Populus spp*.

- **Partial-cutting –** The partial retention of the canopy reduces light transmission to the understory which results in lower soil temperatures and a trend towards reduced vegetation development for some competitors. Aspen development was clearly lower in the partial cut than the clearcut, and it is expected that continued lower light availability should limit the development of other competing vegetation.

Conclusions

Disturbance at the forest floor level, either by mechanical site preparation or by low-intensity burning, significantly altered nutrient availability and rates of N mineralization. Burning and scalping treatments generally increased nutrient availability in the first season of disturbance and the mounding treatment increased N mineralization within the organic layer of the mound. Mixing, in contrast, decreased rates of N mineralization in the surface horizon.

Differences in nutrient availability or cycling of N may affect seedling nutrition and growth in the longer term. High rates of mineralization or nutrient availability caused by the different disturbances may be of more benefit to competing vegetation in the short term, which would be to the detriment of seedling growth. Moreover, higher nutrient availability and rates of mineralization could lead to nutrient leaching and thus a loss in nutrient capital. Nutrient loss may of greatest concern in the mounding treatment where high temperatures favour high rates of mineralization and vegetation development and uptake are limited. The burning treatment may also lead to nutrient losses due to increased nutrient availability, however the limited forest floor consumption from a low intensity burn will not diminish the forest floor nutrient capital substantially.

Forest floor disturbance also had a notable effect on vegetation. An increase in fireweed cover during the first season following fire was seen in the burning treatment. Mounding favoured increased sprouting of rose by the second growing season following site preparation. Scalping promoted vigorous root suckering by aspen. These trends in early vegetation development are important for several reasons. First, it is clear that different disturbances favour different types of vegetation, which will in turn affect the success of planted seedlings. The high aspen cover promoted by scalping would not be suitable for seedling success. Interestingly, a light scalp may be a useful site preparation for regenerating aspen. Second, vegetation control differed between the treatments. Clearly, mixing treatment offering the highest degree of vegetation control by limiting cover and thereby promoting higher light transmission. Mounding also provided a reasonable level of vegetation control. Third, the fact that a certain type of disturbance can increase the dominance of a certain species may be of use for controlling other species that are more aggressive competitors. If a treatment such as a low-intensity burn can be used to increase fireweed cover, and thereby limit the establishment of another aggressive competitor (eg. *Calamagrostis canadensis*), it may be a useful management tool for vegetation control.

The effect of partial canopy retention of vegetation development and nutrient availability was not entirely clear at this early stage. Clear cutting tended to lead to higher Mg and Ca availability relative to the partial cut, which likely increases soil pH and the establishment of competing vegetation. The partial cuts also had an effect on aspen development, limiting its cover and growth relative to the clearcut. Consequently, the retention of a partial canopy was beneficial in reducing competition from aspen. The lower light conditions in the partial cut should limit the development of vegetation compared to the clearcut and thus there should be a benefit of canopy retention to planted seedlings in the longer term.

More detailed information for this study may be found in:

Frey, B.R. (in progress). Impacts of forest floor disturbance on vegetation and nutrient dynamics in clearcut and partial-cut stands. M.Sc. Thesis, Department of Renewable Resources, University of Alberta, Edmonton, Alberta.

Structure and relation of canopy and understory vegetation in boreal mixedwood forests

Steven Kembel and Mark R.T. Dale

Introduction

In many forests, gaps in the canopy can play an important role in determining the distribution of tree seedlings and understory vegetation. Our objectives in this study were to study the spatial structure of, and relationship between canopy trees, understory trees and understory vegetation in old boreal mixedwood forests ranging in canopy composition from conifer-dominated to deciduous-dominated. Specific research objectives were:

1) To quantify the small-scale (sub-stand level) spatial pattern and distribution of canopy and understory vegetation in boreal mixedwood forests.
2) To study the importance of canopy gaps in determining small scale distribution patterns of tree regeneration in these forests.
3) To study the importance of canopy gaps in structuring understory vegetation communities in these forests.
4) To create a model which can predict small-scale understory community structure using canopy variables.

Methods

We established seven permanent 0.5 hectare study plots in old boreal mixedwood forests at the EMEND project. Three plots were established in conifer-dominated forests, two were established in hardwood-dominated forests, and two were established in mixed canopy forests. Within each plot, we measured the spatial coordinates of all living tree stems. Cover of all understory plant species was recorded in 521 0.5-meter2 quadrats placed systematically throughout each plot.

Patterns of tree stems were analyzed using Ripley's K function analysis to determine whether canopy and understory trees occurred in non-random arrangements, and whether seedlings/suckerling of particular species tended to occur more often under canopy gaps than expected by chance. Understory vegetation patterns were analyzed using wavelet analysis and geostatistics to determine scales of pattern and relationships between canopy and understory at several spatial scales. Models of canopy tree influence on understory community structure were created using spatial regression methods.

Results and Discussion

Analyses indicated that canopy trees, understory trees and understory vegetation were all very patchy in their distribution at several spatial scales from 0.5 to 25 meters. In general, spruce seedlings less than 2 meters tall tended to occur more commonly under canopy gaps than under closed canopies. Aspen trees less than 2 meters tall were less restricted in the distribution, often occurring under both canopy gaps and closed canopy. Understory species richness, diversity and total cover were all highest under canopy gaps. Understory vascular plant cover was highest in canopy gaps, while understory non-vascular plant cover was highest under patches of coniferous canopy trees. All of these trends were more pronounced in Conifer-dominated and Mixed stands than in Aspen-dominated stands. Development of the canopy tree influence model is currently underway and should be completed during the summer of 2001.

These results suggest that partial-cutting may have less of a long-term effect on understory plants in Aspen-dominated stands, where canopy trees had much less influence on the distribution of understory trees and vegetation. The canopy tree influence model will allow predictions about the impact of different spatial arrangements of tree harvesting patterns on stand-level distribution of understory species.

More detailed information for this study may be found in:

Kembell, S. (in progress). Structure and relation of canopy and understory vegetation in boreal mixedwood forests. M.Sc. Thesis, Department of Biological Sciences, University of Alberta, Edmonton, Alberta.

The impact of alternative harvesting on the abundance and diversity of white spruce (*Picea glauca*) ectomycorrhizae in a boreal forest ecosystem

Lance Lazaruk and S. Ellen Macdonald

Introduction

Ectomycorrhizae, the symbiotic association between the roots of many species of woody plants and dikaryomycotan fungi, have been deemed essential to the establishment and survival of many boreal and temperate forest tree species. Past research has suggested that this may be attributed to the increased uptake of essential nutrients, including nitrogen and phosphorus, observed in ectomycorrhizal (ECM) plants. Furthermore, current knowledge suggests that the subsequent translocation of carbon and nitrogen between ECM plants via interconnecting mycelia may have implications for the productivity, stability and sustainability of forest ecosystems. In addition, ectomycorrhizae are involved in numerous other ecological processes such as nutrient cycling; elevating the plants resistance to drought, herbivoury and pathogens; and enhancing the growth of otherwise subordinate plant species. They are also an important food source for microarthropods and small mammals. As such, the formation of ectomycorrhizae is thought to be particularly important for young seedlings as vigorous growth helps to ensure the early occupation of space and subsequent access to resources such as light and water. However, due to their symbiotic association, ectomycorrhizae have been shown to be highly sensitive to disturbances such as wildfire and timber harvesting. For example, past research has shown that the biodiversity of ectomycorrhizae is significantly lower in both clear-cut sites and burned sites compared to the undisturbed control sites. In both situations this can be attributed to an increase of 'early stage' ECM fungi and subsequent decrease of 'late stage' ECM fungi. Thus, disturbances often result in a shift in the ECM community.

In order to maintain the diversity and abundance of ectomycorrhizae following harvesting and, thus, ensure the success of both naturally regenerating and outplanted white spruce seedlings it is essential to adopt alternative harvesting techniques that retain a sufficient percentage of healthy trees on the site following harvesting. Harvesting practices designed to emulate natural disturbances should be successful in accomplishing this.

Objectives:

The objectives of this study were to: 1) quantify the impact of alternative harvesting practices on the density of white spruce fine root tips;

2) quantify the impact of alternative harvesting practices on the biodiversity of white spruce ectomycorrhizae;

3) provide guidelines which will assist forest managers in determining the best silvicultural practices for ensuring successful white spruce regeneration based on observed relationships between white spruce regeneration and the biodiversity of ECM fungi.

Methods

A total of 150 sampling locations were established in the spring of 2000 (1 field season post harvest) throughout the Ecosystem Management by Emulating Natural Disturbance (EMEND) research site. They were randomly established within the following conifer dominated stands: unharvested control, clearcut, three partial cuts (with 20%, 50% and 75% live residual remaining) and one burned stand. In addition, both the residual strips and machine corridors in the partial cuts as well as both the burned and unburned portions of the burned stand were sampled.

In the spring of 2000, 2cm (diameter) x 15cm (deep) soil cores were obtained from each of the sampling locations. The soil cores were then transported to the University of Alberta and stored at 4^oC until processing. This involved, i) extracting the white spruce fine root tips by gently washing the soil cores over a soil sieve, and ii) characterizing the white spruce fine root tips as active or inactive (with the aid of a stereoscope) based on the morphology of the fine root tips.

In the fall of 2000, 4cm (diameter) x 15cm (deep) soil cores were obtained from each of the sampling locations. The soil cores were then transported to the University of Alberta and stored at 4^oC until processing. This involved, i) extracting the white spruce fine root tips by gently washing the soil cores over a soil sieve, ii) characterizing the ectomycorrhizae associated with active root tips based on morphological (with the aid of a stereoscope) and anatomical (with the aid of a microscope) features, and iii) identifying the ectomycorrhizae by comparing the morphological and anatomical characterizations to published ectomycorrhizal classifications.

Results

White spruce fine root tip density

The total number of fine root tips observed in the soil cores varied for the different treatments, however, a slight trend was observed (Figure 9). Samples obtained from the burn, clearcut and machine corridors (partial cuts) had the lowest number of root tips per core (between 450 to 600) while the samples from the control and the residual strips (partial cuts) had the highest number of root tips per core (between 800 to 1100). When the total number of root tips was separated into active and inactive root tips this trend became somewhat clearer. Samples obtained from the burn, clearcut and machine corridors had only 3 to 7 active root tips per core while samples from the control and residual strips had significantly more root tips per core (approximately 15 in the 20% and 50% residual samples and 24 in the 75% residual and control samples).

The white spruce ECM community

A total of 19 distinct groups of ectomycorrhizae were observed throughout the study site. Of these, 12 were similar to published descriptions. The identity of the remaining 7 is unknown at this time. These community assemblage of these groups differed throughout the research site. The mean number of groups (richness) was significantly greater in the residual strips, the unburned portion of the burned site and the control site compared to the other sites (clearcut, the machine corridors and the burned portion of the burned site) (Figure 10). Similarly, the diversity of these groups (calculated using Shannon's diversity index) was significantly greater in the residual strips, the unburned portion of the burned site and the control sites. The actual species which comprised most of the community varied among the treatments (Figure 10). For example the only common species found in burns was *Tomentella* sp. Ordination techniques are being used in the future to further examine the community assemblage in these different sites.

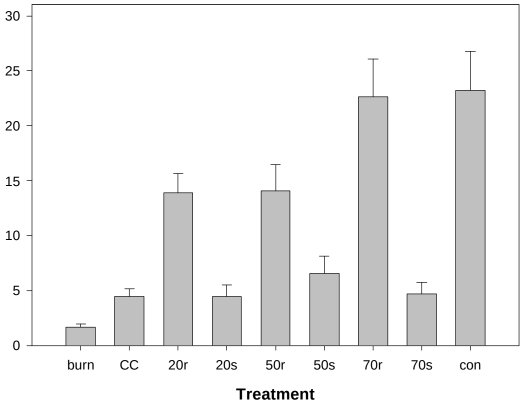

Figure 9. Mean percentage of active white spruce root tips per core for the various treatments (burn, CC=clearcut, 20, 50, 70 = % live tree retention, r = residual strip, s – machine corridor, con = unharvested control).

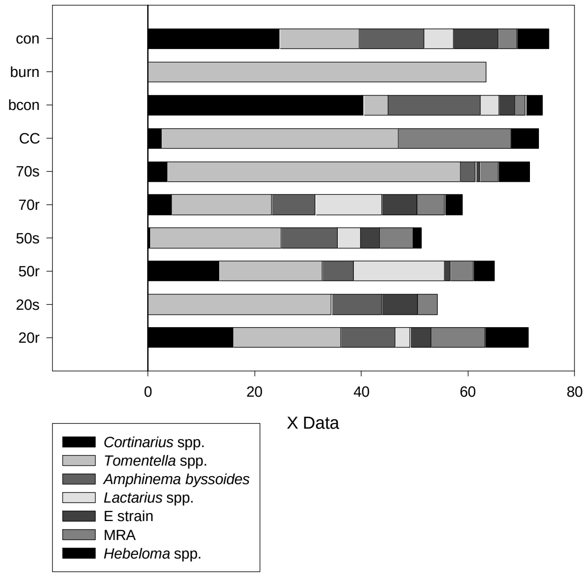

Figure 10. Relative abundance of the seven most common morphotype of mycorrhizae within each of the treatments (treatment codes as in Figure 9).

Conclusions

The results from this study suggest that the total number white spruce fine root tips, the percentage of active white spruce fine root tips, the richness of white spruce ectomycorrhizae and the diversity of white spruce ectomycorrhizae decrease with increasing harvesting intensity. Within thinned compartments the magnitude of this decrease will be greater in the machine corridors compared to the residual strips. Furthermore, the density of fine root tips and ECM diversity was the lowest in the burned portion of the burned site. Both the removal of the ECM fungi's host (ie. white spruce trees) and the compaction associated with the harvesting equipment are thought to have contributed to the results of this study.

Further Research

Further research will be focused on, i) determining the potential for residual structures (ie. ellipses) located in the clearcut sites to act as sources of ECM inoculum and ii) the impact of site preparation on the diversity of ectomycorrhizae observed on regenerating white spruce seedlings. The field sampling associated with these two projects was completed in May 2001.

More detailed information for this study may be found in:

Lazaruk, L. (in progress). The impact of alternative harvesting on the abundance and diversity of white spruce (*Picea glauca*) ectomycorrhizae in a boreal forest ecosystem. M.Sc. Thesis, Department of Renewable Resources, University of Alberta, Edmonton, Alberta.

Factors affecting bryophyte species diversity in the boreal forest

Suzanne E. Mills, S. Ellen Macdonald, Dale H. Vitt

Introduction

Bryophytes (mosses and liverworts) play an important functional role in the boreal forest, slowing decomposition, storing carbon, and interacting with fungi insects and other plants (Longton 1984). Bryophyte species are also a significant component of the species diversity in the boreal forest. In Scandinavia, many red-listed species in the boreal forest are bryophytes (Stokland 1991). The sensitivity of many bryophyte species to forest management has been linked to a reduction in size and diversity of dead woody material.

The first step towards ensuring the retention of bryophyte species diversity in the managed boreal forest in Alberta, is to identify locations with high bryophyte species diversity (diversity hotspots) and understand where they occur. Because of their cryptic nature, bryophytes are not commonly included in broad-scale vegetation surveys. Understanding the relation between bryophyte species diversity and more visible and easily quantifiable forest attributes is thus a more practical way to specify diversity hotspots.

The boreal forest is variable at many spatial scales. Bryophyte species may respond to processes occurring at small scales such as log decay or the creation of gaps (Jonsson and Esseen 1990), and to large scale processes such as forest fires, and climatic variation. In order to predict bryophyte species diversity using habitat parameters we need to first determine the scale(s) of variation in bryophyte species diversity. The next process is to discover how much of this variation in bryophyte species diversity is governed by habitat.

The occurrence of bryophyte species at small scales has been related to the characteristics of specific substrates (Kimmerer 1993, Herben 1994, Watson 1980, Vitt et al.1995, Vitt and Belland 1997). Substrates important for moss colonization are often associated with structural elements of the forest floor (microsites) (Vitt and Belland 1997). These include logs, stumps, tree bases and disturbed patches of soil. Microsites vary in abundance, and quality.

At large spatial scales, bryophyte species diversity has been linked to climate (Lee and La Roi 1979, Molau and Alatalo 1998, Pitkänen 2000), and large scale disturbance (anthropogenic and natural) (Rambo and Muir 1998, Ohlson et al. 1997, Lesica et al. 1991).

Though habitat may influence species diversity, other factors controlling species dispersal, establishment and persistence may hold equal importance (Soderstrom and Jonsson 1989) and (Kimmerer 1994). Bryophyte species diversity of an area will be constrained by the local species pool and the distribution of species diversity within an area will be dependent on the dispersal limitations of individual species. We therefore expect a portion of the variation in bryophyte species diversity to be unexplainable by habitat.

The objective of this study is to determine the best predictors of bryophyte species diversity at different spatial scales. We will establish whether environmental factors thought to be important for bryophyte species vary at measured spatial scales in the boreal forest, determine if bryophyte species diversity is varying at each scale, and construct predictive models to determine how much of the variation in bryophyte species diversity is linked to microclimate and substrate characteristics. The relevance of results to forest management will be discussed.

Methods

Study area

We assessed patterns of bryophyte diversity in North Western Alberta, north of Hines Creek, in the P2 forest management area, township 90, Range 03, W6M. The dominant vegetation of this area is mixed boreal forest characterized by a high proportion of *Populus tremuloides* mixed with *Picea glauca* and *Picea mariana* in the canopy.

We focused our study on three, 10 ha conifer dominated stands (70-95% conifer composition) that had not been previously harvested, within the EMEND (Ecosystem Management Emulating Natural Disturbance), study area. We limited the scope of our study to older boreal forest stands because older stands often have a greater degree of stand complexity and are likely have higher bryophyte species diversity than younger stands (Laaka 1992).

Sample design

We used a nested sample design to look at scale dependent determinates of bryophyte species diversity. I determined bryophyte species richness at three scales: the stand (10 ha), the mesosite (25 x 25 m plots to capture within stand variation), and the microsite (structural elements of the boreal forest providing unique substrates for moss colonization: logs, stumps, trees, disturbed patches of forest floor and $1m^2$ patches of undisturbed forest floor). Each scale was nested within the scale of the next order of magnitude. We sampled up to 25 microsites in each mesosite, and six mesosites in each of three stands.

We placed five centre points randomly within each mesosite. The five center points were used to measure environmental variables and to chose microsites (the nearest microsite to the centre point (<5m away). In total, 22 patches of disturbed soil, 72 stumps, 86 logs, 90 trees and 90 patches of undisturbed soil were sampled.

Data collection

Environmental parameters (substrate availability, light, soil moisture, soil pH, surface moisture, moss depth, *Hylacomnium splendense* growth, were taken from each circle plot. Bryophyte species richness was assessed at each scale: the stand, mesosite and microsite. At the stand scale, bryophyte species diversity was assessed using Floristic Habitat Sampling (FHS) (Newmaster 2000). Bryophyte species diversity at the mesosite scale was assessed using FHS and plot sampling.

Microsite level (within mesosite). At the microsite scale moss species diversity was evaluated by collecting all species and estimating the total abundance of each species to nearest 7.9 cm^2 using a 5.4 X 5.4cm flexible plastic grid. Species abundance measurements were converted to % of occupied surface area to account for differences in microsite size.

Analysis

Nested ANOVAS (SAS V. 8.01 TS Level 01M0, 1999-2000), were performed on microclimate and substrate availability parameters to determine the percent variation explained by stand and mesosite scales.

We used mixed Analysis of Deviance (ANODEV) and Analysis of Variance (ANOVA) models for two purposes, to test whether bryophyte species richness and evenness varied significantly at each scale, and to describe the relationship of mesosite and microsite species richness and evenness to microclimate, substrate availability, and microsite characteristics.

We used generalized linear models (ANODEV models) with Poisson error distribution to analyze all richness data using the glimmix macro (SAS V. 8.01 TS Level 01M0, 1999-2000). Evenness (E) was calculated using Peilou's method (1977), and was analyzed using mixed ANOVA models using PROC MIXED (SAS V. 8.01 TS Level 01M0, 1999-2000), with the ddfm=satterth option.

Beta diversity was calculated between stands, mesosites, and microsite types using the gradient length of the first DCA axis and Whitaker's method (1972) adjusted to remove sample size biases. In order to compare the β diversities of scales and substrate types that had different sample sizes using Whitaker's method, we generated values of total species richness for the sample size of the smallest comparison group using the species area curve function of PC-ORD for Windows, V3.20 (McCune and Mefford 1997). Within mesosite β diversity for all microsite types was analyzed using nested ANOVA to determine if β diversity varied significantly across microsite types and/or stands.

Species-area curves and first order jacknife estimates of species richness (Palmer 1995) were generated using PC-ORD, V3.20 (McCune and Mefford 1997). SPSS for Windows (Release 10.05) was used to determine the values of constants of species-area curves fit to the power function. and logarithmic functions.

Results

Environmental variables

Percent variation explained by the stand, mesosite and microsite (error) scales differed amongst microclimate and substrate variables (Tables 1 and 2). Stand differences explained a significant amount of the variation in soil moisture, surface moisture and ph as well as the number of modules and growth of *Hylacomnium splendens*. Percent available of log, wood and deciduous tree base substrate, as well as light, litter and feather moss depth varied between mesosites but not between stands. Measured microclimatic variables were more variable than substrate availability variables.

Table 1. Percent of total variation of selected environmental variables at stand, mesosite and microsite (error) scales

	All env. Variables	Soil moisture	Soil PH	Light (%PPFD)	Surface moisture % dry wt	Temp.[2]	No. *Hyla. spl* platforms	*Hyla. spl* 1999 Growth	Litter depth	Feather moss depth
Source	*d. f.*	% Var.	% Var.	% Var.	% Var.	% Var.	% Var.	% Var.	% Var.	% Var.
Stand	2	72**	30**	0	20**	2	20*	26**	9	2
Meso (stand)	15	4*	6	57**	2	19*	12*	0	12*	42**
Error	72	22	63	42	76	79	67	73	78	55

[1] Variable was log transformed using Ln(Y+1). * p<.05, **p<.01 .
[2] Variable could not be normalized.

Table 2. Partitioning of total variation in substrate availability at stand, mesosite and microsite (error) scales

% area/ cm^2		Log area[1]	Log area[1] Dec 3,4,5	Wood area[1]	Stump area[2]	Tree base area[1]	Deciduous tree base area[2]
Source	*d.f.* (all)	% Var.	% Var.	% Var.	% Var.	% Var.	% Var.
Stand	2	0	6	0	0	0	0
Meso(stand)	25	28**	5	30**	0	12 (p=.07)	18*
Error	72	72	89	70	95	88	82

[1] Variable was log transformed using Log(Y+.01). * p<.05, **p<.01 .
[2] Variable could not be normalized.

Species richness

The greatest amount of variation in bryophyte species richness was explained by microsite type and not by mesosite or stand scales. Logs had the highest mean species richness, while undisturbed patches of forest floor had the lowest. (Figure 11).

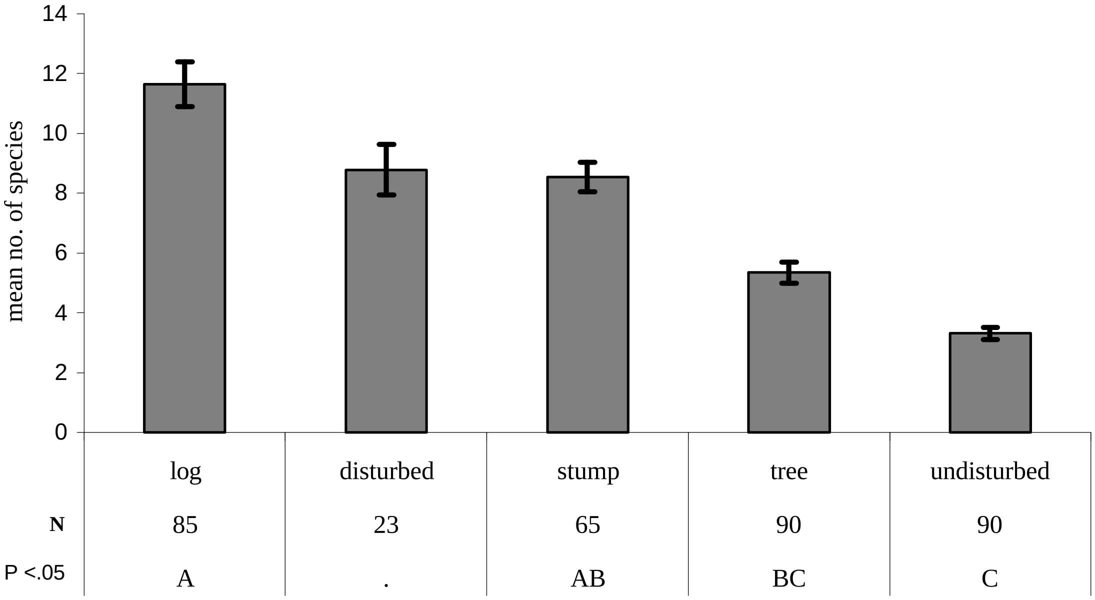

Figure 11 Unadjusted mean microsite species richness (standard error). Significant differences (Tukey-Kramer adjusted p values) between mean species richness (adjusted for stand, mesosite and circle plot scales) indicated by different letters.

Stand species richness was highest in stand 1 followed by stands 3 and 2 (77, 66 and 59 species respectively). At the mesosite scale, percent area of tree bases was the only significant covariate, having a strong negative relationship with species richness. Habitat predictors of species richness at the microsite scale were specific to each microsite type (Table 3).

Log species richness was adequately predicted by log decay class, log surface area, total bryophyte cover, and deciduous/coniferous nature of logs. Deciduous logs had higher species richness than conifer logs and logs of decay class 5 had higher species richness than decay classes 4 or 2 (Figure 12). Both bryophyte cover and log surface area were positively related to bryophyte species richness.

Table 3. Final ANODEV models of bryophyte species richness for mesosite and microsite scales by microsite type. 0=no estimate produced, ns= no significant variation, *=significant at p<.05. Random factors retained in all models to guard against spatial autocorrelation, significance tested using Wald's test. Fixed factors only retained when type III tests were significant when added in a stepwise fashion. Cover=% total bryophyte cover, Area=surface area of microsite, D/C=deciduous or coniferous nature, pff=patch of forest floor

Units of species richness (Y)	Random factors		Fixed factors			G^2 *at* ($÷^2_{(X)}$)	R^2
Mesosite	Stand^0		Tree area*			$5.27_{(17)}$	.64
Log	Stand^0	Meso^0 Meso*D/C*	Area*	Cover*	D/C*	72.35 ($_{67}$).	.81
Stump	Stand^0	Meso^0 Meso*Decay	Decay*	Area	Decay*Area	$58.86_{(56)}$	.48
Tree	Stand^{ns}	Meso^{ns}+	Cover*	Cover^2*	Area*+	85.11 $_{(87)}$	.34
Undisturbed pff	Stand^{ns}	Meso^{ns}+	.	.	.	56.24 $_{(89)}$	.42
Disturbed pff	Stand^{ns}		pH*	.	.	22.64 $_{(21)}$.	.52

Measured parameters were only able to explain half of the total deviance in stump species richness, G^2=58.74 at $÷^2_{(56)}$, R^2=.49 (Table 2.9); 35% of the total variation was stump surface area and decay class.

The best fitting model of tree species richness (G^2=85.11 indicating no lack of fit at $÷^2_{(87)}$), included bryophyte cover (as a polynomial) and tree base surface area (positive relationship) as predictors of bryophyte species richness (Table 2.10). Deciduous/coniferous nature of trees and tree base area were significant explanatory variables in a second, less well fitting model.

Variation in undisturbed patch species richness was not related to any measured environmental parameters, G^2=56.2364 at $÷^2_{(89)}$ (Table 2.10). Isolating stand one (the most variable in terms of soil moisture), a well fitting model of undisturbed patch species richness was constructed using soil moisture and soil ph. Species richness of undisturbed patches in stand 1 was positively related to both soil moisture and soil pH. This relationship was not apparent in either stand 2 or 3.

Both pH and area of disturbed patches of forest floor had positive significant relationships with bryophyte species richness of disturbed patches in univariate models. Overall model fit was good (G^2=22.64) indicating no lack of fit relative to $\div^2_{(21)}$.

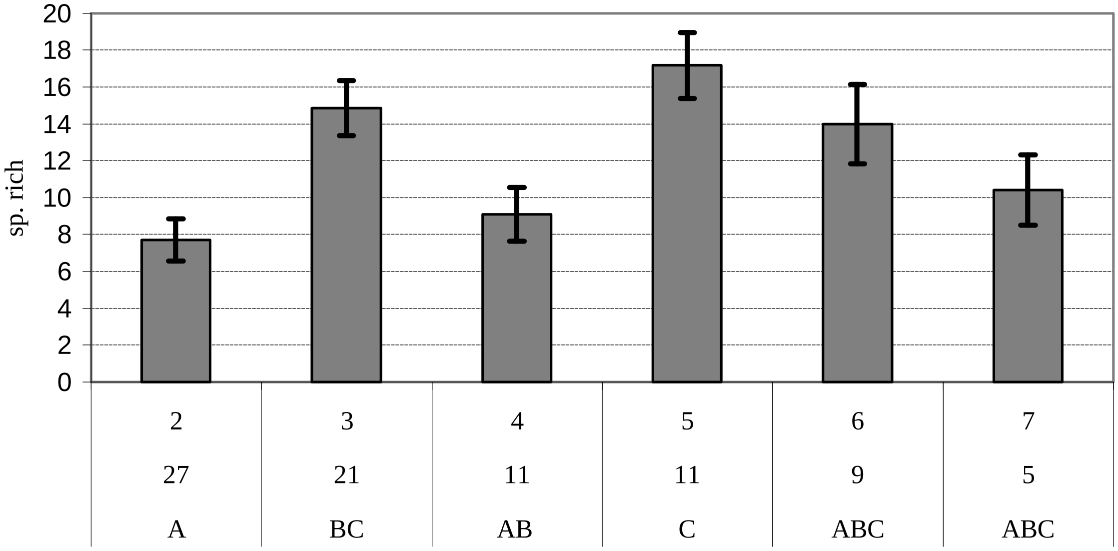

Figure 12. Unadjusted mean species richness (standard error) for log decay classes 2-7. Significant differences (Tukey-Kramer adjusted p values) between adjusted mean species richness indicated by different letters. Mean species richness adjusted for area, bryophyte cover and deciduous/coniferous logs.

Species evenness

Species evenness was not related to species richness at any of the study grains. Microsite types were not significantly different in terms of species evenness, however there was a significant interaction between microsite type and mesosite.

Log species evenness and stump species evenness were both adequately explained by total bryophyte cover (negative relationship) and by the coniferous/deciduous nature of the stump or log. Species evenness of stumps and of logs from deciduous trees were significantly higher than their coniferous counterparts (Adjusted least squares means).

Species evenness of tree bases and undisturbed patches was not related to any of the measured environmental parameters. Area of disturbed patch was negatively related to bryophyte species evenness in disturbed patches (R^2=.54).

Beta diversity

Microsite beta diversity, was higher than either stand or mesosite beta diversity, using both DCA and Whitaker's method (Table 4). Of the three stands, stand 1 had the highest beta diversity, Whitaker â = 1.73 at n=6. Stands 2 and 3 were less heterogeneous with â = 1.55 and 1.57 respectively. Trees had the highest beta diversity of all microsite types, followed by disturbed patches, stumps, undisturbed patches and logs.

Table 4. Beta diversity calculated between stands, mesosites, all microsite types, logs, stumps, tree bases, undisturbed patches of forest floor and disturbed patches of forest floor using the gradient length of the first DCA axis and Whitaker's method (1972) n=3 and n=23

Technique	Stands	Mesosites	All microsite types	Logs	Stumps	Tree Bases	Undisturbed pff	Disturbed pff
1. DCA	0.71	1.70	6.45	4.89	3.63	4.23	4.14	5.36
2. Whitaker	1.13	2.00	11.24	5.68	7.5	9.8	9.7	5
3. Whitaker n=3	1.13	1.47	2.32	2.09	2.19	2.14	2.06	2.28
4. Whitaker n=23			6.7	4.8	5.68	6.62	5.47	5.8

Results obtained from a nested ANOVA analysis of within mesosite microsite beta diversity confirmed the existence of significant differences in beta diversity among microsite types (Table 5). Within mesosite beta diversity for each microsite type did not differ significantly between stands.

Table 5. Nested ANOVA results: within mesosite beta diversity of each substrate type using Whitaker's method (n=5). Type = sampled substrates: log, stump, tree, disturbed, and undisturbed forest floor

		Beta diversity	
Source	*d.f.*	**F – Value**	*P > F*
Stand	2	1.31	.3331
Microsite	3	11.11	.0072
Microsite*Stand	6	1.76	.1284
Error	48		

Species area-curves

All species area curves fit the power function adequately (R^2 values ranged from 0.86 to 0.99). The slope of the species area curve constructed with all 18 mesosites did not approach zero, but did decline dramatically after the addition of 9 mesosites (72-80 species). The second-order jackknife estimate of total species richness was 93.6 (observed species = 82). Stands differed in total species richness, however the shape of generated species area curves remained fairly constant.

The slopes of species area curves for all microsite types, except undisturbed forest floor, began to approach zero (Figure 13). Stumps had the highest estimated species richness (76.8), followed by logs, disturbed patches, trees and undisturbed patches.

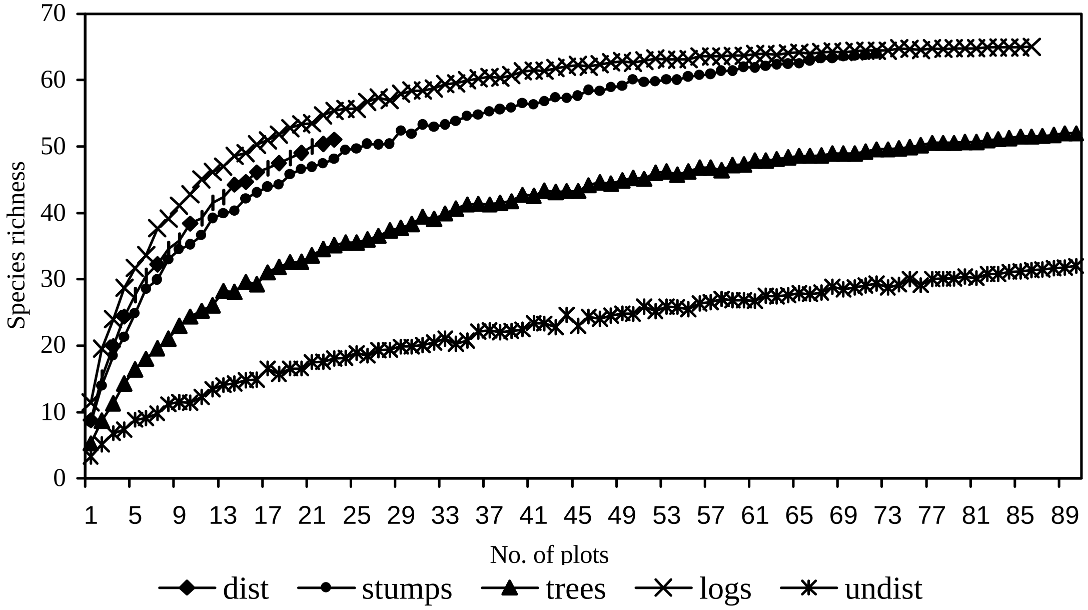

Figure 13. Species area curves for disturbed patches of forest floor, stumps, trees, logs and undisturbed patches of forest floor using number of plots as a surrogate for area. First order jackknife estimates of species richness (total observed species richness): disturbed patches: 64.4 (32), stumps 76.8 (64), trees 52.0 (62.9), logs 65.0 (68.0), undisturbed patches 45.8 (32.0), all microsite types 87 (80).

Application for management

We found that the most important spatial scale for bryophytes in the sampled boreal forest was the microsite scale. Though habitat parameters (substrate availability and climate), varied at stand and mesosite they were not clearly related to patterns of bryophyte species diversity these scales. Habitat descriptors at the microsite scale predicted bryophyte species richness moderately well, however it seems that bryophyte species evenness is more closely linked to the habits of specific bryophyte species, than to microsite properties. Microsite types were different in terms of species composition and disturbed patches of forest floor had exceptionally high species turnover. Species area curves show logs to have the fastest accumulation of new species and undisturbed patches of forest floor to have the lowest. Our results imply that the presence large woody debris in different stages of decay (both coniferous and deciduous) and disturbed patches of forest floor, are the most important indicators of bryophyte species diversity. At intermediate spatial scales in conifer dominated stands of the boreal forest bryophyte species diversity is fairly homogenous and only loosely linked to microclimate and substrate availability.

Where is the diversity?

The number of bryophyte species present on a microsite was first and foremost related to the type of microsite. Large deciduous and coniferous logs in different stages of decay are very important for bryophyte species diversity. Logs accumulated species more quickly than any other microsite type with increased numbers of sample units (Figure 13). This is likely do to the large size of logs and their close proximity to one another facilitating colonization. Of all logs, deciduous logs of decay class five had the highest mean species richness. Disturbed patches were also quite diverse, with high variability in species composition between patches. The greatest variation in species composition also occurred at the microsite scale between microsite types.

At the mesosite scale, gaps appeared to be important. Decreasing tree abundance increased bryophyte species richness. This may be linked to a number of factors including higher soil moisture, dead woody material and light. Overall, species composition between stands and mesosites was relatively uniform (low beta diversity). Microsite species diversity was not related to variation at larger spatial scales.

Implications for bryophyte species inventories

1. The stability of microsite species diversity across mesosites and stands suggests that sampling efforts should focus on the number and variety of microsites and not their location. Differences in stand and mesosite species richness were related to physiographic differences (streams and wet depressions) that affected species composition of undisturbed forest floor (rare species were not often captured in sampled undisturbed patches because of their random placement). Care should be taken that forest floor bryophytes are sampled from all unique areas in the boreal forest.

2. Because of the high compositional turnover (change in which species are present) between disturbed patches and the low occurrence of treefall disturbance in boreal forest stands, all disturbed patches should be sampled if possible to maximize species capture.

3. Since stump species composition was more variable than that of logs, and since species accumulation on stumps did not reach an asymptote, more stumps should be surveyed than logs.

4. Emphasis should be made to sample logs and stumps of different tree species

Implications for forest management

From our study it is apparent that tree fall disturbances, deciduous and coniferous large sized dead woody debris in a variety of decay classes, and a moist understory are essential for the maintenance of bryophyte species diversity. Higher species richness found in older non-managed stands has been linked to the presence of larger sized decaying wood resultant of longer stand integrity (Rambo and Muir 1998, Ohlson et al. 1997). Andersson and Hytteborn (1991) also found higher bryophyte species diversity to be linked to a greater amount of wood in all decay classes especially *Populus tremula*.

Forest management over the long term often reduces the structural heterogeneity of the forest (Dettki and Esseen 1998), and decreases the age structure over the landscape often resulting in higher bryophyte species richness in non-managed stands (Rambo and Muir 1998, Ohlson et al. 1997). It is therefore necessary to maintain areas of forest in older age classes that are sufficient to maintain the bryophyte species pool. Because the high compositional turnover within specific microsite types suggests that some species may be dispersal limited, special care should be taken that older forest patches are not small and isolated.

Mixed wood management of the boreal forest is also necessary for the maintenance of bryophyte species diversity in the boreal forest. Many bryophyte species are dependent on large live and dead Aspen within the favourable moisture regime of a conifer dominated canopy, thus the aspen component of the forest contributed substantially to the species diversity of the study sites.

Maintaining structural heterogeneity in the boreal forest over the course of forest management is the most important single consideration for the preservation of bryophyte species diversity.

More detailed information for this study may be found in:

Mills, S. (in progress). Factors affecting bryophyte species diversity in the boreal forest. M.Sc. Thesis, Department of Renewable Resources, University of Alberta, Edmonton, Alberta.

Understory vascular plant richness and composition in boreal forest stands of varying composition: response to partial-cut harvesting treatments

Treena Fenniak and S. Ellen Macdonald

Introduction

The site conditions provided by a given disturbance help to determine which plants can establish, which may in turn exert an influence on the course and rate of later vegetational development. Driving variables of understory plant re-establishment following disturbance can be broadly categorized as: 1) availability of reproductive propagules, 2) micro- to meso-site environmental conditions. Factors influencing the first include: pre-disturbance plant community (presence of seed bed and rhizomes) and nearby residual plant community (source populations for seed dispersal or clonal expansion). Important environmental factors which are expected to vary at the meso- to micro-site scale are light, soil temperature, nutrient and moisture availability, and establishment substrate (presence of mineral soil). The nature of the disturbance will have a major impact on all driving variables of plant re-establishment. Of particular importance will be: surface soil disturbance, removal of organic matter, residual live and dead canopy [density, dispersion, and composition (Constable and Lieffers 1996)], creation of downed coarse woody material, and the spatial heterogeneity of these.

Partial-cut harvesting removes the canopy, resulting in creased light penetration. In addition, new microsite for regeneration will be established and below-ground resource availability may increase. The response of the understory community to partial harvesting will likely depend upon how different the post-harvest understory environment is from that occurring pre-harvest. In addition, the ability of the pre-disturbance understory community to acclimate to the changed environment will be important. This study aimed to discern whether environmental variables and understory vascular composition differed following different harvesting intensities, and whether or not there was a relationship between environmental changes and species composition changes within treatments.

Methods

In this study we sampled only a portion of the EMEND site, including deciduous dominated (>75% deciduous canopy), conifer dominated (>75% conifer canopy) and mixedwood (coniferous and deciduous each 35-65%) community types, and the control, clearcut, 20% residual and 75% residual partial harvesting treatment types. There were three replicates of each combination of treatment and community, with the exception of the control treatment (four replicates per community type), for a total of 39 compartments. 8 plots (1x1m herb plot and 2x2m shrub plot nested within a 50m^2 tree plot) per compartment were located semi randomly, and sampled one-year preharvest and two years postharvest. Soil temperature and moisture levels, available nutrients (including NO_3^-, NH_4^+ and PO_4^{3+}), CWM diameter, cover, and decay class, decomposition rate, mineral soil cover, litter cover and type, moss and lichen cover and species abundance for each shrub and herb were measured at each plot in each year, as were canopy cover, basal area, live tree and snag densities. Species diversity (Shannon-Weiner and Simpson's) and richness were calculated for each plot and each compartment. All of the canopy structure and environmental variables were analyzed using repeated measures ANOVA, to investigate variation relating to time and treatment.

Results

Blowdown proved to be a major concern in the feasibility of the strip harvesting process, as the 20% residual harvests showed similar live densities to clearcuts by the second year postharvest. Results of ANOVA analysis showed that specific environmental variables exhibited change within the various harvesting regimes over time. Soil temperature and moisture showed the same patterns in all forest types, with higher values in clearcuts, lower values in controls, and intermediate values in the partial harvests. Number of CWM pieces was significantly higher in conifer clearcuts and CWM cover was higher in deciduous 20% treatments than other treatments. The other environmental variables showed no significant change over time with relation to the treatments.

Species diversity and richness per plot were significantly lower postharvest in clearcuts in the mixedwood and conifer communities in the second year postharvest, while clearcut richness and Shannon-Weiner diversity per compartment was only significantly lower in the herb layer of the mixedwood and conifer communities. Detrended canonical correspondence analysis showed that within each forest types, treatments that overlapped in composition preharvest exhibited substantial segregation by the second year postharvest (Figure 14). Results indicate that environmental variables are not strongly correspondent with any changes in the understory community, with the expection of those relating to canopy structure. Detrended correspondence analysis of plot scores calculated using per compartment species abundance values showed a segregation of the deciduous plots from the coniferous and mixedwood plots that remained from pre- to postharvest (Figure 15). Results also suggest that the establishment and success of understory species after partial and total canopy harvesting may be different in different community types, emphasizing a need to approach harvesting in each community with respect for its unique processes, not just based on community composition.

Management Applications

The results suggest that partial-cut harvesting will have less impact on deciduous dominated forests than on those with a significant component of conifer in the canopy, in terms of changes in the understory vascular plant community. In all forest types partial-cut harvesting will tend to result in homogenization at the within-stand scale; understory plant composition becomes more similar among plots throughout the stand. In addition, partial-cut harvesting results in forest stands of different pre-harvest canopy composition becoming more similar; conifer-dominated, mixedwood and deciduous-dominated stands developed relatively similar understory plant communities following partial-cut harvesting or clearcutting.

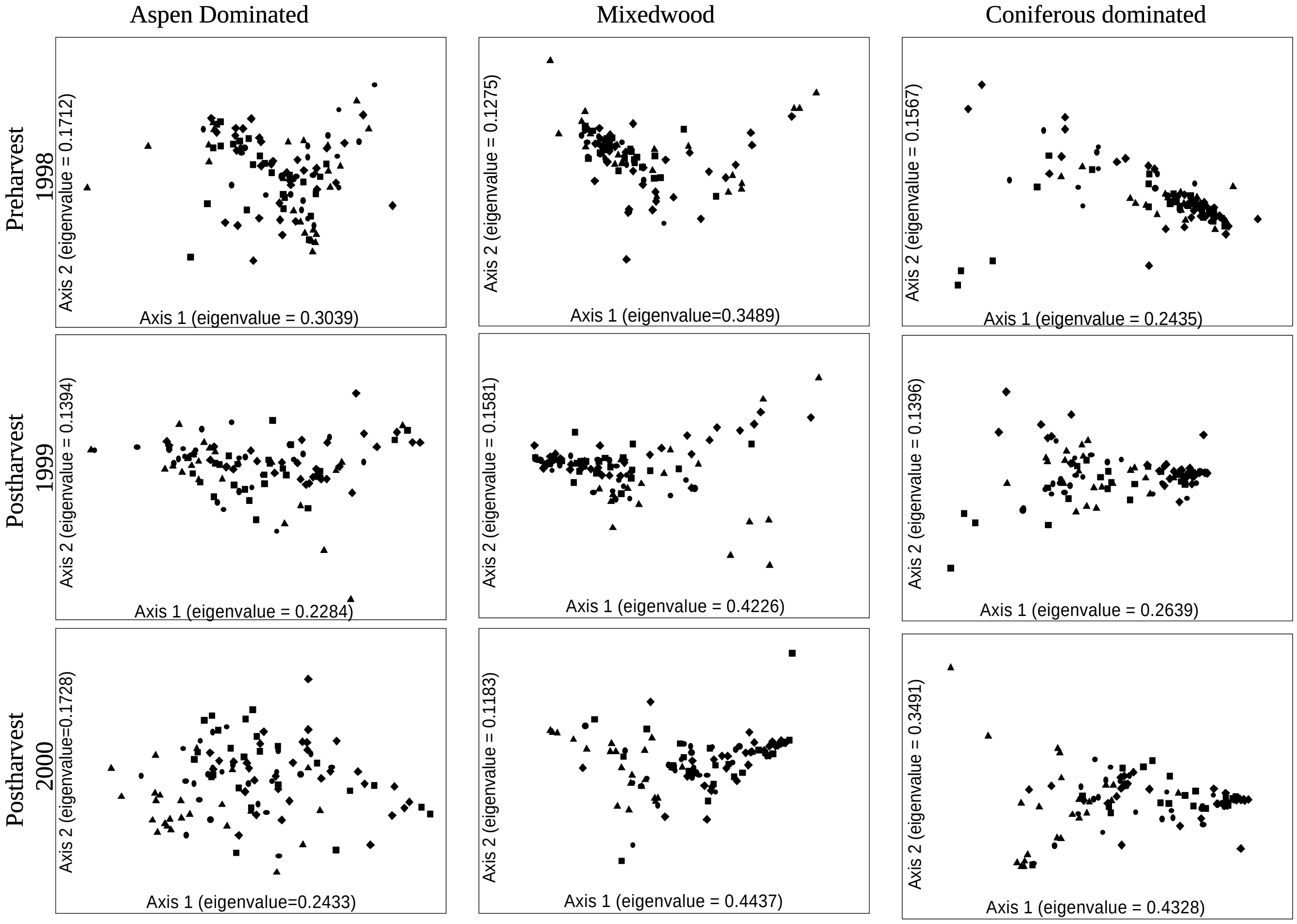

Figure 14. Ordination of species composition showing separation of treatments for the three different forest types in the pre-harvest year (1998) and the first (1999) and second (2000) post-harvest years. Square = unharvested control, diamond = 75 % retention, circle = 20 % retention, triangle = clearcut.

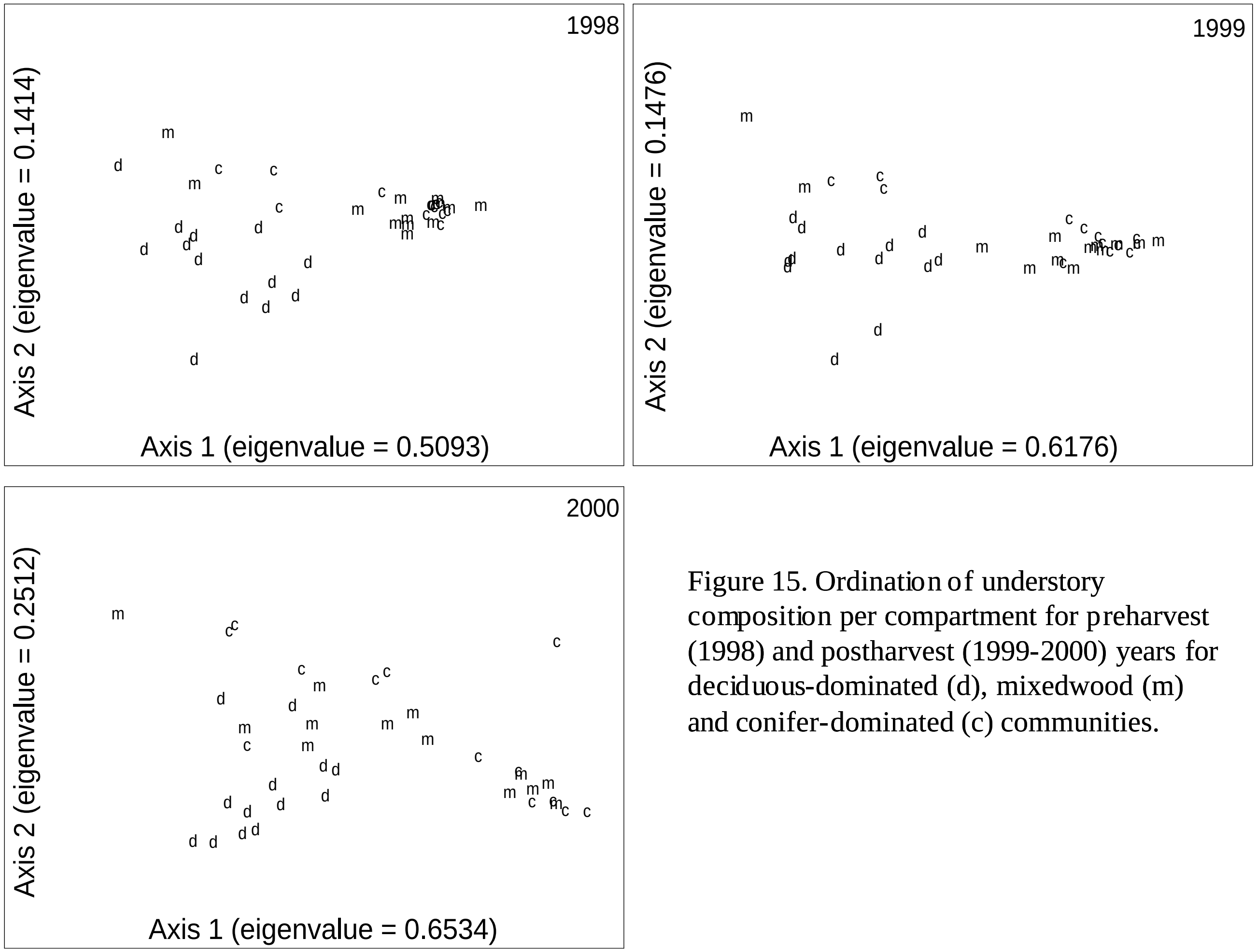

Figure 15. Ordination of understory composition per compartment for preharvest (1998) and postharvest (1999-2000) years for deciduous-dominated (d), mixedwood (m) and conifer-dominated (c) communities.

References

Anderson, L.I., and Hytteborn, H. 1991. Bryophytes and decaying wood - a comparison between managed and natural forest. Holarctic Ecology 14: 121-130.

Bérubé, J.A. and Dessureault, M. 1988. Morphological characterization of *Armillaria ostoyae* and *Armillaria sinapina* sp.nov. Can. J. Bot. 66: 2027-2034

Binkley, D. 1984. Does forest removal increase rates of decomposition and nitrogen release? Forest Ecology and Management 8: 229-233.

Blenis, P.V., Titus, S.J. and Mallett, K.I. 1995. Impact of *Armillaria* root rot in intensively managed white spruce/aspen stands. A joint publication of CFS and Land and Forest service. A5023-129

Brand, D.G and P.S. Janas. 1987. Growth and acclimation of planted white pine and white spruce seedlings in response to environmental conditions. Can. J. For. Res. 18: 320-329.

Constabel, A.J. and Lieffers, V.J. 1996. Seasonal patterns of light transmission through boreal mixedwood canopies. Can. J. For. Res. 26:1008-1114.

DeLong, H.B., V.J.Lieffers and P.V. Blenis. 1997. Microsite effects on first-year establishment and overwinter survival of white spruce in aspen-dominated boreal mixedwoods. Can. J. For. Res. 27: 1452-1457.

Dettki, H. and Esseen, P.-A. 1998. Epiphytic macrolichens in managed and natural forest landscapes: a comparison at two spatial scales. Ecography 21: 613-624.

Dyrness, C.T. and R.A. Norum. 1983. The effects of experimental fires on black spruce forest floors in interior Alaska. Can. J. For. Res. 13: 879-893.

Eis, S. 1981. Effects of vegetation competition on revegetation of white spruce. Can. J. For. Res. 11: 1-8.

Feller, M.C. 1982. The ecological effects of slashburning with particular reference to British Columbia: a literature review. B.C. Ministry of Forests Land Management Report No. 13.

Grime, J.P. 1979. Plant strategies and vegetation processes. John Wiley and Sons, New York. NY.

Grubb, P.J. 1977. The maintenance of species richness in plant communities: the importance of the regeneration niche. Biol. Rev. 52: 107-145.

Harper, J.L. 1977. Population bioogy of plants. Academic Press, U.K.

Herben, T. 1994. The role of reproduction for persistence of bryophyte populations in transient and stable habitats. J. Hattori Bot. Lab. 76: 115-126.

Hogg, E.H. and V.J.Lieffers. 1991. The impact of *Calamagrostis canadensis* on soil thermal regimes after logging in northern Alberta. Can. J. For. Res. 21: 382-394.

Jonsson, B.G. and Esseen, P.-A.. 1990. Treefall disturbance maintains high bryophyte diversity in a boreal spruce forest. J. Ecol. 78: 924-936.

Kimmerer, R.W. 1993. Disturbance and dominance in *Tetraphis pellucida*: a model of disturbance frequency and reproductive mode. The Bryologist 96: 73-79.

Kimmerer, R.W. 1994. Ecological consequences of sexual versus asexual reproduction in *Dicranum flagellare* and *Tetraphis pellucida*. The Bryologist 97: 20-25.

Laaka, S. 1992. The threatened epixylic bryophytes in old primeval forests in Finland. Biological Conservation 59: 151-154.

Landhausser, S.M. and V.J. Lieffers. 1994. Competition between *Calamagrostis canadensis* and *Epilobium angustifolium* under different soil temperature and nutrient regimes. Can. J. For. Res. 24: 2244-2250.

Lee, D. and La Roi, G.H. 1979. Bryophyte and understory vascular plant beta diversity in relation to moisture and elevation gradients. Vegetatio 40: 29-38.

Legendre, P. and Legendre, L. 1998. Numerical Ecology 2nd English Edition. Elsevier, Amsterdam.

Lesica, P., McCune, B., Cooper S.V., and Hong, W.S. 1991. Differences in lichen and bryophyte communites between old-growth and managed second-growth forests in the Swann Valley, Montana. Can. J. Bot. 69: 1745-1755.

Lieffers, V.J., S.E. MacDonald and E.H. Hogg. 1993. Ecology and control strategies for *Calamagrostis canadensis* in boreal forest sites. Can. J. For. Res. 23: 2070-2077.

Lieffers, V.J. and K.J. Stadt. 1994. Growth of understory *Picea glauca*, *Calamagrostis canadensis*, and *Epilobium angustifolium* in relation to overstory light transmission. Can. J. For. Res.24: 1193-1198.

Longton, R.E. 1984. The role of bryophytes in terrestrial ecosystems. Journ. Hattori. Bot. Lab. 55: 147-163.

Mallett, K.I. 1990. Host range and geographic distribution of *Armillaria* root rot pathogens in the Canadian prairie provinces. Can. J. For. Res. 20 (12): 1859-1863.

McCune, B. and Mefford, M..J. 1997. Multivariate Analysis of Ecological Data, PC-ORD for Windows, version 3.20 MjM Software, Gleneden Beach, Oregon, USA.

Molau, U. and Alatalo, J.M. 1998. Responses of subarctic-alpine plant communities to simulated environmental change: biodiversity of bryophytes, lichens, and vascular plants. Ambio 27: 322-329.

Munson, A.D., H.A. Margolis and D.G. Brand. 1993. Intensive silvicultural treatments: impacts on soil fertility and planted conifer response. Soil Sci. Soc. Amer. J. 57:246-255.

Newmaster, S. 2000. Patterns of bryophyte diversity in the interior coastal Cedar-hemlock forests of British Columbia. Ph.D. thesis 372p.

Ohlson, M., Soderstrom, L., Hornberg, G., Zackrisson, O. and Hermansson, J. 1997. Habitat quailities versus long-term continuity as determinants of biodiversity in boreal old-growth swamp forests. Biological Conservation 81: 221-231.

Palik, B.J., R.J. Mitchell, G. Houseal and N. Pederson. 1997. Effects of canopy structure on resource availability and seedling responses in a longleaf pine ecosystem. Can. J. For. Res. 27: 1458-1464.

Palmer, M.W. 1995. How should one count species? Natural Areas Journal 15: 124-135.

Peilou, E.C. 1977. Mathematical Ecology. John Wiley and Sons, USA. pages 307-309.

Pitkänen, S. 2000. Classification of vegetational diversity in managed boreal forests in eastern Finland. 2000. Plant Ecology 146: 11-28.

Prescott, C.E. 1997. Effects of clearcutting and alternative silvicultural systems on rates of decomposition and nitrogen mineralization in a coastal montane coniferous forest. For. Ecol. Manage. 95: 253-260.

Rambo, T.R. and Muir, P.S. 1998. Bryophyte species associations with coarse woody debris and stand ages in Oregon. Bryologist 101: 366-376.

Rayner, A.D.M., and Boddy, L. 1988. Fungal decomposition of wood. Its biology and ecology. John Wiley & Sons, New York.

Soderstrom, L. and Jonsson, B.G. 1989. Spatial pattern and dispersal in the leafy hepatic Ptilidium pulcherrimum. J. Bryol. 15: 793-802.

Spurr, S.H. and B.V. Barnes. 1980. Forest ecology. Wiley, NY.

Stokland, J. N. 1991. Skogbrukets innvirkning pa truede og sarbare arter i barskog. [The impact of modern forestry on endangered species in the boreal forest.] Fauna 44: 11-19.

Thevathasan, N.V., P.E. Reynolds, R. Kuessner and W.F. Bell. 2000. Effects of controlled weed densities and soil types on soil nitrate accumulation, spruce growth, and weed growth. For. Ecol. Manage. 133: 135-144.

Tilman, D. 1988. Plant strategies and the structure and dynamics of plant communities. Princeton University Press, Princeton, NJ.

Van Cleve, K., L. Oliver, R. Schlentner, L.A. Viereck and C.T. Dyrness. 1983. Productivity and nutrient cycling in taiga forest ecosystems. Can. J. For. Res. 13: 747-766.

Vitt, D. H., Li, Y. and Belland, R. 1995. Patterns of bryophyte diversity in peatlands of continental western Canada. The Bryologist 98: 218-227.

Vitt, D.H. and Belland, R. 1997. Attributes of rarity among Alberta mosses: patterns and prediction of species diversity. Bryologist 100: 1-12.

Vitousek, P.M., S.W. Andariese, P.A. Matson, L. Morris and R.L. Sanford. 1992. Effects of harvest intensity, site preparation, and herbicide use on soil nitrogen transformations in a young loblolly pine plantation. Forest Ecology and Management 49: 277-292.

Watson, M.A. 1980. Patterns of habitat occupation in mosses-relevance to considerations of the niche. Bull. Torrey Botanical Club 107(3): 346-372.

Weber, M.G., R.S. McAlpine, B.M. Wotton, J.G. Donnelly and M.W. Hobbs. 1995. Prescribed burning and disk trenching effects on early plantation performance in eastern Ontario, Canada. For. Ecol. Manage. 78: 159-171.

Whittaker, R.H. 1972. Evolution and measurement of species diversity. Taxon 21 (2/3): 213-251.

Whittaker, R.H. 1975. Communities and ecosystems. Macmillan Publishing, NY.