APPROVAL OF DOCUMENT AFTER CONSIDERATION AND/OR INCORPORATION OF ARC REVIEWER'S COMMENTS:

Final Approval: Business Unit Manager: __Larry Roy_____ Date: _March 12/04___

Document Title: **MIXEDWOOD STAND BIODIVERSITY: THE INFLUENCE OF UNDERSTOREY PROTECTION HARVESTING ON FOREST STRUCTURE AND BIODIVERSITY IN ALBERTA BOREAL MIXEDWOOD STANDS – FINAL REPORT**

File Number: 2065M-A03/022/00 Project Code:

Author(s): STEVE BRADBURY; JASON FISHER; SAMANTHA SONG

Initial Input Date: UNKNOWN

Initially Input By: AUTHORS

Revision Dates: Feb 23-04; Feb 24-04; Feb 25-04; Feb 26-04; Feb 27-04; Mar 1-04; Mar 2-04; Mar 3-04; Mar 4-04; Mar 5-04; Mar 8-04; Mar 9-04; Mar 10-04; Mar 11-04; Mar 12-04; Mar 15-04

Revised By: Pat Soldan

Date Title Page Added; Filed Electronically (No Formatting Requested):
Filed by:

For Publication In/As: Client Report
Formatted To:
Comments:

Document Number: FRD05132.CLR
Document Type: Client report – final report
Directory: O:/

Electronic Signature Added:
Draft Removed:

MIXEDWOOD STAND BIODIVERSITY:

THE INFLUENCE OF UNDERSTOREY PROTECTION HARVESTING ON FOREST STRUCTURE AND BIODIVERSITY IN ALBERTA BOREAL MIXEDWOOD STANDS

FINAL REPORT

Mixedwood Stand Biodiversity:

The Influence of Understorey Protection Harvesting on Forest Structure and Biodiversity in Alberta Boreal Mixedwood Stands

Final Report

By

Steve Bradbury
Jason T. Fisher

Sustainable Ecosystems
Alberta Research Council
Vegreville, Alberta

and

Samantha J. Song

Canadian Wildlife Service
Environment Canada
Edmonton, Alberta

March 15, 2004

DISCLAIMER

This study was funded by the Alberta Research Council, Ainsworth Lumber Company, Manning Diversified Forest Products, the Canadian Wildlife Service, and the Alberta Conservation Association. The views, statements and conclusions expressed, and the recommendations made in this report, are entirely those of the authors and should not be construed as the statements, conclusions, or opinions of members of the Alberta Research Council, Ainsworth Lumber Company, Manning Diversified Forest Products Research Trust Fund, Canadian Wildlife Service, or the Alberta Conservation Association.

Address Correspondence to:
Steve Bradbury
Sustainable Ecosystems
Alberta Research Council
P.O. Bag 4000
Vegreville, AB
T9C 1T4
Phone: (780) 632-8305
Fax: (780) 632-8379
Email: bradbury@arc.ab.ca

EXECUTIVE SUMMARY AND MANAGEMENT IMPLICATIONS

This study was conducted in two areas in the boreal forests of northwestern Alberta. The study area south of Grande Prairie, Alberta (Twp 66,67; Rge 4,5; W6M), included deciduous and mixedwood forest cover types. The study area northwest of Manning, Alberta (Twp 94, Rge 24, W5M), included mixedwood and coniferous forest cover types. At each study area, 12 stands were selected: six stands were mixedwood forest, and six stands were either deciduous or coniferous forest. The six stands of each forest cover type were further divided into three to be harvested and three to be reserved throughout the duration of the study. Deciduous and coniferous stands were harvested using traditional clearcutting techniques, and the mixedwood stands were harvested using an understorey protection strategy. At the Grande Prairie study area, pre-harvest sampling occurred during the summer of 2000, and post-harvest sampling occurred during the summer of 2001 and 2002. At the Manning study area, pre-harvest sampling occurred during the summer of 2000 and 2001, and post-harvest sampling occurred during the summer of 2002 and 2003. The following biotic elements were sampled in both study areas: vertical forest structure (*i.e.*, trees and tall shrubs), deadwood resources (*i.e.*, snags and downed woody material), understorey vascular plant communities, songbird communities, fungal communities, red and flying squirrel populations, and bat activity.

Vertical forest structure

All merchantable trees were harvested from deciduous and coniferous stands. The majority of aspen canopy stems, and all merchantable coniferous stems that were accessible from along the skid trails, were harvested in understorey protection cutblocks. Aspen canopy removal targets (70%) were achieved in the Grande Prairie study area understorey protection cutblocks where 69.8% of aspen canopy stems were removed. In the Manning study area, substantially fewer aspen canopy stems were removed (68.3%) compared with the targeted proportion (85%) because many stems were not of a merchantable size. Understorey protection cutblocks in the Grande Prairie and Manning study areas, respectively, had 62.4% (65% was targeted) and 53.2% of understorey conifer stems retained. The high levels of live tree residuals in understorey protection cutblocks provided far more vertical forest structure than traditional clearcuts, or typical structured cutblocks (with < 10% residuals), and thus, provided forest habitat for many forest generalist species.

Deadwood resources

With respect to snag density, understorey protection cutblocks and clearcuts differed in at least two fundamentally important ways: 1) snags were nearly eliminated in both deciduous and coniferous clearcuts (5% remained after harvest), but were retained in substantial numbers (48% in Grande Prairie and 31% in Manning) in understorey protection cutblocks; and 2) the potential for recruitment of new snags in maturing understorey protection cutblocks far exceeds the potential for recruitment of new snags in regenerating clearcuts.

Compared with pre-harvest stands, DWM volume increased substantially in both deciduous and coniferous clearcuts due to the large amount of slash and harvesting debris. Most of the DWM volume in deciduous clearcuts existed as pieces less than 30 cm in diameter, while in coniferous clearcuts the most volume was derived from pieces 20 – 40 cm in diameter. These differences occurred because of the differences in tree sizes and stand age at the time of harvest (deciduous stands were roughly 100 years-old and coniferous stands were roughly 150 years-old). Understorey protection harvesting resulted in fewer changes to DWM volume compared with clearcuts. In addition, abundant live residual trees and dead snags will provide future inputs of DWM in all stages of decay in the interim between understorey

protection harvesting phases. Removal of 70% of the aspen canopy, however, may limit the volume of future DWM in the largest size classes.

Vascular plant communities in deciduous, mixedwood and coniferous forests

Understorey plant communities in mixedwood forests differed from those found in deciduous and coniferous forests in terms of both plant community composition and variation. Plant community differences were driven by changes in forest structure in stands along the boreal deciduous, mixedwood, and coniferous forest continuum. Plant cover, species richness and diversity all decreased as overstorey coniferous stem density and moss cover increased. Deciduous forests had highly variable plant communities and coniferous forests had the lowest variability among vascular plant communities.

Mixedwood stands with higher densities of coniferous stems and higher levels of moss cover, had plant communities that were more similar to coniferous forests. In contrast, mixedwood stands with few coniferous stems and minimal moss cover had similar plant communities to deciduous forests. Variability in mixedwood stand vascular plant communities was associated with variability in mixedwood forest structure (*i.e.*, conifer overstorey and understorey stem density, and moss cover). This structural heterogeneity resulted in a highly variable microhabitat compared with deciduous forests, and thus, resulted in highly variable plant communities. Mixedwood stand plant communities exhibited regional variation, and thus, management of vascular plant communities in mixedwood forests should occur at a regional level.

Vascular plant communities before and after harvest

Clearcutting deciduous and coniferous forests resulted in a greater change to the understorey plant community compared with an understorey protection harvesting strategy. Furthermore, clearcutting coniferous forests caused a greater change to plant communities than clearcutting deciduous forests. Clearcutting coniferous stands produced more homogeneous plant communities, whereas, clearcutting deciduous stands increased plant community variation. After harvest, the deciduous clearcut plant community was dominated by a few species that responded with vigorous growth. In contrast, after coniferous clearcutting, the species-poor vascular plant community responded slowly to the altered microclimate due to the lack of vigorous, competitive herbaceous species.

The plant community in mixedwood forests changed the least (relative to deciduous and coniferous forests) after understorey protection harvesting. The extent to which microclimate changes with different retention levels, influences the magnitude of change to the plant community. Removal of 70% of the deciduous canopy, and roughly 40% of coniferous stems, increased light availability, but the magnitude of this change did little to alter the overall composition of the mixedwood stand plant community.

Plant communities in mixedwood forests, and in understorey protection cutblocks, exhibited regional variation. At the Grande Prairie study area, mixedwood stands had a species-saturated, and highly competitive plant community. At the Manning study area, mixedwood stands had lower representation of all plant species capable of existing in mixedwood forests, and less vigorous plant growth (*i.e.*, less competitive). Variation in plant communities at the Manning study area resulted from individual stands having different plant species assemblages. Variation in plant communities at the Grande Prairie study area resulted from competitive interactions among species producing differences in individual species cover values.

Understorey protection cutblocks had plant communities that were unlike plant communities found in both deciduous and coniferous clearcuts, and provided no habitat where clearcut conditions could be reproduced. Regional differences in plant community response to understorey protection harvesting suggest that regional management objectives should be established.

Songbird communities

Songbird community composition was different in intact mixedwood stands compared with stands with understorey protection; however, the turnover in composition was not as dramatic as compared with a pre- and post-harvest scenario with clearcutting. Density and species richness of songbird communities in understorey protection cutblocks was similar to that found in the pre-harvest mixedwood state, and there were many species that used these stands that also used forested habitat. Communities in understorey protection cutblocks tended to be dominated by generalist and small conifer or shrub associated species such as Chipping Sparrow, Dark-eye Junco, White-throated Sparrow and American Robin, although community composition varied between sites in Manning and Grande Prairie. Understorey protection cutblocks may make a short-term contribution to habitat for these species; however further study of reproductive success is necessary to confirm this. Understorey protection cutblocks did not provide habitat for some sensitive species found in intact, older seral stage, deciduous, mixedwood or coniferous habitats such as Brown Creeper, Black-throated Warbler, Bay-breasted Warbler, Canada Warbler and Cape May Warbler.

Fungal communities

Fungal communities (both decomposer and mycorrhizal species groups) in deciduous, mixedwood and coniferous forest cover types differed. Community differences were associated with fungal-substrate (decomposer) or fungal-host tree (mycorrhizal) relationships. Decomposer and mycorrhizal species both contributed to fungal community variation. Variation in fungal communities was greatest in coniferous stands, followed by deciduous stands. The high variation in fungal communities in coniferous stands was likely a result of patchy distribution of fungal species in response to the structural heterogeneity of the coniferous stands sampled. Regional differences were observed in fungal communities found in mixedwood stands. Fungal community variation was lowest in mixedwood stands within each region. However, overall variation in mixedwood stands from both regions was greater than that observed in deciduous stands.

Understorey protection harvesting influenced decomposer and mycorrhizal fungi to a lesser degree than traditional clearcutting of both deciduous and coniferous stands. Clearcuts provided poor habitat for sporocarp production, due to inappropriate microclimatic conditions. Mixedwood understorey protection cutblocks, on the other hand, retained abundant deadwood resources (and associated microclimatic conditions) for decomposer fungi and high densities of live residual trees for mycorrhizal species. In addition, most of the understorey protection cutblock area was undisturbed by harvest machinery. Understorey protection cutblocks did not lose as much pre-harvest DWM to crushing or to burn piles compared to clearcuts. Furthermore, limited mechanical traffic along skid trails resulted in an undisturbed, and thus, a stable host root system that provided continuity for mycorrhizal species. The fungal community response to understorey protection harvesting exhibited regional variation linked to climate.

Red and flying squirrel populations

Flying squirrel populations were reduced immediately after mixedwood understorey protection harvesting. Understorey protection cutblocks were occupied by mature reproductive individuals in the second year after harvest in Grande Prairie, but not in Manning. These findings suggest that the forest structure remaining in mixedwood understorey protection cutblocks may, in some cases, be facilitating flying squirrel occupation of these stands where foraging and denning sites persist. In contrast, flying squirrels were expected to be largely absent from clearcuts. There were very few differences in red squirrel abundance between mixedwood understorey protection cutblocks and mixedwood reserves, suggesting that understorey protection cutblocks support red squirrel populations in numbers closely approximating unharvested mixedwood stands. In contrast, red squirrels were largely absent from clearcuts. In the first year after harvest, understorey protection cutblocks were occupied by smaller, non-reproductive, and ostensibly less fit individuals, suggesting these stands represented suboptimal habitat for red squirrels. By the second year after harvest, red squirrels attained masses and rates of reproductive maturity that did not differ from coniferous or mixedwood reserves. The similarities between control mixedwood reserves and year 2 understorey protection cutblocks suggests that this harvesting strategy facilitates the maintenance of squirrel populations in some mixedwood stands. Squirrel persistence is likely due to the presence of overstorey trees for cover and nest sites, mature cone-bearing spruce left as residuals, and microclimatic conditions that favour the growth of fungi and lichen.

Bat activity

Activity of larger, less manoeuvrable bat species was greater in clearcuts than in unharvested stands. Overall bat activity was reduced in deciduous clearcuts in comparison with deciduous reserves, suggesting that clearcutting may favour larger species but detrimentally impact overall bat diversity. We found no differences in activity of small *Myotis* or large non-*Myotis* bat species between mixedwood reserves and understorey protection cutblocks. These findings suggest that forest structural attributes created by canopy break-up in old-growth stands, which serve to facilitate bat activity under natural conditions, may be emulated by understorey protection harvesting. The apparent maintenance of bat abundance and diversity in understorey protection cutblocks suggests that this harvesting strategy is a preferred alternative to clearcutting. However, although foraging in understorey protection cutblocks was recorded, roosting activity in harvested sites was not specifically identified. The availability of roost sites in first- and second-phase understorey protection harvesting will limit the long-term population persistence of bats.

Understorey protection beyond the stand level

With the exception of some within-stand plant and fungal regeneration, the rate and extent of recolonisation of mixedwood understorey protection cutblocks - by tree seeds, vascular plant propagules, fungal spores, songbirds, squirrels, bats and other biota - will largely depend on their presence in adjoining stands, and in the surrounding landscape. The dispersal distances for most biota that we studied were not large, thus emphasizing the importance of adjacency effects in determining post-harvest successional trajectories and biotic convergence to preharvest states. If understorey protection cutblocks are clustered in the landscape (and in time), adjacent to one another, and disconnected from source populations in unharvested areas, then recolonisation may be delayed or even prevented for some biota. However, if understorey protection cutblocks are spatially and temporally staggered across the landscape, such that high connectivity is maintained between unharvested population sources and harvested stands within any given rotation, then, recolonisation will be facilitated. This study revealed that understorey protection harvest provides in-stand structure favourable for the maintenance of

biodiversity - however this capacity will only be achieved through careful landscape-level planning that allows this potential to be realised.

Project deliverables

As part of developing and conducting this research we have worked closely with government regulatory agencies and the forest industry to ensure that the results will be applicable to these organizations. Specific deliverables include:

- Three Year-end Reports and one Final Project Report.
- Descriptions of pre-harvest boreal forest stand structure (*i.e.*, deciduous, mixedwood and coniferous stands) and the vegetation, songbird, and fungal communities, flying and red squirrel populations and bat activity found therein.
- Descriptions of post-harvest boreal forest stand structure (*i.e.*, deciduous clearcuts, mixedwood understorey protection cutblocks and coniferous clearcuts) and the vegetation, songbird, and fungal communities, flying and red squirrel populations and bat activity found therein.
- Management implications of understorey protection harvesting strategies at the stand level.
- Presentations of research findings in client reports, primary journals, and at conferences.
- Participation in discussion groups that assess alternative harvest practices in Alberta.

Steve Bradbury
Jason Fisher
Samantha Song
March 15, 2004

RESEARCH TEAM

STEVE BRADBURY, Ph.D., Project Leader, Plant/Fungal Ecologist.
Sustainable Ecosystems, Alberta Research Council, Vegreville, Alberta, T9C 1T4,
phone (780) 632-8305, fax (780) 632-8379, email bradbury@arc.ab.ca.

JASON T. FISHER, M.Sc., Mammalogist.
Sustainable Ecosystems, Alberta Research Council, Vegreville, Alberta, T9C 1T4,
phone (780) 632-8374, fax (780) 632-8379, email fisherj@arc.ab.ca.

SAMANTHA J. SONG, Ph.D., Boreal Ecologist.
Canadian Wildlife Service, Environment Canada, Room 200, 4999-98 Ave. Edmonton, Alberta,
T6B 2X3, phone (780) 951-8965, fax (780) 495-2615, email Samantha.Song@ec.gc.ca.

SHARON KENDALL, B.Sc., Technician.
Sustainable Ecosystems, Alberta Research Council, Vegreville, Alberta, T9C 1T4,
phone (780) 632-8320, fax (780) 632-8379, email sharonk@arc.ab.ca.

LUKE NOLAN, Dipl. Tech., Technician.
Sustainable Ecosystems, Alberta Research Council, Vegreville, Alberta, T9C 1T4,
phone (780) 632-8386, fax (780) 632-8379, email luke@arc.ab.ca.

LEONARD PELESHOK, Dipl. Tech., Technician.
Sustainable Ecosystems, Alberta Research Council, Vegreville, Alberta, T9C 1T4,
phone (780) 632-8312, fax (780) 632-8379, email len@arc.ab.ca.

COLIN TWITCHELL, Dipl. Tech. Technician.
Sustainable Ecosystems, Alberta Research Council, Vegreville, Alberta, T9C 1T4,
phone (780) 632-8356, fax (780) 632-8379, email colin@arc.ab.ca.

Additional scientist contribution:

Lisa Wilkinson, M.Sc. Regional Endangered Species Specialist, Alberta Sustainable Resource Development, Edson, Alberta.
Philip Lee, Ph.D. Forest Ecologist, University of Alberta, Edmonton, Alberta.

Additional technical assistance:

Cris Gray, B.Sc., former Technician, Alberta Research Council
Dave McKinnon, B.Sc., former Technician, Alberta Research Council
Kelly Sturgess, B.Sc., former Technician, Alberta Research Council
Lindsay Tomyn, B.Sc., former Technician, Alberta Research Council
Gavin Berg, B.Sc., Summer Field Technician, Alberta Research Council
Delinda Ryerson, B.Sc., Summer Field Technician, Alberta Research Council
Dan Sturgess, B.Sc., Summer Field Technician, Alberta Research Council

FUNDING SOURCES

April 2000 - March 2004

Alberta Research Council, Sustainable Ecosystems, Bag 4000, Vegreville, Alberta, T9C 1T4.
Larry Roy, phone (780) 632-8250, fax (780) 632-8379, email Larry@arc.ab.ca.

Manning Diversified Forest Products Research Trust Fund, Manning Diversified Forest Products, Box 370, Manning, Alberta, T0H 2M0.
Andy Shandro, MDFP Research Trust Fund Secretariat, phone (780) 836-3111, fax (780) 836-3202, email mdfpwood@telusplanet.net.

Ainsworth Lumber Company, Bag 6700, Grande Prairie, Alberta, T8V 6Y9.
Dave Beck, Silviculture Forester, phone (780) 831-2522, fax (780) 831-2501, email daveb@ainsworth.ca.
Fred Radersma, Planning Superintendent, phone (780) 831-2516, fax (780) 831-2501, email fredr@ainsworth.ca.

September 2002 – March 2004

Environment Canada, 4999-98 Ave. Edmonton, Alberta, T6B 2X3.
Samantha Song, Boreal Ecologist, Western Boreal Conservation Initiative, phone (780) 951-8965, fax (780) 495-2615, email Samantha.Song@ec.gc.ca.

April 2001 - March 2002

Alberta Conservation Association, Bag 900 – 26, Provincial Building, Peace River, Alberta, T8S 1T4
Paul Hvenegaard, Regional Programs Manager, phone (780) 624-6405, fax (780) 624-6455, email paul.hvenegaard@gov.ab.ca.

GENERAL ACKNOWLEDGEMENTS

This project has required and received strong commitments from the forest industry, the Alberta Research Council, and Environment Canada.

We appreciate the administrative and funding support provided by the Alberta Research Council. Special thanks are extended to Dick Peter, Larry Roy, Melanie Thibault, Gerry Lofthaug, Duane Nakonechny, Pat Soldan, Elaine Cannan, Sonia Hunka, Nanc Fraser-Hrynyk, Connie Jackson, Val Golka, Lorraine Robert, Susan Stecyk, Brenda Dziwenka, Patricia Ferleyko, and Kathy Ilkiw for their assistance.

We thank our technical staff for their hard work in the field and input during analysis and preparation of this document. Technicians include Len Peleshok, Sharon Kendall, Luke Nolan, Colin Twitchell, Cris Gray, Dave McKinnon, Gavin Berg, Delinda Ryerson, Kelly Sturgess, Dan Sturgess, and Lindsay Tomyn.

The following people and organizations helped with logistical support in the field, equipment storage, equipment supply, providing knowledge of the study areas, and assisted with study site selection and GPS: Fred Radersma, Dave Beck, Dave Cook, Andrew Allison, Bryan Telford, Noel Roberts, and Joe Hustler of Ainsworth Lumber Company, Grande Prairie; JP Bielech, Clarence Budal, Jeff Horner, Steve Blanton, Andy Shandro and Shane Drupinski of Manning Diversified Forest Products, Manning; Robert Schmidt of Canadian Northwest Carriers, Manning; and Peter Vogan of the Grande Prairie Regional College, Grande Prairie.

Jim Schieck, Alberta Research Council, Vegreville, initiated the project concept long before it became a reality. His early efforts, ideas and support are gratefully acknowledged. Lisa Wilkinson, Alberta Sustainable Resource Development, Edson, and Phil Lee, University of Alberta, Edmonton, contributed a great deal of time, effort and thought into the first year of the project; their input has improved the project substantially. Lisa Wilkinson also co-authored the bat chapter.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Page

CHAPTER 1. PROJECT BACKGROUND AND SCIENTIFIC RATIONALE

Steve Bradbury

Background

Boreal mixedwood forests occupy approximately one-third of the productive landbase of western Canada and consist largely of understorey immature white spruce growing under a canopy consisting of aspen, balsam poplar and white birch. From a forest industry perspective, these stands represent an important source of aspen fibre for pulp and oriented strand board production, or, if left unharvested these stands would provide significant volumes of conifer sawlogs in 40 – 60 years (Navratil *et al*. 1994).

Traditional white spruce management has focused on clearcut harvesting mixedwood stands and establishing white spruce plantations to re-establish the conifer component. In mixedwood stands, this can be costly due to the number of re-entries required to control aspen suckering so that white spruce can reach the free-to-grow stage. Furthermore, many of the understorey white spruce that would have been economically merchantable in 40 – 60 years, are clearcut as sub- and marginally-merchantable stems (Navratil *et al*. 1994). In doing so, understorey white spruce trees are replaced by trees that may not be merchantable for another 100 years.

Alternative harvesting strategies have been developed to protect the understorey white spruce while removing the mature aspen (Peterson and Peterson 1992; Navratil *et al*. 1994). In these understorey protection harvest scenarios, tree harvesting occurs during two periods. At the first stage of harvest (65 - 85 years after the stand initiating event) large deciduous trees and merchantable white spruce are removed to capture these trees before they senesce, and to reduce competition for sub-canopy and understorey white spruce. Following this initial understorey protection harvest, aspen and poplar suckers will likely regenerate in available spaces (*i.e*., skid trails, decking areas and roads), and conifers could be planted in inadequately stocked areas. In the second harvesting stage, 40 – 60 years after the deciduous harvest, released white spruce would be harvested and the area could be managed either for hardwood, mixedwood, conifer or an uneven aged stand scenario (J.P. Bielech, *pers. comm.*).

The rationale for adopting an understorey protection harvest strategy is to ensure that the maximum volume of mature aspen is harvested, and the rotation period for spruce sawlogs is minimized. In doing so, this strategy may alleviate problems where different companies on the same landbase hold coniferous and deciduous harvest rights, and where protection of the understorey spruce component is a priority for the softwood user. However, while mixedwood harvest strategies appear economically feasible (Navratil *et al*. 1994) we do not know the ecological implications of such a harvest strategy.

Scientific Rationale

Wildfire is the dominant natural disturbance in the boreal forests of North America (Eberhart and Woodard 1987; Hunter 1993), and has shaped the pattern of boreal stands on the landscape. Within Alberta's boreal mixedwood forest, flora and fauna have evolved within complex habitats resulting from natural successional processes following wildfire. Biota that require young forests with many structural legacies from old forests (*i.e*., biota that live in young forests but require snags for nesting or foraging) reach high abundance during the first 30 years following natural disturbance (Stelfox 1995; Schieck *et al*. 1995; Kirk et al. 1996; Song 2002). Different biotic communities are present 30-60 years after natural disturbance because snags produced from previous disturbances have disappeared, and stands in the resulting forest have little structural diversity. In addition, the dense canopy during this period allows little light to penetrate to the forest floor, resulting in

poorly developed forb and shrub communities (Peterson and Peterson 1992). By 100 years after fire, boreal mixedwood stands regain their complex forest structures. During this time, many aspen trees die creating large standing snags, large downed logs, and gaps in the canopy. Canopy gaps allow increased light levels to reach understorey layers resulting in accelerated understorey spruce growth, but a high understorey spruce density continues to restrict forb and shrub development to shade tolerant species. Logs from fallen trees create a diverse forest floor with a wide variety of substrates and microclimates for plants, fungi, invertebrates and mammals.

Many birds and mammals nest in cavities excavated within rotten centres of large trees, snags, and downed logs (Hansen *et al.* 1991). In addition, fungi, vascular and nonvascular plants live within and on large snags and downed logs and are part of complex food webs that are dependent on these dead wood structures (Crites and Dale 1998). Due to the diversity of habitats, many species may reach their highest abundance in older mixedwood stands compared to any other boreal stand type (Song 2002).

Managing biodiversity in the complex and dynamic boreal mixedwood forest is not simple. Ecosystem management typically strives to mimic natural disturbance regimes (Hunter 1993). However, substantial differences in forest structure have been documented between stands resulting from natural disturbance and stands created by traditional clearcut harvesting that targets either deciduous or coniferous species (Lee *et al.* 1997; Lee 1999; Song 2002). Concomitant with differences in forest structure are differences in the response of biotic communities and abiotic environments following natural and anthropogenic disturbances (Hobson and Schieck 1999; Lee 1999; Song 2002).

The greatest fundamental difference between harvested and burned sites is that post-fire sites have high densities of both fire-killed snags and live residuals (Lee 1999), but it is unlikely that any harvest scenario will leave high densities of fire-killed trees after harvest. Wildfires may burn vast areas of land, but within the margins of even the largest burns, high densities of live residual trees are found (Eberhart and Woodard 1987). Burned areas leave live residuals in a wide range of sizes and distributions from individual trees to large seemingly undisturbed patches several hectares in size. On average, in large areas (>60 ha) of burned boreal forests, live residuals represent 37% of the total burned area (C. Smyth, *pers comm.*).

In an attempt to mimic the existence of live residuals found in burned areas, structured harvesting techniques are designed to leave a range of live standing residual trees on-site (although, typically less than 10%). Live residuals in cutblocks may serve as remnant habitat providing continuity with pre-harvest forests, refugia for species dependent upon old-growth structure, and may serve as "stepping stones" to facilitate movement across cutover areas (Saunders *et al*. 1991; Spies *et al*. 1991; deMaynadier and Hunter 1995; Schieck 2000; Song 2002; Bradbury 2004). Depending on the amount and distribution of live residuals, biotic communities and abiotic conditions are generally influenced to a lesser degree than those measured following clearcutting, and incorporation of residuals in cutblocks may facilitate a quicker convergence between natural and anthropogenic successional trajectories (Song 2002; Bradbury 2004). If convergence occurs prior to the second rotation, then harvest prescriptions may be reasonably successful in maintaining natural communities on a managed landbase.

Understorey protection harvest leaves substantial densities of live and dead standing residuals; at least 40% of the pre-harvest understorey spruce remains undamaged and 0 – 35% of the overstorey aspen may be left as wind buffers (Navratil *et al*. 1994; D. Beck, *pers. comm.*). However, while understorey protection harvest sites may have similarly high densities of living residuals compared with burned sites, it is not known if these residuals are capable of maintaining mixedwood forest structure and biotic communities. Furthermore, understorey protection residuals are anthropogenic in structure, both in terms of tree species

composition and stand level distribution (*i.e.*, parallel skid trails and residual strips). In contrast, wildfires kill both overstorey and understorey trees regardless of species, and do not leave parallel linear rows of standing residuals. It is not known if the parallel trail system created during understorey protection harvest will fragment the residuals at a level detectable and intolerable by biotic communities, and whether abundant parallel skid trails create uniform edge habitat throughout the cutblock. Nevertheless, several physical aspects of understorey protection trials may benefit biodiversity and wildlife relative to traditional harvesting (Vanha-Majamaa and Jalonen 2001); high densities of residuals are conserved relative to traditional harvesting techniques, and the amount of residual left *in situ* will undoubtedly result in less dramatic changes to abiotic conditions on the forest floor and lower vertical strata (Halpern *et al*. 1999).

While numerous trials exist in Alberta measuring the growth rate of released white spruce following understorey protection harvest, few studies examining their ecological consequences have been completed. It is unknown how pre-harvest biotic communities respond to removal of the deciduous overstorey and to the density of live residual trees left after understorey protection trials, and without this knowledge, accurate decisions about the economic and ecological consequences of understorey protection harvesting cannot be made.

Objectives

The objectives of this study were:

1) to evaluate the biotic consequences of mixedwood understorey protection harvest, by testing the hypothesis that understorey protection harvest maintains forest structural components (*i.e.*, live and dead residuals) that provide habitat for biotic communities found in natural mixedwood stands. This was accomplished by examining a number of specific forest elements including forest structure, songbirds, bat activity, squirrel populations, vascular plants and fungal communities.

2) to determine if boreal mixedwood stands support unique assemblages of bird and plant species. This was accomplished by examining species assemblages found in boreal deciduous, mixedwood and coniferous stands.

3) to compare magnitude of biotic responses to understorey protection to those found after clearcutting. For many biotic communities, the differences found in clearcuts compared to pre-harvest stands are significant; we determined if understorey protection harvest resulted in a less dramatic change relative to clearcutting, and if understorey protection blocks provided habitat, even temporarily, for species that lost habitat in a clearcut scenario.

4) to provide a discussion of the management implications of regional and provincial implementation of mixedwood harvest strategies.

By replicating this study in two different regions of northwestern Alberta, the scope of inference was enhanced. This particular study examined pre-harvest stands for one year at the Grande Prairie study area and two years at the Manning study area, and examined post-harvest stands for two years at each study area. Within this time frame we can only document the initial biotic responses to harvesting, but by revisiting the study area over time, changes to successional trajectories prior to the second phase of harvesting can be monitored.

Literature Cited

Bradbury, S. 2004. Understorey plant communities in boreal cutblocks with different sizes and numbers of residual patches. Can. J. For. Res. *In press*.

Crites, S., and Dale, M.R.T. 1998. Diversity and abundance of bryophytes, lichens and fungi in relation to woody substrate and successional stage in aspen mixedwood

boreal forests. Canadian Journal of Botany. 76: 641-651.

deMaynadier, P.G., and Hunter, M.L. 1995. The relationship between forest management and amphibian ecology: a review of the North American literature. Environmental Review. 3: 230-261.

Eberhart, K.E., and Woodard, P.M. 1987. Distribution of residual vegetation associated with large fires in Alberta. Canadian Journal of Forest Research. 17: 1207-1212.

Halpern, C.B., Evans, S.A., Nelson, C.R., McKenzie, D., Liguori, D.A., Hibbs, D.E. and Halaj, M.G. 1999. Response of forest vegetation to varying levels and patterns of green-tree retention: an overview of a long-term experiment. Northwest Sci. 73:27-44.

Hansen, A.J., Spies, T.A., Swanson, F.J., and Ohmann, J.L. 1991. Conserving biodiversity in managed forests. BioScience. 41: 382-392.

Hobson, K.A. and Schieck, J. 1999. Changes in bird communities within boreal mixedwood forest during the fist thirty years: contrasting the effects of harvest and wildfire.

Hunter, M.L. 1993. Natural fire regimes as spatial models for managing boreal forests. Biological Conservation. 65: 115-120.

Kirk, D.A., Diamond, A.W., Hobson, K.A., and Smith, A.R. 1996. Breeding bird communities of the western and northern Canadian boreal forest: relationship to forest type. Canadian Journal of Zoology. 74: 1749-1770.

Lee, P.C., Crites, S., Nietfeld, M., Van Nguyen, H., and Stelfox, J.B. 1997. Characteristics and origins of deadwood material in aspen-dominated boreal forests. Ecological Applications. 7: 691-701.

Lee, P. (Editor). 1999. Fire and harvest residual (FAHR) project: the impact of wildfire and harvest residuals on forest structure and biodiversity in aspen-dominated boreal forests of Alberta. Alberta Research Council, Vegreville, AB.

Navratil, S., L.G. Brace, E.A. Sauder and S. Lux. 1994. Silvicultural and harvest options to favour immature white spruce and aspen regeneration in boreal mixedwoods. Natural Resources Canada, Canadian Forest Service, Northwest Region, Northern Forestry Centre, Edmonton, Alberta. Information Report NOR-X-327.

Peterson, E.B. and Peterson, N.M. 1992. Ecology, management, and use of aspen and balsam poplar in the prairie provinces, Canada. For. Can., Northwest Reg., North. For. Cent., Edmonton, Alberta. Spec. Rep. 1.

Saunders, D.A., Hobbs, R.J., and Margules, C.R. 1991. Biological consequences of ecosystem fragmentation: a review. Conservation Biology. 5: 18-32.

Schieck, J., Nietfeld, M., and Stelfox, J.B. 1995. Differences in bird species richness and abundance among three successional stages of aspen dominated boreal forests. Canadian Journal of Zoology. 73: 1417-1431.

Schieck, J. (Editor). 2000. Biodiversity in cutblocks with few large versus many small residual patches of trees and snags: 1999/2000 final report. Alberta Research Council, Vegreville, AB.

Song, S.J. (Editor). 2002. Ecological basis for stand management: a synthesis of ecological responses to wildfire and harvesting. Alberta Research Council, Vegreville, AB.

Spies, T.A., Tappeiner, J., Pojar, J., and Coates, D. 1991. Trends in ecosystem management at the stand level. *In* Transactions of the fifty-sixth North American wildlife natural resources conference. *Edited by* R.E. McCabe, Wildlife Management Institute, Washington DC. pp. 628-639.

Stelfox, J.B. 1995. Relationships between stand age, stand structure, and biodiversity in aspen mixedwood forests in Alberta. Jointly published by Alberta Environmental Centre (AECV95-R1), Vegreville, AB, and Canadian Forest Service (Project No. 0001A), Edmonton, AB. 301 pp.

Vanha-Majamaa, I., and Jalonen, J. 2001. Green tree retention in Fennoscandian forestry. Scand. J. For. Res. Suppl. 3:79-90.

CHAPTER 2: GRANDE PRAIRIE AND MANNING STUDY AREAS AND GENERAL METHODS

Steve Bradbury

Study Areas

This study was conducted in two areas in the boreal forests of northwestern Alberta. The study area south of Grande Prairie, Alberta (Twp 66,67; Rge 4,5; W6M), was composed of two forest types: pure deciduous stands dominated by aspen (*Populus tremuloides* Michx.) but with small patches of balsam poplar (*Populus balsamifera* L.), and mixedwood stands with an aspen dominated canopy and a white spruce understorey (*Picea glauca* (Moench) Voss). The study area is located on soils that are grey (solodic to solodized solonetz) clay loam to clay over lacustro-till (Odynsky *et al*. 1956). Daily mean temperature in the coldest month (January) is -15.0˚C and in the hottest month (July) is 15.9˚C. Average annual precipitation is 447 mm, with approximately 36% of total annual precipitation falling as snow (Environment Canada, 2004: Grovedale weather station). Twelve stands, ranging in size from 20.2 to 57.6 ha (mean of 40.1 ha), were selected in the Grande Prairie study area: six stands were mixedwood forest, and six were deciduous forest. The two forest types were further divided into three stands to be harvested and three stands to be reserved throughout the duration of the study (Figure 2.1). At the initiation of the study, and prior to harvest, canopy trees in all twelve stands were approximately 100 years old.

The study area northwest of Manning, Alberta (Twp 94, Rge 24, W5M), also had two forest types. Conifer stands were dominated by mature white spruce with minor canopy components of aspen, balsam poplar and lodgepole pine (*Pinus contorta* Loudon var. *latifolia* Engelm.). Mixedwood stands had an aspen overstorey and a white spruce understorey. The study area is located on poorly drained grey (solodic to eluviated gleysol) clay loam to clay soils (Reeder and Odynsky 1969). The daily mean temperature in the coldest month (January) is -18.8˚C and in the hottest month (July) is 15.9˚C. Average annual precipitation is 391 mm, with approximately 28% of total annual precipitation falling as snow (Environment Canada, 2004: Notikewin weather station). Twelve stands ranging from 11 to 49 ha, with a mean of 27.3 ha were selected in the study area. The two forest types were further divided into three reserve stands and three harvested stands (Figure 2.2). At the initiation of the study, and prior to harvest, canopy trees in the conifer stands were approximately 150 years old. Canopy trees in the mixedwood stands were approximately 75 years old.

In the Grande Prairie study area, stands were harvested between September 2000 and February 2001. Deciduous stands were clearcut using traditional methods, and mixedwood stands were harvested using an understorey protection system. The objective of the mixedwood harvest was to remove 70% of the deciduous stems while protecting as much coniferous understorey as possible. Skid trails were cut 25 m apart, and were approximately 4 m wide. A Timco feller-buncher with the ability to reach up to 10 m off the skid trail was used for harvest.

In the Manning study area, cut stands were harvested in November and December 2001. Coniferous stands were clearcut as per standard practice, and mixedwood stands were harvested using an understorey protection system. The objective of the mixedwood harvest was to remove 85% of the deciduous stems while protecting at least 55% of the conifer understorey. Skid trails were also cut 25 m apart, but were approximately 5 m wide. A Timberjack feller-buncher with the ability to reach up to 7 m off the trail was used for harvest.

In both study areas, skidder traffic was confined to the skid trails, except where the feller-buncher could move into the residual strips without damaging the understorey. Rub posts were left along skid trails to protect adjacent understorey from damage during skidding. Areas with heavy

coniferous understorey and minor deciduous volume were left unharvested. Merchantable coniferous stems that reached or exceeded the height of the deciduous canopy were harvested, if accessible.

General Survey Methods

Pre-harvest sampling was conducted during the spring and summer of 2000 in both study areas, and in spring and summer 2001 in the Manning study area (Table 2.1). Post-harvest sampling was conducted during the spring and summer of 2001 and 2002 in the Grande Prairie study area, and during the spring and summer of 2002 and 2003 in the Manning study area.

In the Grande Prairie study area a grid pattern of 10 ha was established in the centre of each stand (Figure 2.3). In the Manning study area a strip transect of 7 ha was established in the centre of each stand (Figure 2.4). All pre-harvest and post-harvest sampling was conducted along transects within each grid (Grande Prairie) or strip (Manning).

Vertical forest structure (*i.e.*, trees and tall shrubs - Chapter 3), and deadwood resources (*i.e.*, snags and downed woody material - Chapter 4), were sampled along transects totalling 800 m in the Grande Prairie study area and 500 m in the Manning study area. Understorey vegetation (Chapters 5 and 6) was sampled in a series of nested plots (Figures 2.3 and 2.4). Breeding birds (Chapter 7) were sampled and territories were mapped within the grid in the Grande Prairie study area (Figure 2.3) and along the strip in the Manning study area (Figure 2.4). Fungal communities were sampled along a 500 m x 2 m belt transect (Chapter 8) within each grid or strip in both study areas; the fungal belt transect coincided with the squirrel live trapping matrix (see Figures 2.3 and 2.4). Red squirrels were surveyed in conjunction with the bird surveys, and both red and flying squirrels were live trapped within the grid or strip in both study areas (Chapter 9). Bats were sampled using automatic remote bat detectors within the grid or strip in each study area (Chapter 10).

Literature Cited

Environment Canada. 2004. Environment Canada. Canadian climate normals (online). Grovedale and Notikewin stations. Available at: http://www.climate.weather office.ec.gc.ca/ Welcome_e.html.

Odynsky, W., Wynnyk, A., and Newton, J.D. 1956. Soil survey of the Grande Prairie and Sturgeon Lake sheets. Research Council of Alberta Report No. 74. University of Alberta, Edmonton, AB.

Reeder, S.W. and Odynsky, W. 1969. Soil survey of the Hotchkiss and Keg river area. University of Alberta Bulletin No. SS-9, University of Alberta, Edmonton, AB.

Table 2.1. Sampling schedule for forest structure and biota during the project.

	2000		2001		2002		2003	
	Grande Prairie	Manning	Grande Prairie	Manning	Grande Prairie	Manning	Grande Prairie	Manning
	(Pre-harvest)		(Post-harvest)	(Pre-harvest)	(Post-harvest)		(Post-harvest)	
Trees and shrubs	extensive	none	moderate	extensive	extensive	extensive	none	cursory
Snags and DWM	extensive	extensive	moderate	moderate	extensive	extensive	none	cursory
Vascular plants	extensive	extensive	moderate	moderate	extensive	none	none	extensive
Songbirds	extensive	extensive	extensive	extensive	extensive	extensive	none	extensive
Fungi	extensive	extensive	extensive	extensive	extensive	extensive	none	extensive
Squirrels	cursory	cursory	extensive	extensive	extensive	extensive	none	extensive
Bat activity	extensive	extensive	extensive	none	none	extensive	none	none

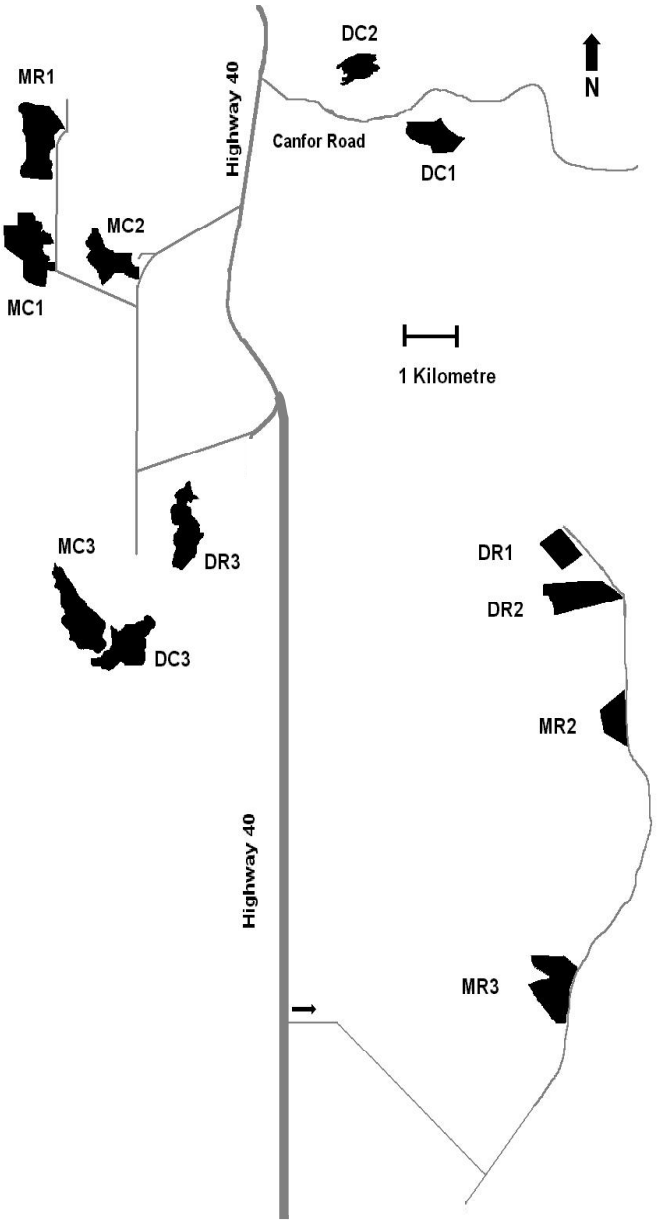


Figure 2.1. Locations of stands in the Grande Prairie study area. Letters refer to stand type (DR-deciduous reserve, DC-deciduous clearcut, MR-mixedwood reserve, MC-mixedwood understorey protection cutblock) and numbers refer to replicates.

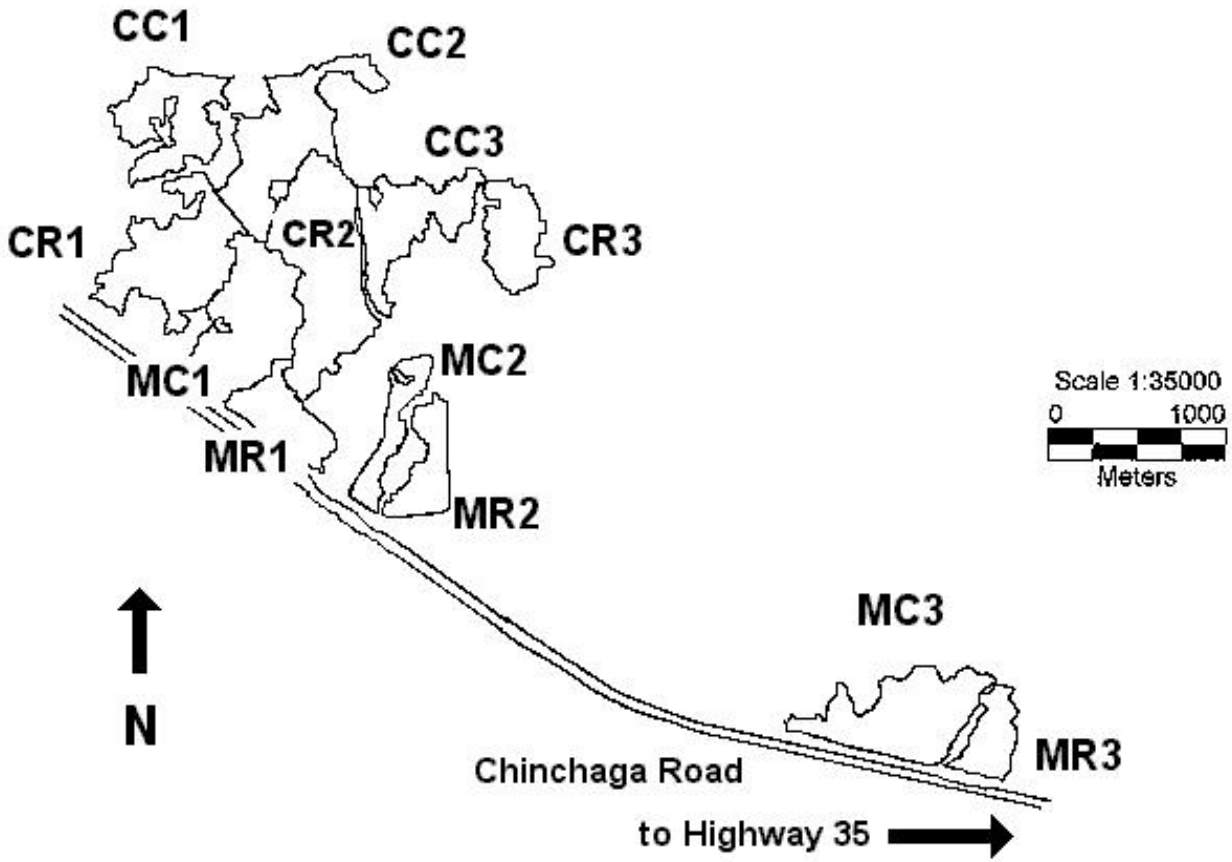


Figure 2.2. Locations of stands in the Manning study area. Letters refer to stand type (CR- coniferous reserve, CC-coniferous clearcut, MR-mixedwood reserve, MC-mixedwood understorey protection cutblock) and numbers refer to replicates.

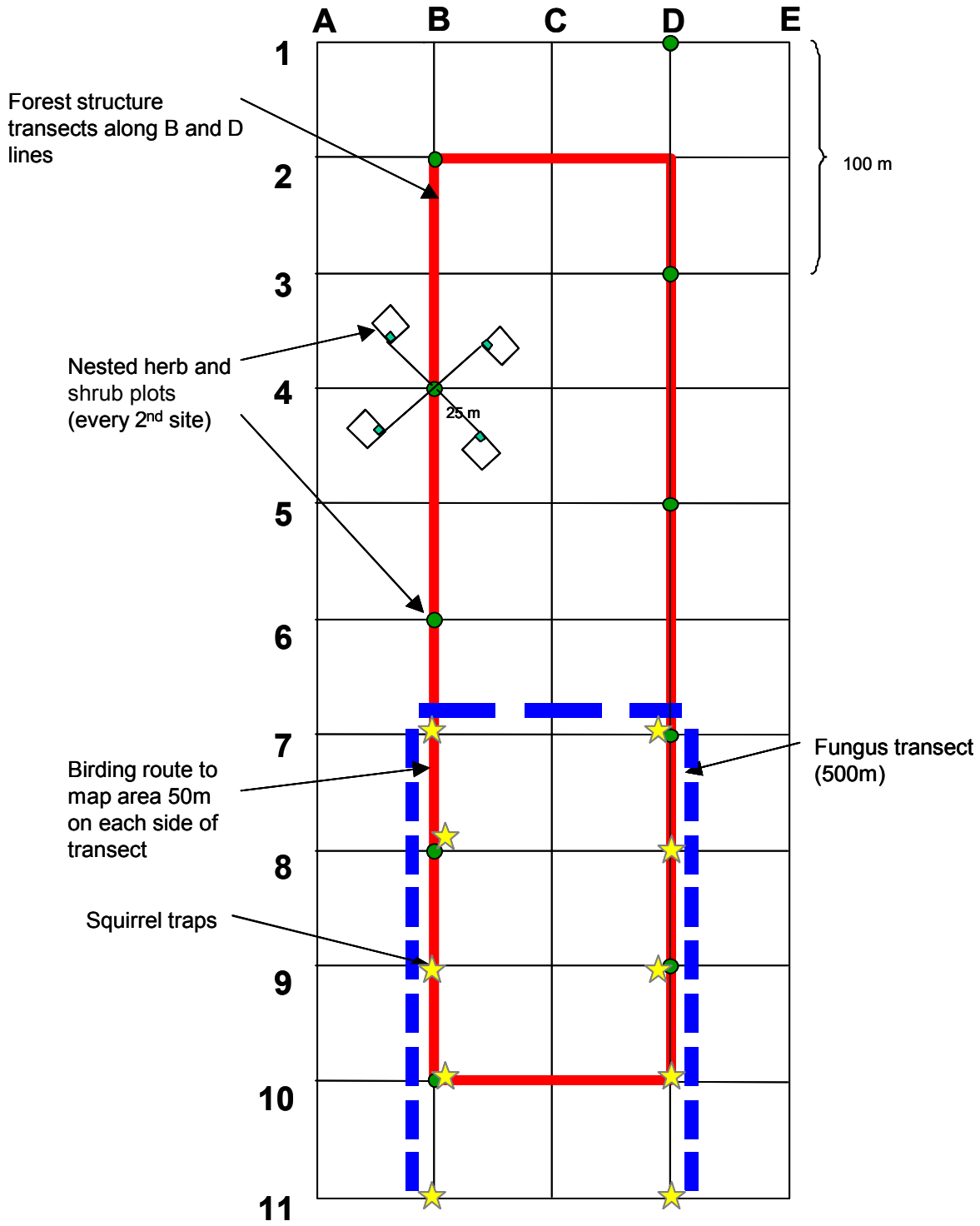


Figure 2.3. Grid layout for sampling in the Grande Prairie study area. Note: In addition to the sampling information depicted, bat detectors were set at positions C2 and C10; the shape of DR3 required re-organizing the grid shape, but sampling area remained constant.

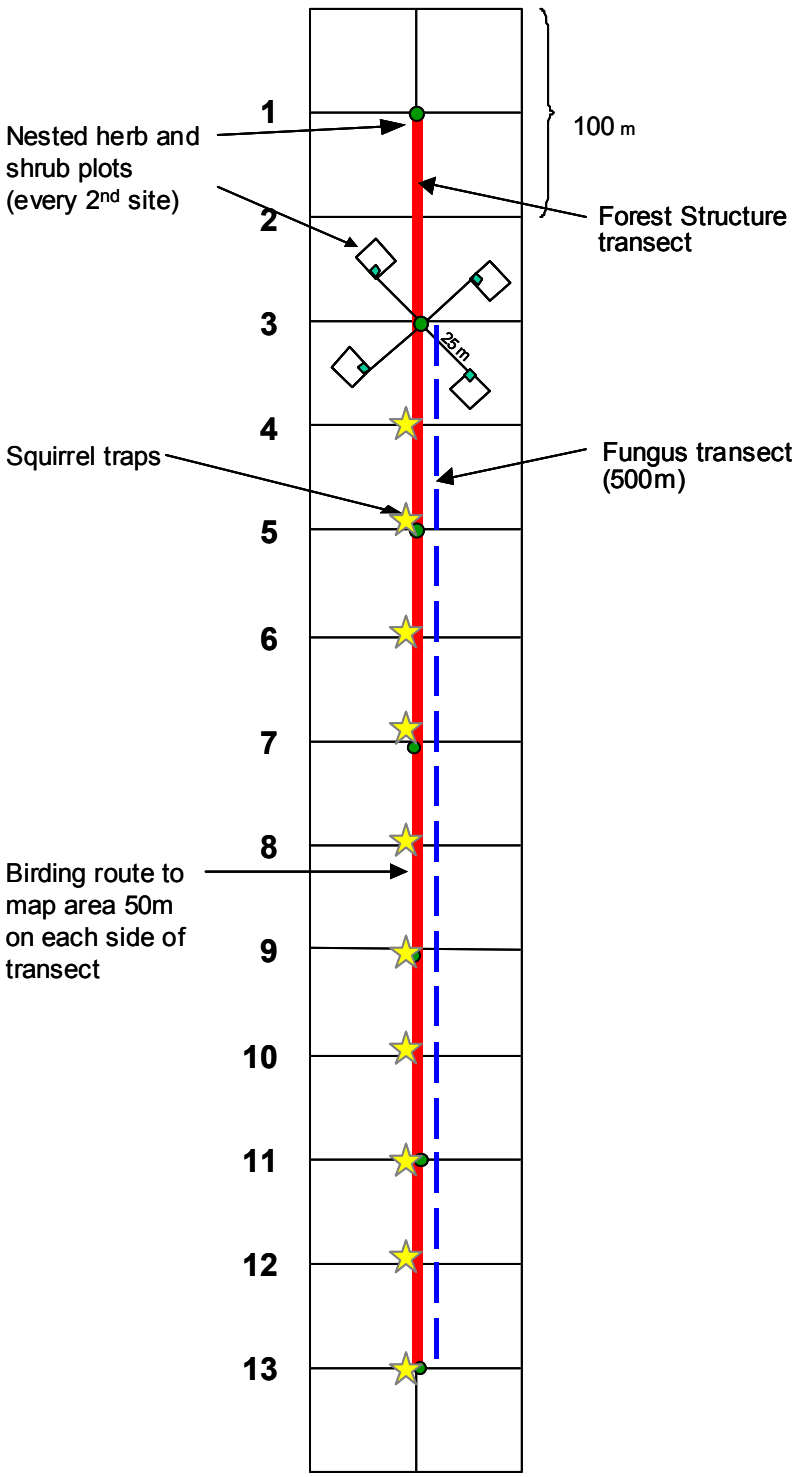


Figure 2.4. Strip layout for sampling in the Manning study area. Note: In addition to the sampling information depicted, bat detectors were set at positions 1 and 13; not all stands were a continuous line due to the shape of the stand but hectare area (7 ha) was consistent throughout.

CHAPTER 3: VERTICAL FOREST STRUCTURE IN DECIDUOUS, MIXEDWOOD AND CONIFEROUS STANDS BEFORE AND AFTER HARVEST, WITH SPECIFIC ATTENTION TO UNDERSTOREY PROTECTION CUTBLOCKS

Steve Bradbury

Introduction

Successional development of boreal stands in western Canada is generally considered to include a conversion from aspen dominated stands to conifer dominated stands over time. This switch takes place as the aspen canopy breaks up and an understorey of conifer trees grows into the canopy breaks (Strong and La Roi 1983; Peterson and Peterson 1992). Understanding the relationships between dominant tree species, as successional processes change one boreal forest type to another over time, are critical if land managers expect to implement anthropogenic disturbance on the landbase with the smallest of footprint. Maintenance of biodiversity on a managed landbase requires that we minimize our anthropogenic footprint by duplicating natural processes (to the best of our ability), and by maintaining natural variability and heterogeneity (Roberts and Gilliam 1995; Hartley 2002).

From a biodiversity perspective, clearcut stands in the first decade after harvest, are generally considered to be poor surrogates to recently burned natural stands (Bradbury 2002; Fisher and Wilkinson 2002; Lee, 2002; Schieck and Song 2002). The most striking reason for this discrepancy is the lack of vertical forest structure (*i.e.*, trees and tall shrubs), either living or dead, in clearcut stands relative to recently burned stands (Lee 2002). While certain aspects of naturally burned stands can never be accounted for in managed stands (*e.g.,* abundant fire-killed snags), other characteristics after wildfire can (*e.g.*, variable amounts of live residual trees within cutblock boundaries). By leaving variable densities of live trees within cutblock boundaries, cutblocks not only appear more like natural stands, but live residuals (at appropriate densities and distributions) may be used by a variety of forest dwelling species (Bradbury 2002; Fisher and Wilkinson 2002; Schieck and Song 2002; Bradbury 2004).

This project is not specifically concerned with mimicking natural processes by leaving residual trees in cutblocks. However, a cursory understanding of the role of residuals in post-harvest stands provides context, because, the amount of residual forest structure found in understorey protection cutblocks is substantial (Navratil *et al.* 1994), and a short-term benefit to biodiversity is likely. Understorey protection cutblocks, as a consequence, may provide forest structure and habitat for a variety of mixedwood dwelling species.

This chapter describes the vertical structure of deciduous and mixedwood stands in the Grande Prairie study area, and coniferous and mixedwood stands in the Manning study area, before and after harvest. The objectives were: 1) to provide data describing vertical forest structure (tree and tall shrub density in different height strata and diameter classes) in boreal deciduous, mixedwood and coniferous stands; 2) to describe the vertical forest structure found in understorey protection cutblocks; and, 3) to provide forest structural data as covariables in analysis of other biotic elements studied in this project.

Materials and Method

Data collection

Vertical forest structure was captured by assessing stem densities in vertical strata greater than 1.3 m above the ground; conifer stem density was additionally sampled from 0.2 - 1.3 m (referred to as regenerating conifer). All vegetation below 1.3 m was captured by the understorey vascular plant sampling protocol (Chapters 5 and 6). Tree and tall shrub (Moss 1999) sampling occurred during June and July 2000 and 2002 in both the Grande Prairie and Manning study areas.

In the Grande Prairie study area, all deciduous and mixedwood stand sampling was executed along the B and D transects, starting midway between site one and two, and ending midway between site ten and eleven (Chapter 2, Figure 2.3). Each site was delineated into two different sized plots: a 50 m x 3 m plot (150 m^2) for trees and tall shrubs (above 10 m) and regenerating conifer; and, a 50 m x 2 m plot (100 m^2) for trees and tall shrubs below 10 m. Plots were centred along the transect, hence, sampling occurred in a continuous strip. A similar procedure was followed in the Manning study area along the 7-ha strip (Chapter 2, Figure 2.4).

In each plot, all tree species, and shrub species that tended to grow taller than 3 m in height, were sampled; only trees and tall shrubs with more than half of their stem within the plot boundary were measured. Tree and tall shrub species diameter at breast height (DBH) and height class were recorded for each individual stem. Height classes were designated as: 1 = 1.3 - 3 m, 2 = 3 - 5 m, 3 = 5 - 10 m, 4 = 10 - 20 m, and 5 = 20+ m. In addition, "regenerating conifer" between 0.2 m and 1.3 m in height were counted. For analysis purposes DBH classes were designated as: 1 = 0 - 10 cm, 2 = 10 - 20 cm, 3 = 20 - 30 cm, 4 = 30 - 40 cm, and 5 = 40+ cm.

Data analysis

One-way ANOVA, with a *post hoc* Student's t-test, was used to investigate differences between pre-harvest and post-harvest deciduous and mixedwood stands in the Grande Prairie study area, and between coniferous and mixedwood stands in the Manning study area. Differences were judged as significant if $p < 0.05$. Analyses were performed using the JMP statistical package (SAS 2000).

Results

Individual tree and shrub data were summed by species for each height class, and a stem density per ha conversion was performed. A summary of deciduous, coniferous and shrub stem density per height class (Tables 3.1 and 3.2) and per DBH class (Tables 3.3 and 3.4) are provided for all 12 pre-harvest stands within each study area; in addition, summaries of post-harvest stem densities are provided for clearcut stands and understorey protection stands for both study areas. Only data from harvested stands are explored in further detail.

At the Grande Prairie study area, overall tree stem density did not differ between deciduous forests and clearcut stands, but did differ between mixedwood understorey protection stands and mixedwood forests ($F = 4.647$; d.f. = 3, 211; $p = 0.004$). A loss of conifer and shrub density in clearcut stands (10.1% and 18.2% of pre-harvest levels, respectively) was compensated for by a significant increase in aspen sucker density (Figure 3.1); it should be noted that the shortest sampled height class was 1.3 – 3 m, and thus, thousands of aspen suckers per ha shorter than 1.3 m were not counted. Decreased stem density was observed in mixedwood understorey protection stands compared to mixedwood forests, and this was due largely to a loss of shrub density (Figure 3.1).

Stem density varied within each height strata both between forest types and before and after harvest. In the Grande Prairie study area in the lowest stratum sampled (*i.e.*, 1.3 – 3 m), stem density increased (Figure 3.2) after clearcutting the deciduous forest, but did not differ in the mixedwood understorey protection cutblocks compared to mixedwood forests ($F = 4.521$; d.f. = 3, 211; $p = 0.004$). Despite a substantial loss of shrub density, vigorous aspen sucker growth after deciduous clearcutting resulted in an overall increase in stem density. Understorey protection cutblocks had reduced conifer and shrub densities and increased deciduous density; sucker growth was largely confined to the skid trails, haul roads and decking areas. In the 3 –5 m and 5 – 10 m height strata (Figure 3.2), stem density decreased after clearcutting deciduous forests, but remained the same in understorey protection cutblocks compared to mixedwood forests (Height class 2: $F = 15.022$; d.f. = 3, 211; $p < 0.001$; Height class 3: $F = 14.744$; d.f. = 3, 211; $p < 0.001$). In the two taller height strata (*i.e.*, 10 – 20 m and +20 m), stem density

decreased (Height class 4: F = 17.057; d.f. = 3, 211; p = < 0.001; Height class 5: F = 73.225; d.f. = 3, 211; p < 0.001) after harvest in both deciduous and mixedwood forests (Figure 3.2). As planned in the mixedwood understorey protection harvesting strategy, understorey conifer stems from all height strata (*i.e.*, all stems > 0.2 m in height) were well retained; understorey conifer density changed from an average of 1589 stems/ha before harvest to 992 stems/ha after harvest (62.4% of pre-harvest density).

At the Manning study area (Figure 3.3), overall tree stem density decreased after harvest in both coniferous and mixedwood forests (F = 35.637; d.f. = 3, 141; p < 0.001). Deciduous, conifer and shrub stems were lost in clearcut stands (6.2%, 13.1% and 24.3% of pre-harvest levels, respectively), whereas a much greater proportion of stems in understorey protection cutblocks were conserved (33.4% deciduous stems, 53.2% conifer stems, and 57.9% shrub stems, respectively).

Stem density varied within each height class strata both between forest types and before and after harvest. In the Manning study area (Figure 3.4) in the lowest stratum sampled (*i.e.*, 1.3 – 3 m), stem density decreased after clearcutting in the coniferous forest (F = 18.848; d.f. = 3, 141; p < 0.001), but did not differ in the mixedwood understorey protection cutblocks compared to mixedwood forests. Clearcutting removed most small stems from coniferous forests, but understorey protection cutblocks maintained much of the shortest woody stems; aspen sucker growth was largely confined to skid trails, haul roads and decking areas, but had little influence on density estimates because stem heights had not reached 1.3 m at the time of sampling (one year after harvest). In the 3 –5 m and 5 – 10 m height strata (Figure 3.4), stem density decreased after clearcutting coniferous forests, but remained the same in understorey protection cutblocks compared to mixedwood forests (Height class 2: F = 5.351; d.f. = 3, 141; p = 0.002; Height class 3: F = 8.416; d.f. = 3, 141; p < 0.001). In height class 4 (*i.e.*, 10 – 20 m), stem density decreased (F = 32.503; d.f. = 3, 141; p = < 0.001) after conifer stand harvest, but did not differ after understorey protection harvest (Figure 3.4). In height class 5 (*i.e.*, +20 m), stem density decreased (F = 193.975; d.f. = 3, 141; p < 0.001) after harvest in both coniferous and mixedwood stands. In the mixedwood understorey protection harvesting strategy, understorey conifer stems were well retained in all height strata (*i.e.*, all stems > 0.2 m in height); understorey conifer density changed from an average of 1941 stems/ha before harvest to 1033 stems/ha after harvest (53.2% of pre-harvest density, approximating the planned level of 55%).

Discussion

All merchantable trees were harvested from deciduous and coniferous stands. The majority of aspen canopy stems, and all merchantable coniferous stems, that were accessible from along the skid trails, were harvested in understorey protection cutblocks. Aspen canopy removal targets (70%) were achieved in the Grande Prairie study area understorey protection cutblocks where 69.8% of aspen canopy stems were removed; in the Manning study area substantially fewer aspen canopy stems were removed (68.3%) compared with the target proportion (85%) because many stems were not of a merchantable size. Understorey protection cutblocks in the Grande Prairie and Manning study areas, respectively, had 62.4% (65% was targeted) and 53.2% of understorey conifer stems retained. The combination of higher retention in the Grande Prairie understorey protection cutblocks, but higher pre-harvest conifer stem density in the Manning study area mixedwood forests resulted in a post-harvest conifer density of 1012 ± 28 stems/ha from both study areas.

Aspen suckering was clearly higher in deciduous clearcuts compared to mixedwood understorey protection cutblocks and coniferous clearcuts. This result was not unexpected and has been previously described (Frey *et al.* 2003; Prévost and Pothier 2003; Bradbury 2004). In the second growing season, a total of 2712 aspen stems/ha were counted in deciduous clearcuts; of that total, 2502 aspen stems/ha were from the

shortest height class (1.3 – 3 m, the shortest height class measured in this study), and many thousands more were uncounted below 1.3 m. Because of the density of residual aspen stems in understorey protection cutblocks (202 stem/ha), and the dominance maintained by these live trees, only a quarter of the density of aspen suckers (622 aspen stems/ha) was measured following understorey protection harvest compared to deciduous clearcutting. Even fewer aspen suckers (11 aspen stems/ha) were measured in the Manning study area understorey protection cutblocks. While many aspen suckers were not counted below 1.3 m, the very low density of suckers that had reached this height suggests that either apical dominance was not broken (492 canopy aspen stems/ha were retained), or microclimatic conditions were not conducive to vigorous aspen suckering (Peterson and Peterson 1992; Prévost and Pothier 2003).

The density of retained deciduous and coniferous stems in all height classes in the understorey protection cutblocks far exceeded densities found after traditional harvesting methods (see Lee 2002 for a review of large tree stem densities after harvest). Previous mixedwood understorey protection cutblocks in Alberta (Navratil *et al.* 1994) preserved between 40% and 61% of pre-harvest understorey spruce stems. Such high levels of retention have a dramatic influence on the microclimatic conditions found in post-harvest cutblocks. For instance, Prévost and Pothier (2003) studied changes to light availability in partial cuts in eastern boreal forests of Quebec. Partial cutting 65% of merchantable stems resulted in 48% of full light being transmitted to the understorey plant community compared with less than 20% of full light in unharvested control stands and 35% merchantable stem harvest cuts. In partial cuts (35%, 50%, 65% harvest), post-harvest conditions changed rapidly due to crown expansion of residual canopy trees, and vigorous growth of aspen suckers and tall shrubs; in all partial cut treatments, light transmitted to the understorey plant communities decreased each year for the first five years after harvest (Prévost and Pothier 2003).

Green tree retention has been shown to provide within block habitat for flora and fauna associated with pre-harvest forests (Halpern *et al*. 1999; Schieck 2000; Schieck and Song 2002; Bradbury *et al*. 2003; Bradbury 2004), however, the efficacy of residual habitat depends on species life history requirements, the amount of retention and the intensity of disturbance. The high levels of live tree residuals in understorey protection blocks provides far more vertical forest structure than traditional clearcuts, or typical structured cutblocks (with < 10% residuals), and thus, will likely provide forest habitat for many forest generalist species. However, residual strips in the understorey protection cutblocks are separated by parallel 4 - 5 m wide skid trails every 25 m throughout the cutblock. It is unknown if the density of these strips influences floral and/or faunal dispersal. Furthermore, as aspen suckers develop along skid trails over time, the influence of these dense strips of vegetation on light levels reaching understorey communities is unknown (Mourelle *et al*. 2002).

An understorey protection strategy aims to harvest both deciduous and coniferous stems off the same landbase, by using a two-harvest system separated by a number of decades. During the interim between harvest phases, released understorey conifer stems reach merchantability sooner than under natural conditions. Paramount to a successful harvesting strategy is the expectation that coniferous volume during the second phase of harvest is at least equal to the volume that would have been harvested if the stand had developed naturally; that is, any potential understorey conifer volume lost or damaged during the first harvest phase is regained after release due to the improved conifer growing conditions within the understorey protection cutblock. The acceleration of conifer tree growth rate can be perceived as an acceleration of forest structural successional rate. However, it is unknown if plant and animal populations and communities can keep pace with this successional rate.

Management Implications and Future Research

- High levels of live residual trees, particularly understorey conifer stems, can be maintained using an understorey protection harvesting strategy, and these residuals provide abundant within-block forest structure. This residual structure may provide benefits towards management area biodiversity objectives.

Future research should be conducted to: 1) measure understorey conifer spruce growth and dynamics during the interim between understorey protection harvest phases; 2) measure aspen sucker growth and dynamics during the interim between understorey protection harvest phases; 3) measure blowdown levels of retained deciduous and coniferous stems; 4) assess the development rate of forest structure within understorey protection cutblocks and ultimately determine the suitability of this structure for the maintenance of biodiversity prior to the second phase of harvest.

Acknowledgements

I am grateful to our technical staff for their hard work in the field with data collection. Technicians over the course of the study included Kelly Sturgess, Gavin Berg, Cris Gray, Sharon Kendall, Dave McKinnon, Luke Nolan, Len Peleshok, Dee Ryerson, Dan Sturgess, and Lindsay Tomyn. Constructive criticism of earlier versions of this chapter was provided by J.P. Bielech, and Fred Radersma. Phil Lee provided invaluable input into the initial study design. Pat Soldan formatted the text, figures and tables.

Literature Cited

Bradbury, S. 2002. Response of understorey vascular plants to wildfire and harvesting. In: Ecological basis for stand management. Alberta Research Council, Vegreville, AB.

Bradbury, S. 2004. Understorey plant communities in boreal cutblocks with different sizes and numbers of residual patches. Can. J. For. Res. *In press*.

Bradbury, S., L. Peleshok and L. Nolan. 2003. Consequences of different sized live tree residual patches in harvested aspen stands of northwestern Alberta: nonvascular plants and cumulative falldown. Alberta Research Council, Vegreville.

Fisher, J.T. and Wilkinson, L. 2002. Mammalian responses to wildfire and harvesting. In: Ecological basis for stand management. Alberta Research Council, Vegreville, AB.

Frey, B.R., Lieffers, V.J., Munson, A.D. and Blenis, P.V. 2003. The influence of partial harvesting and forest floor disturbance on nutrient availability and understorey vegetation in boreal mixedwoods. Can. J. For. Res. 33:1180-1188.

Halpern, C.B., Evans, S.A., Nelson, C.R., McKenzie, D., Liguori, D.A., Hibbs, D.E. and Halaj, M.G. 1999. Response of forest vegetation to varying levels and patterns of green-tree retention: an overview of a long-term experiment. Northwest Sci. 73:27-44.

Hartley, M.J. 2002. Rationale and methods for conserving biodiversity in plantation forests. For. Ecol. Manage. 155:81-95.

Lee, P. 2002. Forest structure after wildfire and harvesting. In: Ecological basis for stand management. Alberta Research Council, Vegreville, AB.

Moss, E.H. 1994. Flora of Alberta. A manual of flowering plants, conifers, ferns and fern allies found growing without cultivation in the province of Alberta, Canada. 3rd Edition. Revised by J.G. Packer. University of Toronto Press. Toronto, ON.

Mourelle, C., Macdonald, E., Dankert, B., and Major, M. 2002. Stand structure and plant diversity under two forest management practices: salvage thinning and understorey protection in the Canadian western boreal.

In: Proceedings from Sustainable Forest Management Network Conference "Advances in forest management: from knowledge to practice", Edmonton 2002. pp 154-159.

Navratil, S., Brace, L.G., Sauder, E.A., and Lux, S. 1994. Silvicultural and harvesting options to favor immature white spruce and aspen regeneration in boreal mixedwoods. Nat. Resour. Can., Can. For. Serv., Northwest Reg., North. For. Cent., Edmonton, Alberta. Inf. Rep. NOR-X-327.

Peterson, E.B. and Peterson, N.M. 1992. Ecology, management, and use of aspen and balsam poplar in the prairie provinces, Canada. For. Can., Northwest Reg., North. For. Cent., Edmonton, Alberta. Spec. Rep. 1.

Prévost, M. and Pothier, D. 2003. Partial cuts in a trembling aspen-conifer stand: effects on microenvironmental conditions and regeneration dynamics. Can. J. For. Res. 33: 1-15.

Roberts, M.R. and Gilliam, F.S. 1995. Patterns and mechanisms of plant diversity in forested ecosystems: implications for forest management. 5:969-977.

Schieck, J. (Editor). 2000. Biodiversity in cutblocks with few large versus many small residual patches of trees and snags. Alberta Research Council, Vegreville, AB.

Schieck, J. and Song, S.J. 2002. Responses of boreal birds to wildfire and harvesting. In: Ecological basis for stand management. Alberta Research Council, Vegreville, AB.

Strong, W.L. and La Roi, G.H. 1983. Rooting depths and successional development of selected boreal forest communities. Can. J. For. Res. 13:577-588.

SAS. 2000. JMP Statistics and Graphics Guide, Version 3.2.1, SAS Institute, Cary, NC.

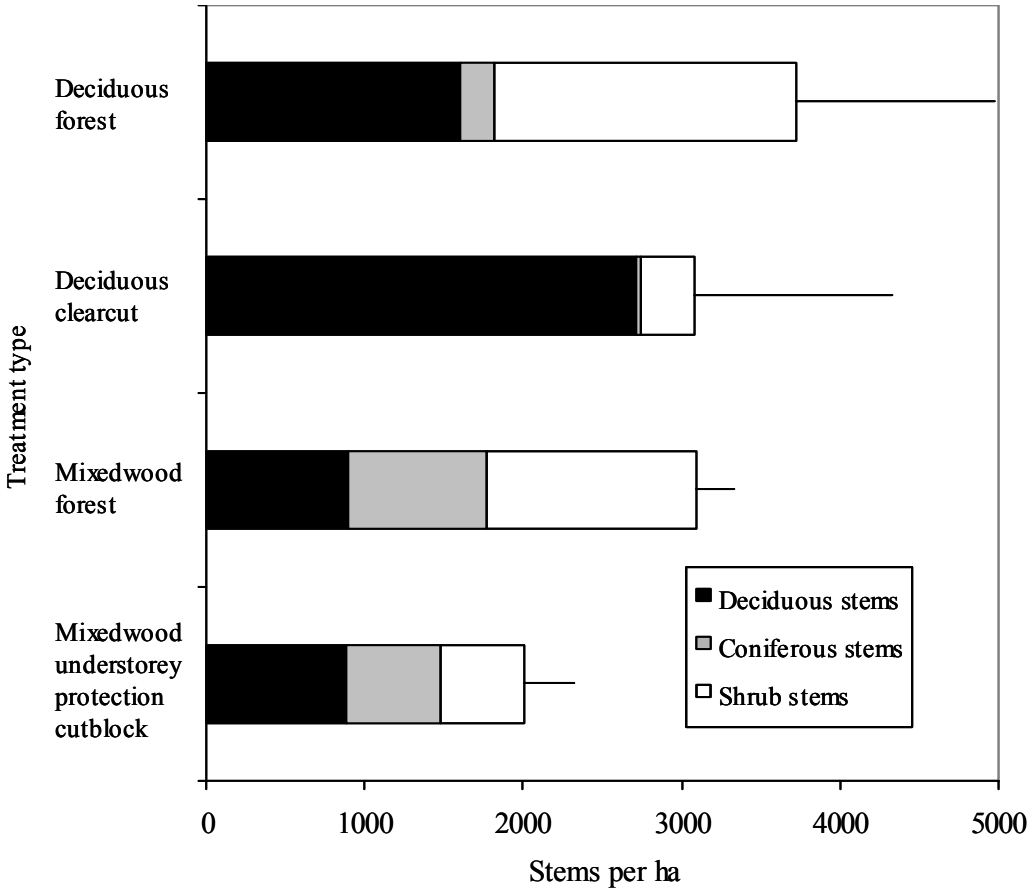


Figure 3.1. Mean woody stem density (stems/ha) in the Grande Prairie study area deciduous forests, deciduous clearcuts, mixedwood forests, and mixedwood understorey protection cutblocks. Values were derived from data in five height classes ranging from 1.3 m to > 20 m. Deciduous stems include aspen, balsam poplar and birch; coniferous stems include black and white spruce and balsam fir; shrub stems include alder, willow, saskatoon and minor occurrences of other tall shrubs. Error bars indicate standard error of total stem density.

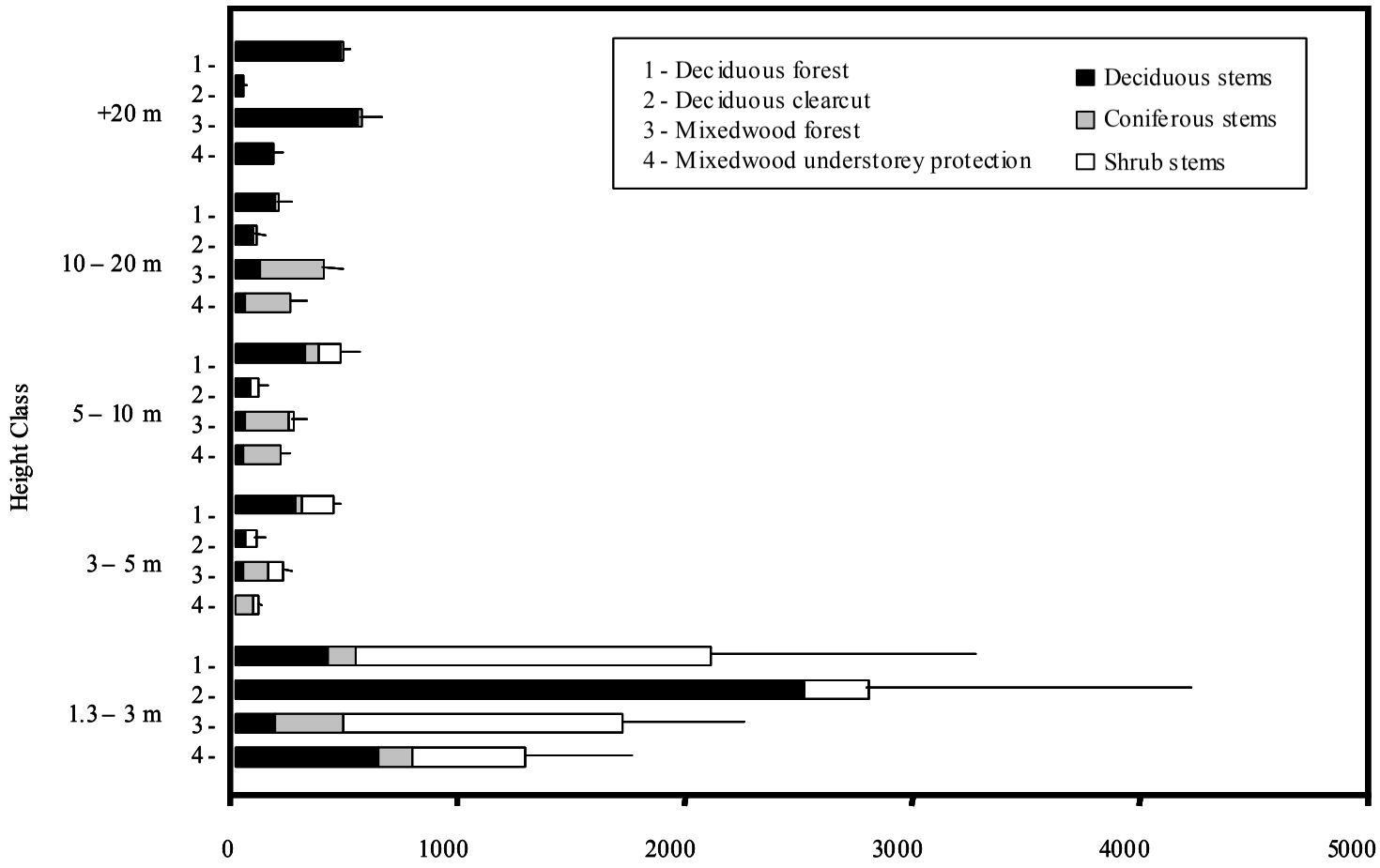


Figure 3.2. Mean woody stem density (stems/ha) in each of five height strata in the Grande Prairie study area deciduous forests, deciduous clearcuts, mixedwood forests, and mixedwood understorey protection cutblocks. Error bars indicate standard error of stem density in each height strata in each forest type.

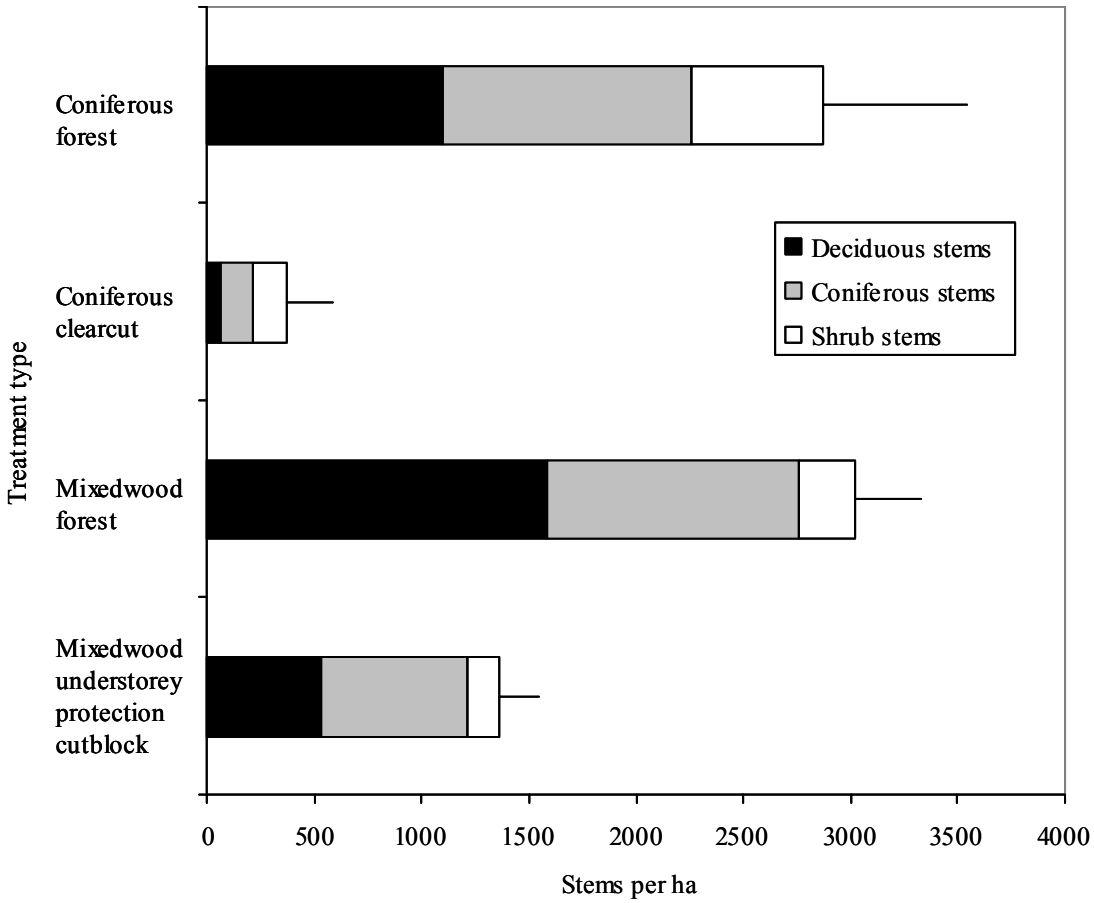


Figure 3.3. Mean woody stem density (stems/ha) in Manning study area coniferous forests, coniferous clearcuts, mixedwood forests, and mixedwood understorey protection cutblocks. Values were derived from data in five height classes ranging from 1.3 m to > 20 m. Deciduous stems include aspen, balsam poplar and birch; coniferous stems include black and white spruce, lodgepole pine and balsam fir; shrub stems include alder, willow, saskatoon and minor occurrences of other tall shrubs. Error bars indicate standard error of total stem density.

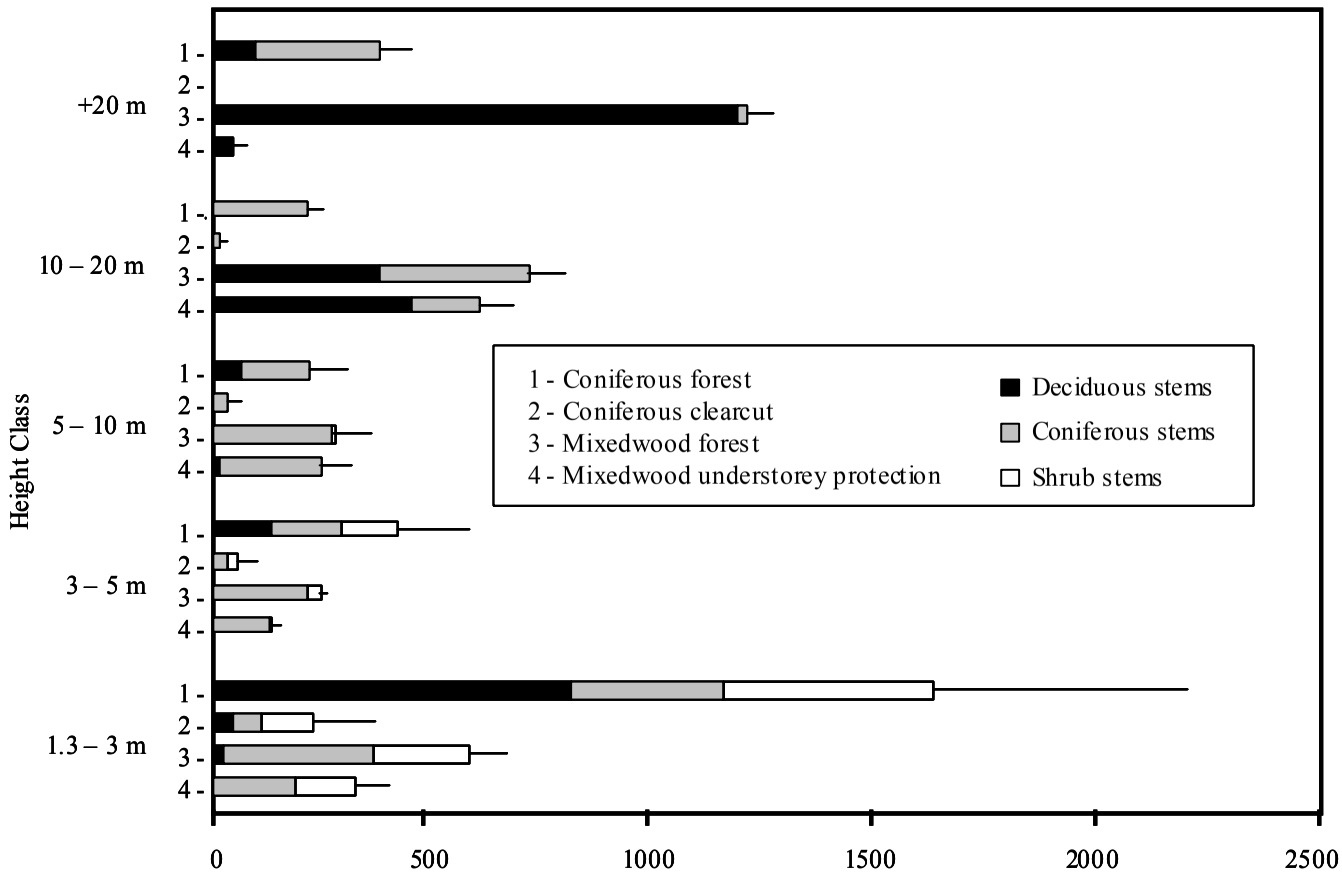


Figure 3.4. Mean woody stem density (stems/ha) in the Manning study area coniferous forests, coniferous clearcuts, mixedwood forests, and mixedwood understorey protection cutblocks. Error bars indicate standard error of stem density in each height strata in each forest type.

CHAPTER 4: DEADWOOD RESOURCES (SNAGS AND DOWNED WOODY MATERIAL) IN DECIDUOUS, MIXEDWOOD AND CONIFEROUS STANDS BEFORE AND AFTER HARVEST, WITH SPECIFIC ATTENTION TO UNDERSTOREY PROTECTION CUTBLOCKS

Steve Bradbury

Introduction

Deadwood resources (snags and downed woody material) represent critical habitat for many indigenous forest dwelling species, including cavity builders (Conner *et al.* 1975), cavity nesters (Barclay *et al.* 1988; Gibbs *et al.* 1993; Schieck and Roy 1995), and plants (Crites and Dale 1998; Lee and Sturgess 2001). Utilization of deadwood by forest organisms, results in the breakdown of organic matter and excretion of nutrients into soil, and maintains the cycles of growth and decomposition in boreal forests (Freedman *et al*. 1996). Interruption of this cycle (by eliminating large volumes of deadwood resources of particular species, sizes or decay stages) would not stop the process, but would result in a re-organization of the diversity of species associated with decomposition, and an alteration in the rate of decay (and thus rate and timing of nutrient release) (Freedman *et al*. 1996).

Intensively managed stands have reduced snag density, less downed woody material (DWM) volume and reduced forest floor thickness compared with mature and old-growth natural stands (Freedman *et al*. 1996; Lee 2002). In cases where managed stands are harvested early in rotation, when trees first reach merchantability, the stand has generally not reached an age where substantial natural mortality occurs to the largest trees. Harvesting, thus, leads to increasingly fewer deadwood resources; this process has been described as being among the most notable, longer term ecological effects observed in intensively managed forests (Freedman *et al*. 1996).

Management of deadwood resources requires the maintenance of a range of snag densities and DWM volume in post-harvest stands. On a managed landbase where traditional clearcut methods are employed, it may be difficult to leave abundant snags because of the safety threat they impose, and much of the DWM volume is damaged during harvesting operations. Understorey protection harvesting, however, may provide a management option where high snag density maybe preserved amongst abundant levels of live residuals, and with machinery limited to skid trails, fewer pieces of DWM may be destroyed.

This chapter describes deadwood resources of deciduous and mixedwood stands in the Grande Prairie study area and mixedwood and coniferous stands in the Manning study area. In both locations, the objectives of this research were to: 1) describe the deadwood resources in boreal deciduous, mixedwood and coniferous stands; and, 2) describe the deadwood resources in deciduous clearcuts, coniferous clearcuts, and mixedwood understorey protection cutblocks. In addition, deadwood resource data was used as covariable data in analysis of other biotic elements studied in this project.

Materials and Method

Snag and DWM data were collected in June and July of 2000 and 2002 in both the Grande Prairie and Manning study areas. Sampling followed the site plan previously described in the general experimental layout (Chapter 2, Figures 2.3 and 2.4).

Snags

The layout for sampling snags was similar to that used for trees and shrubs, however, the plot size was much larger, 20 m x 50 m (1000 m^2). A snag was defined as any completely dead tree or tall shrub ≥1.3 m in height, ≥10 cm DBH, and not leaning more than 45° from vertical. For each snag encountered in the plot, species, height class, DBH, decay class, and bole condition were recorded. Snags on the boundary of the plot were counted if at least half of the

bole was within the plot. Unidentifiable snags were recorded as deciduous or coniferous. Height classes were the same as those designated for trees and tall shrubs: 1 = 1.3 - 3 m, 2 = 3 - 5 m, 3 = 5 - 10 m, 4 = 10 - 20 m, and 5 = 20+ m. Likewise, diameter classes (based on DBH) were the same as those designated for trees and tall shrubs: 1 = 1 - 10 cm, 2 = 10 - 20 cm, 3 = 20 -30 cm, 4 = 30 - 40 cm, and 5 = 40+ cm. Decay stage classifications were designated as: 1 = recently dead; 2 = only major branches remaining; 3 = bole mostly intact; and 4 = bole broken, wood soft. Bole condition was recorded as intact or broken.

Downed woody material

Downed woody material was sampled using a line-intercept method. Downed wood pieces intercepting a straight line running from site to site were sampled, with each 1-ha site having 50 m of transect. DWM was defined as a dead piece of wood ≥5 cm diameter and less than 45° from horizontal. Species, diameter-at-line-intercept, and decay class were recorded for all pieces of DWM. Unidentifiable pieces were described as deciduous or coniferous. Diameter classes were designated at the line-intercept as: 1 = 5 - 10 cm, 2 = 10 - 20 cm, 3 = 20 - 30 cm, 4 = 30 - 40 cm, and 5 = 40+ cm. Decay stage classifications were designated as: 1 = bark and fine branches intact, wood hard; 2 = only major branches remain, wood hard to soft; and 3 = colonized by nonvascular and/or vascular plants, wood generally soft. Although decay along DWM is often uneven, a single value was assigned to characterize the state of decay directly at the transect intercept.

Volume of DWM was calculated using the formula:

$$V = (9.8696 \times \sum d^2/8L) \times 10000$$

where V is DWM volume (m^3ha^{-1}), d is the diameter (m) of each piece of DWM sampled along the transect, and L is the transect length.

Data analysis

One-way ANOVA, with a *post hoc* Student's t-test, was used to investigate differences between pre-harvest and post-harvest deciduous and mixedwood stands in the Grande Prairie study area, and between coniferous and mixedwood stands in the Manning study area. Differences were judged as significant if $p < 0.05$. Analyses were performed using the JMP statistical package (SAS 2000).

Results

In total at the Grande Prairie study area, pre-harvest and reserve deciduous stands had 110 snags/ha, and pre-harvest and reserve mixedwood stands had 144 snags/ha; deciduous clearcuts had 6 snags/ha (5% of pre-harvest density) and mixedwood understorey protection cutblocks had 69 snags/ha (48% of pre-harvest density). In deciduous forests, 99% of snags were deciduous, and in mixedwood forests, 98% of snags were deciduous.

In total at the Manning study area, pre-harvest and reserve coniferous stands had 154 snags/ha and pre-harvest and reserve mixedwood stands had 93 snags/ha; coniferous clearcuts had 8 snags/ha (5% of pre-harvest density) and mixedwood understorey protection cutblocks had 29 snags/ha (31% of pre-harvest density). In coniferous forests, 49% of snags were deciduous with the remainder being coniferous, and in mixedwood forests, 99% of snags were deciduous.

Snag density by diameter class

At the Grande Prairie study area, snag density was determined in four diameter classes (Table 4.1); no snags were sampled in the fifth diameter class (*i.e.*, +40 cm). In the two smaller diameter classes (Figure 4.1) significantly fewer snags remained after harvest in both deciduous and mixedwood stands (diameter class 1: $F = 47.5$, $p < 0.001$; diameter class 2: $F = 14.7$, $p < 0.001$), but nearly all small snags were lost in deciduous clearcuts. For snags 20 – 30 cm and 30 – 40 cm in diameter, density decreased in deciduous

clearcuts (diameter class 3: $F = 8.6$, $p < 0.001$; diameter class 4: $F = 7.2$, $p < 0.001$) but did not change significantly in mixedwood understorey protection cutblocks (Figure 4.1), although only small volumes of DWM were observed. In general, harvesting affected deciduous, coniferous and shrub snags equally in all diameter classes.

At the Manning study area, snag density was determined in five diameter classes (Table 4.2). In the smallest diameter class (Figure 4.1) significantly fewer snags remained after harvest in both coniferous and mixedwood stands ($F = 14.5$, $p < 0.001$). For snags 10 – 20 cm and 20 – 30 cm in diameter, density decreased in coniferous clearcuts (diameter class 2: $F = 63.3$, $p < 0.001$; diameter class 3: $F = 38.9$, $p < 0.001$) but did not change significantly in mixedwood understorey protection cutblocks (Figure 4.1); in both diameter classes 2 and 3, very few snags (<1 snag/ha) were observed in mixedwood stands before and after harvest. Snags in the two largest diameter classes were only observed in coniferous stands before harvest (Figure 4.1). The ratio of deciduous snags to coniferous snags in coniferous forests increased with increased snag size. Mixedwood stands in the Manning study area were less than 75 years old, and as a result, had little time to recruit large snags; this was clearly reflected in the results. In general, harvesting affected deciduous, coniferous and shrub snags equally in all diameter classes.

Snag density by decay class

At the Grande Prairie study area, snag density was determined in four decay stage classes (Table 4.3). Significantly fewer snags (Figure 4.2) remained after harvest in both deciduous and mixedwood stands (decay class 1: $F = 26.8$, $p < 0.001$; decay class 2: $F = 36.3$, $p < 0.001$; decay class 3: $F = 28.8$, $p < 0.001$; decay class 4: $F = 11.2$, $p < 0.001$), with a greater density of snags in each decay class being preserved in understorey protection cutblocks compared to deciduous clearcuts. Understorey protection cutblocks preserved more than 30% of snags in all decay classes (Figure 4.2).

At the Manning study area the same trends were observed (Table 4.4). Snag density in each decay class (Figure 4.2) decreased significantly after harvest in both coniferous and mixedwood stands (decay class 1: $F = 26.8$, $p < 0.001$; decay class 2: $F = 13.9$, $p < 0.001$; decay class 3: $F = 29.9$, $p < 0.001$; decay class 4: $F = 64.1$, $p < 0.001$), but a greater density of snags in each decay class were preserved in understorey protection cutblocks. At least 30% of snags were preserved in understorey protection cutblocks in decay classes 1 - 3, but only 20% of snags in decay class 4 were preserved (Figure 4.2).

Downed woody material volume by size class

In total at the Grande Prairie study area, pre-harvest and reserve deciduous stands had 85.6 m^3/ha of DWM and pre-harvest and reserve mixedwood stands had 59.3 m^3/ha; deciduous clearcuts had 256.2 m^3/ha of DWM and mixedwood understorey protection cutblocks had 193 m^3/ha. On average, DWM volume increased 300% after harvest in deciduous clearcuts, and 325% after harvest in mixedwood understorey protection cutblocks.

In total at the Manning study area, pre-harvest and reserve coniferous stands had 179.6 m^3/ha of DWM and pre-harvest and reserve mixedwood stands had 44.4 m^3/ha; coniferous clearcuts had 227.4 m^3/ha of DWM and mixedwood understorey protection cutblocks had 181.3 m^3/ha. On average, DWM volume increased 125% after harvest in coniferous clearcuts, and 400% after harvest in mixedwood understorey protection cutblocks.

At the Grande Prairie study area, DWM volume was determined in five diameter classes (Table 4.5). Deciduous clearcuts had significantly higher DWM volume in all diameter classes (diameter class 1: $F = 95.4$, $p < 0.001$; diameter class 2: $F = 26.3$, $p < 0.001$; diameter class 3: $F = 11.5$, $p < 0.001$; diameter class 4: $F = 7.0$, $p < 0.001$; diameter class 5: $F = 5.8$, $p < 0.001$), whereas, mixedwood understorey protection cutblocks had increased DWM volume only in diameter classes 1 – 3 (Figure 4.3); DWM volume in diameter class 4 did not differ significantly, and no pieces of DWM in diameter

class 5 were observed in mixedwood stands. Deciduous clearcutting and understorey protection harvesting produced similar volumes of DWM in the two smaller diameter classes, but less DWM volume in the larger diameter classes remained after understorey protection harvesting.

At the Manning study area, DWM volume was determined in five diameter classes (Table 4.6). Understorey protection cutblocks had significantly higher DWM volume in all diameter classes (diameter class 1: $F = 81.7$, $p < 0.001$; diameter class 2: $F = 19.3$, $p < 0.001$; diameter class 4: $F = 5.4$, $p < 0.001$; diameter class 5: $F = 3.2$, $p < 0.001$) with the exception of diameter class 3 where DWM volume did not change. Coniferous clearcuts had higher DWM volume in diameter class 1, but volume did not differ significantly in the other larger diameter classes (Figure 4.3). There was a striking increase in DWM volume in the two largest diameter classes following understorey protection harvesting.

Downed woody material volume by decay class

At the Grande Prairie study area, DWM volume was measure in three decay classes (Table 4.7). Understorey protection cutblocks had higher DWM volume in each decay class (Figure 4.4) compared to mixedwood forests (decay class 1: $F = 6.9$, $p < 0.001$; decay class 2: $F = 21.4$, $p < 0.001$; decay class 3: $F = 12.3$, $p < 0.001$). Deciduous clearcuts had significantly higher DWM volume in decay classes 2 and 3 (Figure 4.4).

At the Manning study area, DWM volume was also observed in three decay classes (Table 4.8). Downed WM volume increased significantly in all decay classes (decay class 1: $F = 17.3$, $p < 0.001$; decay class 2: $F = 17.3$, $p < 0.001$; decay class 3: $F = 8.3$, $p < 0.001$) after harvest in both coniferous and mixedwood forests, with the exception of DWM in decay class 3 in coniferous clearcuts where it decreased (Figure 4.4).

Discussion

Snags and DWM are inexorably linked, with all snags becoming DWM at some stage in their decay; additional inputs of DWM also come from fallen live trees. Deadwood resources come in a wide range of sizes (*i.e.*, volume) and decay stages which results in a heterogeneous assortment of microhabitat types all mediated by stand age and local environmental conditions (Lee 2002). In addition, different tree (or shrub) species have different chemical compositions, and this chemical microenvironment not only affects the decomposition process (*i.e.*, rate and nutrient release), but also the types of organisms capable of using the resource during decomposition (Söderström 1988a; Andersson and Hytteborn 1991; Crites and Dale 1998; Lee and Sturgess 2001). In fact, many species that dependent on DWM select either deciduous or coniferous substrates, while other species are capable of using both substrates (Söderström 1988b). As a result, microhabitat produced by decaying deadwood resources in natural forests increases heterogeneity.

Snag density before harvest in deciduous, mixedwood and coniferous forests fell within the range measured previously in boreal forests (Lee 1998; but see Lee 2002 for a review). Over successional timeframes in natural forests, snag density reaches a peak immediately after disturbance (*e.g.*, fire, insect outbreak), decreases rapidly as these initial snags fall down, and then increases slowly as stands age (Lee 2002). In comparison, snag densities are generally very low after harvest (Lee 2002), and increase slowly only if regenerating stands surpass the age when the largest trees begin to die (Freedman *et al*. 1996). The decrease in snag density in clearcuts, certainly compared with natural fire-killed stands where snags are most abundant, substantially reduces forest structural variability during the first few decades after harvest (Lee 2002).

With respect to snag density, understorey protection cutblocks and clearcuts differ in at least two fundamentally important ways: 1) snags were nearly eliminated in both deciduous and coniferous clearcuts, but were retained in substantial numbers in understorey protection cutblocks; and 2) the potential for recruitment of new snags in understorey protection cutblocks far exceeds the potential for recruitment of new snags in clearcuts.

The volume of DWM before harvest in deciduous, mixedwood and coniferous stands, also fell within the range previously measured in boreal forests (Lee 2002). The substantial increase in DWM volume in both deciduous and coniferous clearcuts was due to the large amount of slash and harvesting debris. Most of the DWM volume in deciduous clearcuts existed as pieces less than 30 cm in diameter, while in coniferous clearcuts the most volume was derived from pieces 20 – 40 cm in diameter. These differences likely occurred because of the differences in tree sizes and stand age at the time of harvest (deciduous stands were roughly 100 years-old and coniferous stands were roughly 150 year-old).

In naturally occurring stands, DWM volume increases substantially in the first 10 years after wildfire due to the blow down of fire-killed snags. This large volume of DWM then slowly progresses through the decomposition cycle, with various volumes in all stages of decay; fresh inputs appear throughout succession until total volume begins to accumulate in older stands (> 125 years) (Lee 2002). Harvesting, however, removes potential future DWM volume and, once the initial resources are decomposed, leaves post-harvest stands at a DWM deficit in all stages of decay (Freedman *et al*. 1996; Lee 2002). Understorey protection cutblocks create conditions distinct from clearcuts, wherein DWM dynamics are less dramatically influenced (Mourelle *et al*. 2002). For example, abundant live residual trees and dead snags provide future inputs of DWM (Vanha-Majamaa and Jalonen 2001) in all stages of decay in the interim between understorey protection harvesting phases. This residual material may provide substrate for organisms dependent on deadwood substrates (Kruys *et al*. 1999). The removal of 70% of the aspen canopy, however, may limit the volume of future DWM in the largest size classes.

Management Implications and Future Research

- High levels of both live and dead residual trees in understorey protection cutblocks, provides immediate deadwood resources and future sources of deadwood input.
- Compared to clearcuts, understorey protection cutblocks provide a useful management tool for providing for high levels of retention of deadwood resources in all size classes and decay stages.
- The preservation of existing snags and DWM, and the availability of future inputs of deadwood resources, will contribute to forest structural heterogeneity, and thus biodiversity values, within understorey protection cutblocks, at least until the second phase of harvest.

Additional research should be conducted to: 1) monitor snag density dynamics in existing understorey protection cutblocks; 2) monitor DWM volume dynamics in existing understorey protection cutblocks; 3) determine the response of organisms directly dependent on deadwood resources during the interim between harvest phases and compare the value of deadwood resources in understorey protection cutblocks with those found in clearcuts; and, 4) assess the dynamics of deadwood resources within understorey protection cutblocks and ultimately determine the suitability of these resources for the maintenance of biodiversity prior to the second phase of harvest.

Acknowledgements

I am grateful to our technical staff for their hard work in the field with data collection. Technicians over the course of the study included Kelly Sturgess, Gavin Berg, Cris Gray, Sharon Kendall, Dave McKinnon, Luke Nolan, Len Peleshok, Dee Ryerson, Dan Sturgess, and Lindsay Tomyn. Constructive criticism of earlier

versions of this chapter was provided by J.P. Bielech, and Fred Radersma. Phil Lee provided invaluable input into the initial study design. Pat Soldan formatted the text, figures and tables.

Literature Cited

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

Barclay, R.M.R., Faure, P.A., and Farr, D.R. 1988. Roosting behaviour and roost selection by migrating silver-haired bats (*Lasionycteris noctivagans*). J. Mammal. 69:821-826.

Conner, R.N., Shaw, C.G. and Furniss, M.M. 1975. Woodpecker nesting habitat in cut and uncut woodlands in Virginia. J. Wildl. Manage. 39:144-150.

Crites, S. and Dale, M.R.T. 1998. Diversity and abundance of bryophytes, lichens and fungi in relation to woody substrate and successional stage in aspen mixedwood boreal forests. Can. J. Bot. 76:641-651.

Freedman, B., Zelazny, V., Beaudette, D., Fleming, T., Flemming, S, Forbes, G., Gerrow, J.S., Johnson, G., and Woodley S. 1996. Biodiversity implications of changes in the quantity of dead organic matter in managed forests. Environ. Rev. 4:238-265.

Gibbs, J.P., Hunter, M.J. Jr., Melvin, S.M. 1993. Snag availability and communities of cavity nesting birds in tropical versus temperate forests. Biotropica. 25:236-241.

Kruys, N., Fries, C., Jonsson, B.G., Lämås, T., and Stahl, G. 1999. Wood-inhabiting cryptograms on dead Norway spruce (*Picea abies*) trees in managed Swedish boreal forests. Can. J. For. Res. 29:178-186.

Lee, P. 1998. Dynamics of snags in aspen-dominated midboreal forests. For. Ecol. Manage. 105:263-272.

Lee, P. 2002. Forest structure after wildfire and harvesting. In: Ecological basis for stand management. Alberta Research Council, Vegreville, AB.

Lee, P. and Sturgess, K. 2001. The effects of logs, stumps and root throws on understorey communities within 28-year-old aspen-dominated boreal forests. Can. J. Bot. 79:905-916.

Mourelle, C., Macdonald, E., Dankert, B., and Major, M. 2002. Stand structure and plant diversity under two forest management practices: salvage thinning and understorey protection in the Canadian western boreal. In: Proceedings from Sustainable Forest Management Network Conference "Advances in forest management: from knowledge to practice", Edmonton 2002. pp 154-159.

SAS. 2000. JMP Statistics and Graphics Guide, Version 3.2.1, SAS Institute, Cary, NC.

Schieck, J. and Roy, L. 1995. Changes in snags and downed woody material characteristics in a chronosequence of aspen mixedwood stands in Alberta. In: Relationships between stand age, stand structure, and biodiversity in aspen mixedwood forests in Alberta. Alberta Environmental Centre (AECV95-R1), Vegreville, AB, and Canadian Forest Service (Project No. 0001A), Edmonton, AB.

Söderström, L. 1988a. The occurrence of epixylic bryophyte and lichen species in an old natural and a managed forest stand in northeast Sweden. Biol Cons. 45:169-178.

Söderström, L. 1988b. Sequence of bryophyte and lichen species in relation to substrate variables of decaying and coniferous wood in Northern Sweden. Nord. J. Bot. 8:89-97.

Vanha-Majamaa, I., and Jalonen, J. 2001. Green tree retention in Fennoscandian forestry. Scand. J. For. Res. Suppl. 3:79-90.

Table 4.3. Mean (standard error) snag density per ha per decay class (dc) in deciduous forests and clearcuts, and mixedwood forests and understorey protection cutblocks in the Grande Prairie study area before (pre) and after (post) harvest. Deciduous stems (Dec) include aspen, balsam poplar and birch; coniferous stems (Con) include black and white spruce and balsam fir; shrub stems (Shb) include alder, willow, saskatoon and minor occurrences of other tall shrubs.

Grande Prairie	N	Dec dc 1	Dec dc 2	Dec dc 3	Dec dc 4	Con dc 1	Con dc 2	Con dc 3	Con dc 4	Shb dc 1	Shb dc 2	Shb dc 3	Shb dc 4
DC1 – pre	18	7 (3)	41 (5)	79 (11)	19 (4)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
DC2 – pre	17	9 (3)	33 (7)	35 (6)	12 (2)	0 (0)	1 (1)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
DC3 – pre	18	26 (4)	13 (4)	8 (3)	9 (2)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	2 (1)
Mean	**53**	**14**	**29**	**41**	**13**	**0**	**1**	**0**	**0**	**0**	**0**	**0**	**1**
DR1 – pre	17	8 (2)	31 (5)	59 (8)	9 (2)	0 (0)	1 (1)	0 (0)	0 (0)	0 (0)	4 (3)	6 (3)	2 (1)
DR2 – pre	19	5 (2)	33 (5)	46 (8)	5 (2)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (1)	1 (1)	1 (1)
DR3 – pre	18	31 (7)	86 (11)	33 (7)	3 (2)	0 (0)	0 (0)	0 (0)	0 (0)	1 (1)	1 (1)	1 (1)	0 (0)
Mean	**54**	**14**	**50**	**46**	**6**	**0**	**1**	**0**	**0**	**0**	**2**	**3**	**1**
MC1 – pre	18	20 (5)	47 (7)	84 (11)	13 (3)	2 (1)	1 (1)	1 (1)	1 (1)	0 (0)	0 (0)	0 (0)	0 (0)
MC2 – pre	18	22 (3)	38 (5)	46 (7)	13 (5)	1 (1)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
MC3 – pre	18	36 (6)	46 (7)	37 (9)	18 (3)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (1)	1 (1)
Mean	**54**	**26**	**44**	**55**	**14**	**1**	**1**	**0**	**0**	**0**	**0**	**1**	**0**
MR1 – pre	18	10 (3)	82 (10)	39 (7)	10 (2)	0 (0)	3 (2)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
MR2 – pre	18	11 (3)	81 (5)	67 (7)	14 (4)	1 (1)	3 (1)	1 (1)	0 (0)	0 (0)	0 (0)	1 (1)	0 (0)
MR3 – pre	18	11 (4)	40 (7)	35 (7)	8 (3)	0 (0)	17 (5)	0 (0)	1 (0)	1 (1)	1 (1)	0 (0)	0 (0)
Mean	**54**	**11**	**68**	**47**	**11**	**0**	**8**	**0**	**0**	**0**	**0**	**0**	**0**
DC1 – post	18	0 (0)	0 (0)	1 (1)	2 (1)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
DC2 – post	17	1 (1)	1 (1)	1 (1)	6 (2)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
DC3 – post	18	2 (1)	1 (1)	2 (2)	1 (1)	0 (0)	0 (0)	0 (0)	0 (0)	1 (1)	0 (0)	0 (0)	0 (0)
Mean	**43**	**1**	**1**	**1**	**3**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
MC1 – post	18	15 (3)	18 (3)	16 (3)	12 (3)	2 (0)	1 (1)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
MC2 – post	18	1 (1)	23 (6)	23 (4)	4 (2)	2 (0)	1 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
MC3 – post	18	8 (3)	36 (6)	33 (5)	6 (2)	0 (0)	1 (0)	0 (0)	0 (0)	0 (0)	0 (0)	2 (1)	2 (0)
Mean	**54**	**8**	**26**	**24**	**7**	**1**	**1**	**0**	**0**	**0**	**0**	**1**	**1**

Note: Decay classes were as follows: 1 = recently dead; 2 = only major branches remaining; 3 = bole mostly intact; and 4 = bole broken, wood soft.

Table 4.4. Mean (standard error) snag stem density per ha per decay class (dc) in coniferous forests and clearcuts, and mixedwood forests and understorey protection cutblocks in the Manning study area before (pre) and after (post) harvest. Deciduous stems (Dec) include aspen, balsam poplar and birch; coniferous stems (Con) include black and white spruce and balsam fir; shrub stems (Shb) include alder, willow, saskatoon and minor occurrences of other tall shrubs.

Manning	N	Dec dc 1	Dec dc 2	Dec dc 3	Dec dc 4	Con dc 1	Con dc 2	Con dc 3	Con dc 4	Shb dc 1	Shb dc 2	Shb dc 3	Shb dc 4
CC1 – pre	8	1 (1)	9 (4)	26 (9)	93 (19)	4 (3)	45 (11)	20 (5)	60 (12)	0 (0)	0 (0)	0 (0)	0 (0)
CC2 – pre	11	2 (1)	6 (2)	6 (3)	48 (10)	4 (2)	17 (7)	15 (5)	41 (10)	0 (0)	0 (0)	0 (0)	0 (0)
CC3 – pre	9	0 (0)	10 (4)	22 (7)	54 (10)	13 (6)	43 (20)	18 (7)	13 (7)	0 (0)	0 (0)	0 (0)	0 (0)
Mean	**28**	**1**	**8**	**18**	**65**	**7**	**35**	**18**	**38**	**0**	**0**	**0**	**0**
CR1 – pre	11	0 (0)	4 (2)	13 (4)	26 (8)	15 (5)	24 (7)	5 (2)	39 (13)	0 (0)	0 (0)	0 (0)	(1)
CR2 – pre	11	2 (1)	5 (2)	21 (7)	42 (7)	5 (2)	21 (5)	13 (6)	5 (2)	0 (0)	0 (0)	0 (0)	0 (0)
CR3 – pre	11	4 (2)	17 (4)	22 (5)	72 (7)	3 (1)	3 (1)	1 (1)	5 (4)	0 (0)	0 (0)	0 (0)	0 (0)
Mean	**33**	**2**	**9**	**18**	**47**	**7**	**16**	**6**	**16**	**0**	**0**	**0**	**0**
MC1 – pre	11	21 (5)	28 (5)	15 (4)	31 (8)	1 (1)	1 (1)	0 (0)	1 (1)	0 (0)	0 (0)	0 (0)	0 (0)
MC2 – pre	11	20 (7)	38 (6)	14 (4)	26 (9)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
MC3 – pre	7	3 (2)	14 (4)	16 (4)	9 (3)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Mean	**29**	**15**	**27**	**15**	**22**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
MR1 – pre	11	2 (1)	47 (8)	45 (7)	58 (12)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (1)
MR2 – pre	11	8 (3)	21 (6)	22 (5)	32 (15)	0 (0)	0 (0)	0 (0)	1 (1)	0 (0)	0 (0)	0 (0)	0 (0)
MR3 – pre	7	4 (2)	17 (8)	7 (3)	17 (8)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Mean	**29**	**5**	**28**	**25**	**36**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**
CC1 – post	8	0 (0)	4 (4)	1 (1)	0 (0)	1 (1)	4 (4)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
CC2 – post	11	1 (1)	1 (1)	0 (0)	1 (1)	0 (0)	2 (2)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
CC3 – post	9	0 (0)	0 (0)	3 (2)	1 (1)	3 (2)	0 (0)	3 (2)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Mean	**28**	**1**	**2**	**2**	**1**	**2**	**2**	**1**	**0**	**0**	**0**	**0**	**0**
MC1 – post	11	5 (0)	17 (4)	12 (2)	6 (2)	0 (0)	3 (2)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
MC2 – post	11	4 (2)	6 (3)	4 (2)	1 (1)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (0)	0 (0)	0 (0)
MC3 – post	11	6 (4)	11 (4)	4 (2)	4 (2)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Mean	**33**	**2**	**11**	**7**	**3**	**0**	**1**	**0**	**0**	**0**	**1**	**0**	**0**

Note: Decay classes were as follows: 1 = recently dead; 2 = only major branches remaining; 3 = bole mostly intact; and 4 = bole broken, wood soft.

Table 4.5. Mean (standard error) DWM volume (m^3/per ha) per diameter class in deciduous forests and clearcuts, and mixedwood forests and understorey protection cutblocks in the Grande Prairie study area before (pre) and after (post) harvest. Deciduous (Dec) stems include aspen, balsam poplar and birch; coniferous (Con) stems include black and white spruce and balsam fir; shrub stems (Shb) include alder, willow, saskatoon and minor occurrences of other tall shrubs.

Grande Prairie	N	Dec dia 1	Dec dia 2	Dec dia 3	Dec dia 4	Dec dia 5	Con dia 1	Con dia 2	Con dia 3	Con dia 4	Con dia 5	Shb dia 1	Shb dia 2	Shb dia 3	Shb dia 4
DC1 – pre	18	10.1 (1)	62.6 (7)	47.7 (6)	14.7 (5)	5.6 (6)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)
DC2 – pre	18	8.5 (2)	26.0 (4)	13.8 (5)	7.6 (4)	0.0 (0)	0.1 (0)	0.0 (0)	0.7 (1)	1.8 (2)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)
DC3 – pre	18	7.2 (1)	9.8 (2)	3.2 (1)	2.7 (2)	0.0 (0)	0.2 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	2.9 (1)	0.9 (0)	0.0 (0)	0.0 (0)
Mean	**54**	**8.6**	**32.8**	**21.5**	**8.4**	**1.9**	**0.1**	**0.0**	**0.2**	**0.6**	**0.0**	**1.0**	**0.3**	**0.0**	**0.0**
DR1 – pre	14	9.1 (2)	35.3 (5)	43.6 (7)	19.9 (7)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.9 (0)	1.4 (1)	0.0 (0)	0.0 (0)
DR2 – pre	19	10.3 (1)	51.0 (5)	50.1 (9)	21.6 (7)	7.9 (6)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	2.0 (1)	2.7 (1)	0.0 (0)	0.0 (0)
DR3 – pre	18	12.2 (1)	13.1 (2)	3.4 (2)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	2.7 (1)	0.4 (0)	0.0 (0)	0.0 (0)
Mean	**51**	**10.5**	**33.1**	**32.4**	**13.8**	**2.6**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**1.9**	**1.5**	**0.0**	**0.0**
MC1 – pre	18	14.1 (1)	41.4 (5)	10.0 (3)	2.8 (2)	0.0 (0)	0.9 (0)	1.2 (1)	1.8 (1)	1.4 (1)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)
MC2 – pre	18	7.1 (1)	43.4 (6)	22.5 (5)	5.1 (3)	0.0 (0)	0.0 (0)	0.4 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.3 (0)	0.0 (0)	0.0 (0)	0.0 (0)
MC3 – pre	18	10.3 (2)	11.7 (2)	0.7 (1)	0.0 (0)	0.0 (0)	0.1 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	2.7 (1)	0.3 (0)	0.0 (0)	0.0 (0)
Mean	**54**	**10.5**	**32.2**	**11.0**	**2.6**	**0.0 (0)**	**0.3**	**0.6**	**0.6**	**0.5**	**0.0**	**1.0**	**0.1**	**0.0**	**0.0**
MR1 – pre	18	11.5 (1)	19.6 (3)	3.2 (1)	1.7 (2)	0.0 (0)	0.3 (0)	0.4 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.1 (0)	0.0 (0)	0.0 (0)	0.0 (0)
MR2 – pre	18	11.9 (1)	49.1 (3)	18.3 (4)	7.7 (3)	8.0 (6)	0.2 (0)	0.6 (0)	0.6 (1)	0.0 (0)	0.0 (0)	0.1 (0)	0.0 (0)	0.0 (0)	0.0 (0)
MR3 – pre	18	5.5 (1)	15.2 (3)	10.0 (4)	7.1 (4)	2.8 (3)	1.8 (1)	0.8 (0)	0.0 (0)	0.0 (0)	0.0 (0)	1.0 (1)	0.5 (0)	0.0 (0)	0.0 (0)
Mean	**54**	**9.6**	**28.0**	**10.5**	**5.5**	**3.6**	**0.8**	**0.6**	**0.2**	**0.0**	**0.0**	**0.4**	**0.2**	**0.0**	**0.0**
DC1 – post	18	63.0 (6)	163.6 (15)	128.0 (21)	61.5 (15)	24.2 (12)	0.2 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)
DC2 – post	18	47.3 (6)	63.9 (12)	36.8 (13)	16.3 (10)	15.7 (9)	0.7 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)
DC3 – post	18	44.6 (5)	67.1 (10)	20.5 (4)	2.5 (3)	0.0 (0)	0.3 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	9.5 (1)	1.5 (1)	1.6 (2)	0.0 (0)
Mean	**54**	**51,6**	**98.2**	**61.8**	**26.8**	**13.3**	**0.4**	**0.0**	**0.0**	**0.0**	**0.0**	**3.2**	**0.5**	**0.5**	**0.0**
MC1 – post	18	42.4 (3)	120.5 (14)	33.0 (9)	10.0 (7)	0.0 (0)	4.1 (1)	2.6 (1)	5.0 (3)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)
MC2 – post	18	66.0 (6)	131.1 (19)	81.0 (12)	8.9 (6)	0.0 (0)	0.7 (0)	1.2 (1)	0.0 (0)	0.0 (0)	0.0 (0)	0.1 (0)	0.0 (0)	0.0 (0)	0.0 (0)
MC3 – post	18	24.3 (3)	31.6 (5)	6.8 (4)	0.0 (0)	0.0 (0)	1.1 (0)	1.0 (1)	0.0 (0)	0.0 (0)	0.0 (0)	5.4 (2)	2.2 (1)	0.0 (0)	0.0 (0)
Mean	**54**	**44.2**	**94.4**	**40.3**	**6.3**	**0.0 (0)**	**2.0**	**1.6**	**1.7**	**0.0**	**0.0**	**1.8**	**0.7**	**0.0**	**0.0**

Note: DBH classes were as follows: 1 = 1 -10 cm, 2 = 10 – 20 cm, 3 = 20 – 30 cm, 4 = 30 – 40 cm, 5 = +40 m.

Table 4.6. Mean (standard error) DWM volume (m^3/per ha) per DBH class in coniferous forests and clearcuts, and mixedwood forests and understorey protection cutblocks in the Manning study area before (pre) and after (post) harvest. Deciduous stems (Dec) include aspen, balsam poplar and birch; coniferous stems (Con) include black and white spruce and balsam fir; shrub stems include alder, willow, saskatoon and minor occurrences of other tall shrubs.

Manning	N	Dec dia 1	Dec dia 2	Dec dia 3	Dec dia 4	Dec dia 5	Con dia 1	Con dia 2	Con dia 3	Con dia 4	Con dia 5	Shb dia 1	Shb dia 2	Shb dia 3	Shb dia 4
CC1 – pre	8	3.7 (1)	11.6 (3)	27.7 (8)	14.4 (7)	0.0 (0)	4.4 (1)	16.7 (5)	11.6 (4)	17.8 (7)	5.1 (5)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)
CC2 – pre	12	0.8 (0)	35.5 (5)	91.1 (21)	40.5 (15)	16.5 (7)	1.8 (1)	26.5 (8)	39.5 (11)	26.0 (8)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)
CC3 – pre	11	3.4 (1)	36.1 (7)	50.0 (14)	17.7 (7)	0.0 (0)	2.9 (1)	13.0 (2)	18.9 (6)	4.4 (3)	4.4 (4)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)
Mean	**31**	**2.6**	**27.7**	**56.3**	**24.2**	**5.5**	**3.0**	**18.7**	**23.3**	**16.1**	**3.2**	**0.0**	**0.0**	**0.0**	**0.0**
CR1 – pre	11	3.0 (1)	13.1 (4)	13.9 (5)	17.9 (10)	4.9 (5)	4.3 (1)	10.0 (3)	3.7 (2)	2.7 (3)	30.3 (15)	2.4 (1)	5.1 (2)	(6)	0.0 (0)
CR2 – pre	13	3.1 (1)	24.2 (5)	47.7 (12)	45.2 (15)	10.1 (7)	3.4 (1)	9.3 (2)	14.1 (4)	26.9 (8)	8.2 (6)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)
CR3 – pre	11	2.5 (1)	35.6 (7)	66.6 (11)	36.0 (7)	0.0 (0)	0.3 (0)	8.0 (2)	32.4 (6)	10.7 (6)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)
Mean	**35**	**2.9**	**24.3**	**42.7**	**33.1**	**5.0**	**2.7**	**9.1**	**16.7**	**13.4**	**12.9**	**0.8**	**1.7**	**2.3**	**0.0**
MC1 – pre	11	21.2 (4)	12.4 (3)	16.4 (6)	5.2 (4)	0.0 (0)	0.6 (0)	0.5 (1)	1.6 (2)	0.0 (0)	0.0 (0)	0.7 (0)	0.0 (0)	0.0 (0)	0.0 (0)
MC2 – pre	11	15.6 (2)	5.1 (2)	2.7 (2)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.3 (0)	0.0 (0)	0.0 (0)	3.3 (3)
MC3 – pre	9	12.2 (2)	3.9 (2)	10.5 (7)	2.9 (3)	0.0 (0)	0.2 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.2 (0)	0.0 (0)	0.0 (0)	0.0 (0)
Mean	**31**	**16.3**	**7.2**	**9.8**	**2.7**	**0.0**	**0.3**	**0.2**	**0.5**	**0.0**	**0.0**	**0.4**	**0.0**	**0.0**	**1.1**
MR1 – pre	11	21.6 (4)	33.6 (8)	14.6 (6)	3.1 (3)	0.0 (0)	0.1 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	2.6 (1)	2.1 (1)	0.0 (0)	0.0 (0)
MR2 – pre	11	10.6 (2)	10.4 (3)	3.4 (2)	0.0 (0)	0.0 (0)	0.1 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.8 (0)	0.0 (0)	0.0 (0)	0.0 (0)
MR3 – pre	8	18.8 (3)	7.8 (2)	14.6 (10)	3.2 (3)	0.0 (0)	0.8 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.3 (0)	0.0 (0)	0.0 (0)	0.0 (0)
Mean	**30**	**17.0**	**17.2**	**10.9**	**2.1**	**0.0**	**0.3**	**0.0**	**0.0**	**0.0**	**0.0**	**1.2**	**0.7**	**0.0**	**0.0**
CC1 – post	12	11.4 (4)	20.5 (6)	26.2 (10)	31.2 (12)	9.0 (9)	21.5 (3)	38.4 (8)	15.1 (5)	11.2 (8)	7.3 (7)	0.5 (0)	0.0 (0)	0.0 (0)	0.0 (0)
CC2 – post	14	2.7 (1)	20.4 (5)	63.6 (10)	26.1 (9)	7.8 (8)	10.6 (2)	42.8 (6)	48.0 (13)	11.2 (6)	14.8 (10)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)
CC3 – post	12	3.9 (1)	22.8 (6)	55.0 (20)	50.4 (20)	14.7 (10)	15.0 (6)	25.9 (5)	44.6 (11)	6.5 (6)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)
Mean	**38**	**6.0**	**21.2**	**48.2**	**35.9**	**10.5**	**15.7**	**35.7**	**35.9**	**9.6**	**7.3**	**0.2**	**0.0**	**0.0**	**0.0**
MC1 – post	13	46.3 (7)	37.8 (9)	21.3 (8)	47.9 (18)	29.3 (16)	11.0 (2)	6.3 (2)	2.6 (3)	0.0 (0)	0.0 (0)	2.3 (1)	0.0 (0)	0.0 (0)	0.0 (0)
MC2 – post	13	47.8 (6)	39.4 (7)	13.0 (8)	7.7 (5)	0.0 (0)	5.4 (2)	2.2 (1)	0.0 (0)	0.0 (0)	0.0 (0)	1.2 (1)	0.0 (0)	0.0 (0)	0.0 (0)
MC3 – post	12	63.0 (5)	35.3 (7)	14.5 (6)	40.3 (9)	64.1 (24)	4.2 (1)	4.5 (2)	0.0 (0)	0.0 (0)	0.0 (0)	0.3 (0)	0.0 (0)	0.0 (0)	0.0 (0)
Mean	**38**	**52.4**	**37.5**	**16.3**	**31.9**	**31.1**	**6.8**	**4.3**	**0.9**	**0.0**	**0.0**	**1.3**	**0.0**	**0.0**	**0.0**

Note: DBH classes were as follows: 1 = 1 -10 cm, 2 = 10 – 20 cm, 3 = 20 – 30 cm, 4 = 30 – 40 cm, 5 = +40 m.

Table 4.7. Mean (standard error) DWM volume (m^3/per ha) per decay class (dc) in deciduous forests and clearcuts, and mixedwood forests and understorey protection cutblocks in the Grande Prairie study area before (pre) and after (post) harvest. Deciduous stems (Dec) include aspen, balsam poplar and birch; coniferous stems (Con) include black and white spruce and balsam fir; shrub stems (Shb) include alder, willow, saskatoon and minor occurrences of other tall shrubs.

Grande Prairie	N	Dec dc 1	Dec dc 2	Dec dc 3	Con dc 1	Con dc 2	Con dc 3	Shb dc 1	Shb dc 2	Shb dc 3
DC1 – pre	18	7.2 (3)	59.8 (7)	73.6 (8)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)
DC2 – pre	18	1.5 (1)	23.7 (5)	30.6 (5)	0.1 (0)	0.0 (0)	2.6 (2)	0.0 (0)	0.0 (0)	0.0 (0)
DC3 – pre	18	0.1 (0)	11.0 (2)	11.8 (3)	0.1 (0)	0.0 (0)	0.0 (0)	0.7 (0)	1.5 (0)	1.6 (1)
Mean	**54**	**3.0**	**31.5**	**38.7**	**0.1**	**0.1**	**0.9**	**0.2**	**0.5**	**0.5**
DR1 – pre	14	3.5 (2)	39.5 (9)	64.9 (6)	0.0 (0)	0.0 (0)	0.0 (0)	0.1 (0)	0.1 (0)	2.1 (1)
DR2 – pre	19	5.9 (3)	62.6 (11)	72.5 (8)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	1.9 (1)	2.7 (1)
DR3 – pre	18	0.0 (0)	19.9 (2)	8.7 (1)	0.0 (0)	0.0 (0)	0.0 (0)	0.2 (0)	1.9 (1)	1.0 (0)
Mean	**51**	**3.1**	**40.7**	**48.7**	**0.0**	**0.0**	**0.0**	**0.1**	**1.3**	**2.0**
MC1 – pre	18	2.9 (1)	28.2 (3)	37.1 (5)	1.5 (1)	0.1 (0)	3.6 (2)	0.0 (0)	0.0 (0)	0.0 (0)
MC2 – pre	18	6.2 (4)	37.3 (6)	34.4 (5)	0.0 (0)	0.4 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.3 (0)
MC3 – pre	18	0.6 (0)	13.2 (2)	8.9 (1)	0.0 (0)	0.0 (0)	0.1 (0)	0.0 (0)	1.6 (0)	1.4 (1)
Mean	**54**	**3.2**	**26.2**	**26.8**	**0.5**	**0.2**	**1.2**	**0.0**	**0.5**	**0.6**
MR1 – pre	18	2.6 (1)	15.9 (4)	17.5 (2)	0.3 (0)	0.4 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.1 (0)
MR2 – pre	18	3.5 (2)	35.1 (3)	56.4 (10)	0.8 (1)	0.3 (0)	0.4 (0)	0.0 (0)	0.1 (0)	0.1 (0)
MR3 – pre	18	1.0 (1)	12.6 (2)	27.0 (8)	1.1 (0)	1.5 (1)	0.1 (0)	0.2 (0)	0.8 (1)	0.5 (0)
Mean	**54**	**2.4**	**21.2**	**33.7**	**0.7**	**0.7**	**0.1**	**0.1**	**0.3**	**0.2**
DC1 – post	18	4.0 (2)	41.3 (11)	395.1 (55)	0.0 (0)	0.2 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)
DC2 – post	18	6.3 (6)	145.4 (29)	28.2 (13)	0.2 (0)	0.3 (0)	0.2 (0)	0.0 (0)	0.0 (0)	0.0 (0)
DC3 – post	18	7.3 (3)	97.4 (12)	30.0 (7)	0.0 (0)	0.3 (0)	0.0 (0)	3.2 (2)	8.0 (1)	1.4 (1)
Mean	**54**	**5.9**	**94.7**	**151.1**	**0.1**	**0.2**	**0.1**	**1.1**	**2.7**	**0.5**
MC1 – post	18	10.6 (2)	97.2 (13)	98.0 (15)	3.9 (2)	3.3 (1)	4.5 (2)	0.0 (0)	0.0 (0)	0.0 (0)
MC2 – post	18	13.7 (4)	183.7 (23)	89.7 (12)	1.3 (1)	0.6 (1)	0.0 (0)	0.0 (0)	(0)	0.0 (0)
MC3 – post	18	6.2 (2)	31.6 (6)	24.9 (4)	1.5 (1)	0.5 (0)	(0)	2.3 (1)	(1)	3.2 (1)
Mean	**54**	**10.1**	**104.2**	**70.9**	**2.2**	**1.5**	**1.5**	**0.8**	**0.7**	**1.1**

Note: Decay classes were as follows: 1 = recently dead; 2 = only major branches remaining; 3 = bole mostly intact; and 4 = bole broken, wood soft.

Table 4.8. Mean (standard error) DWM volume (m^3/per ha) per decay class (dc) in coniferous forests and clearcuts, and mixedwood forests and understorey protection cutblocks in the Manning study area before (pre) and after (post) harvest. Deciduous stems (Dec) include aspen, balsam poplar and birch; coniferous stems (Con) include black and white spruce and balsam fir; shrub stems (Shb) include alder, willow, saskatoon and minor occurrences of other tall shrubs.

Manning	N	Dec dc 1	Dec dc 2	Dec dc 3	Con dc 1	Con dc 2	Con dc 3	Shb dc 1	Shb dc 2	Shb dc 3
CC1 – pre	8	9.3 (4)	12.2 (7)	36.0 (9)	12.9 (5)	9.5 (4)	33.1 (11)	0.0 (0)	0.0 (0)	0.0 (0)
CC2 – pre	12	1.1 (1)	75.3 (15)	108.0 (18)	19.8 (5)	50.5 (9)	23.5 (9)	0.0 (0)	0.0 (0)	0.0 (0)
CC3 – pre	11	6.2 (2)	37.8 (12)	63.3 (14)	16.2 (8)	21.2 (7)	6.1 (3)	0.0 (0)	0.0 (0)	0.0 (0)
Mean	**31**	**5.5**	**41.7**	**69.1**	**16.3**	**27.1**	**20.9**	**0.0**	**0.0**	**0.0**
CR1 – pre	11	14.5 (7)	9.3 (4)	28.9 (9)	10.5 (3)	14.2 (11)	26.3 (9)	0.8 (1)	3.2 (2)	10.2 (6)
CR2 – pre	13	25.6 (9)	53.3 (17)	51.4 (11)	22.6 (7)	26.4 (6)	12.9 (5)	0.0 (0)	0.0 (0)	0.0 (0)
CR3 – pre	11	20.3 (10)	51.3 (12)	69.2 (13)	1.0 (1)	13.5 (4)	37.1 (8)	0.0 (0)	0.0 (0)	0.0 (0)
Mean	**35**	**20.1**	**38.0**	**49.8**	**11.3**	**18.0**	**25.4**	**0.3**	**1.1**	**3.4**
MC1 – pre	11	0.9 (0)	21.0 (4)	33.2 (8)	2.6 (2)	0.1 (0)	0.0 (0)	0.2 (0)	0.4 (0)	0.1 (0)
MC2 – pre	11	3.2 (1)	12.7 (2)	7.5 (2)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.3 (0)	3.3 (3)
MC3 – pre	9	0.5 (0)	10.5 (2)	18.6 (12)	0.2 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.2 (0)	0.0 (0)
Mean	**31**	**1.5**	**14.7**	**19.8**	**0.9**	**0.0**	**0.0**	**0.1**	**0.3**	**1.1**
MR1 – pre	11	1.3 (1)	39.0 (9)	32.5 (10)	0.0 (0)	0.1 (0)	0.0 (0)	1.1 (1)	3.0 (2)	0.5 (0)
MR2 – pre	11	0.4 (0)	12.2 (2)	11.7 (4)	0.1 (0)	0.0 (0)	0.0 (0)	0.1 (0)	0.5 (0)	0.2 (0)
MR3 – pre	8	0.4 (0)	19.7 (4)	24.3 (15)	0.2 (0)	0.6 (0)	0.0 (0)	0.0 (0)	0.3 (0)	0.0 (0)
Mean	**32**	**0.7**	**23.6**	**22.8**	**0.1**	**0.2**	**0.0**	**0.4**	**1.3**	**0.2**
CC1 – post	12	29.5 (10)	14.4 (4)	54.4 (20)	43.2 (8)	32.9 (10)	17.3 (8)	0.0 (0)	0.1 (0)	0.2 (0)
CC2 – post	14	9.9 (4)	54.3 (14)	56.5 (14)	24.0 (6)	85.5 (18)	17.8 (7)	0.0 (0)	0.0 (0)	0.0 (0)
CC3 – post	12	11.6 (5)	91.7 (29)	43.4 (15)	26.7 (11)	48.2 (10)	17.1 (8)	0.0 (0)	0.0 (0)	0.0 (0)
Mean	**38**	**17.0**	**53.4**	**51.4**	**31.3**	**55.5**	**17.4**	**0.0**	**0.1**	**0.1**
MC1 – post	13	26.7 (9)	44.3 (7)	111.7 (22)	16.3 (4)	3.4 (3)	0.2 (0)	0.0 (0)	1.9 (1)	0.4 (0)
MC2 – post	13	36.7 (8)	43.8 (6)	27.3 (9)	7.0 (2)	0.6 (0)	0.0 (0)	0.3 (0)	0.3 (0)	0.6 (0)
MC3 – post	12	53.3 (8)	38.7 (4)	125.1 (31)	8.7 (3)	0.0 (0)	0.0 (0)	**0.1** (0)	0.0 (0)	0.2 (0)
Mean	**38**	**38.9**	**42.2**	**88.0**	**10.6**	**1.3**	**0.1**	**0.1**	**0.7**	**0.4**

Note: Decay classes were as follows: 1 = recently dead; 2 = only major branches remaining; 3 = bole mostly intact; and 4 = bole broken, wood soft.

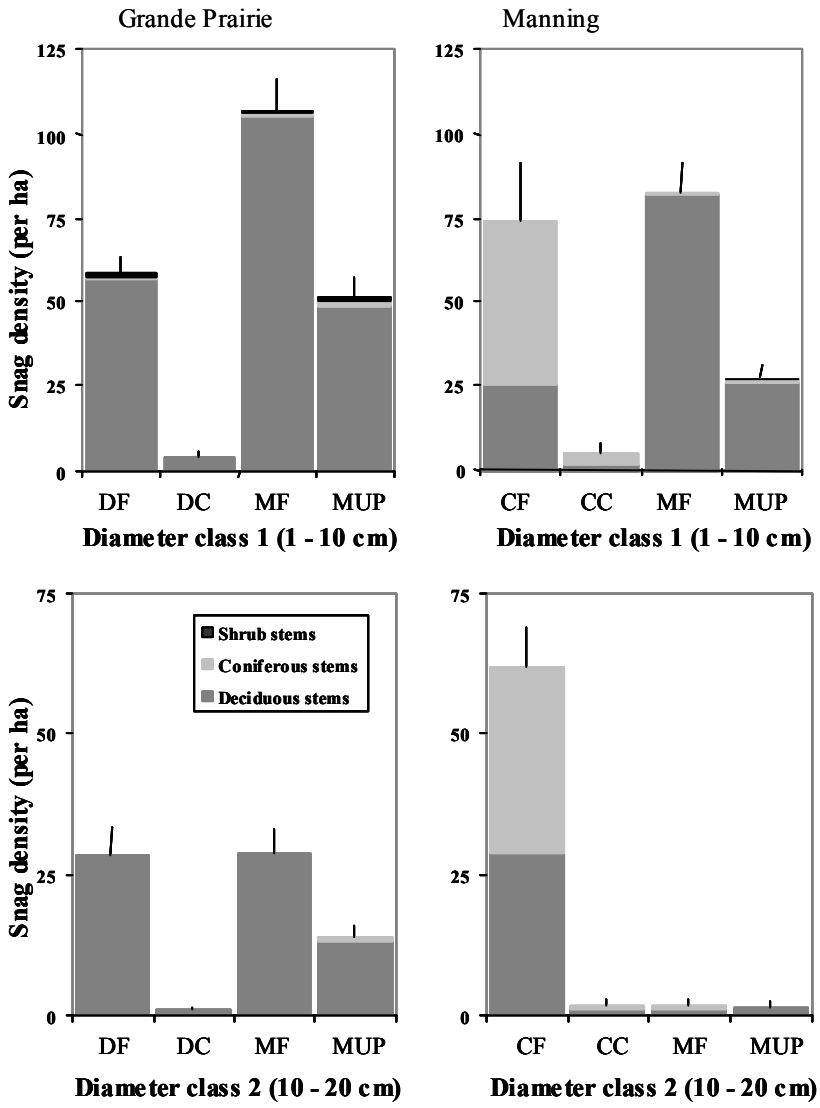


Figure 4.1. Mean snag density (stems/ha) in each of two diameter classes in the Grande Prairie (left hand graphs) and Manning (right hand graphs) study areas. Bars represent deciduous forests (DF), deciduous clearcuts (DC), mixedwood forests (MF), mixedwood understorey protection cutblocks (MUP), coniferous forests (CF) and coniferous clearcuts (CC). Error bars indicate standard error of snag density in each diameter class in each forest type.

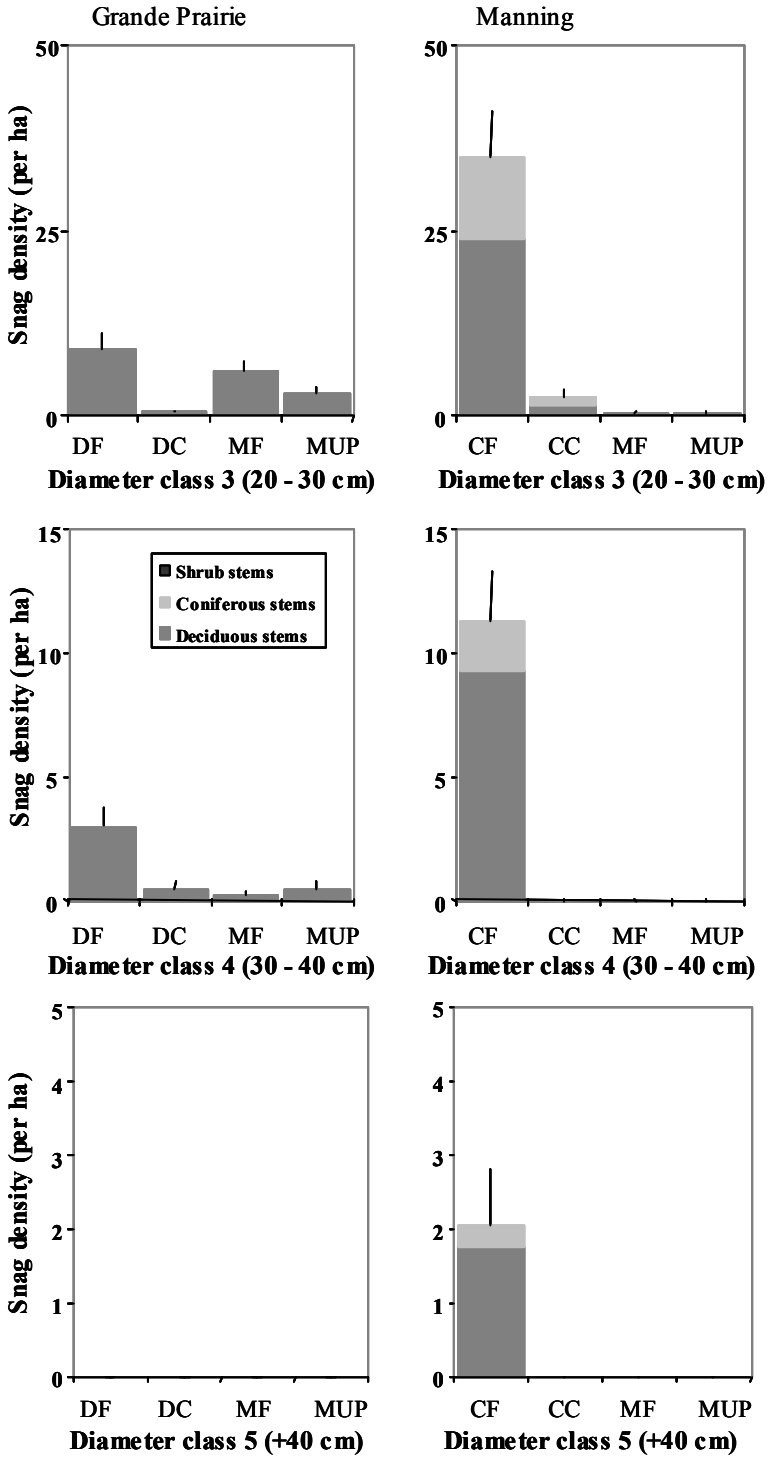


Figure 4.1 Cont. Mean snag density (stems/ha) in each of three diameter classes in the Grande Prairie (left hand graphs) and Manning (right hand graphs) study areas. Bars represent deciduous forests (DF), deciduous clearcuts (DC), mixedwood forests (MF), mixedwood understorey protection cutblocks (MUP), coniferous forests (CF) and coniferous clearcuts (CC). Error bars indicate standard error of snag density in each diameter class in each forest type.

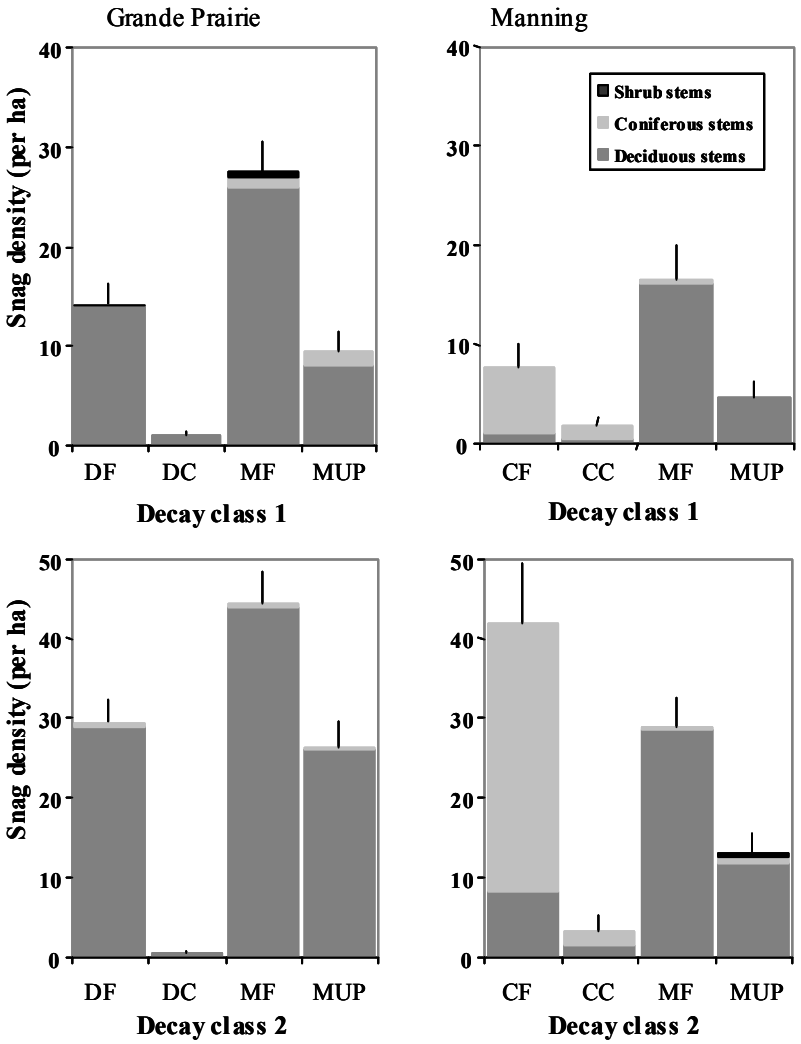


Figure 4.2. Mean snag density (stems/ha) in each of two decay classes in the Grande Prairie (left hand graphs) and Manning (right hand graphs) study areas. Bars represent deciduous forests (DF), deciduous clearcuts (DC), mixedwood forests (MF), mixedwood understorey protection cutblocks (MUP), coniferous forests (CF) and coniferous clearcuts (CC). Error bars indicate standard error of snag density in each diameter class in each forest type.

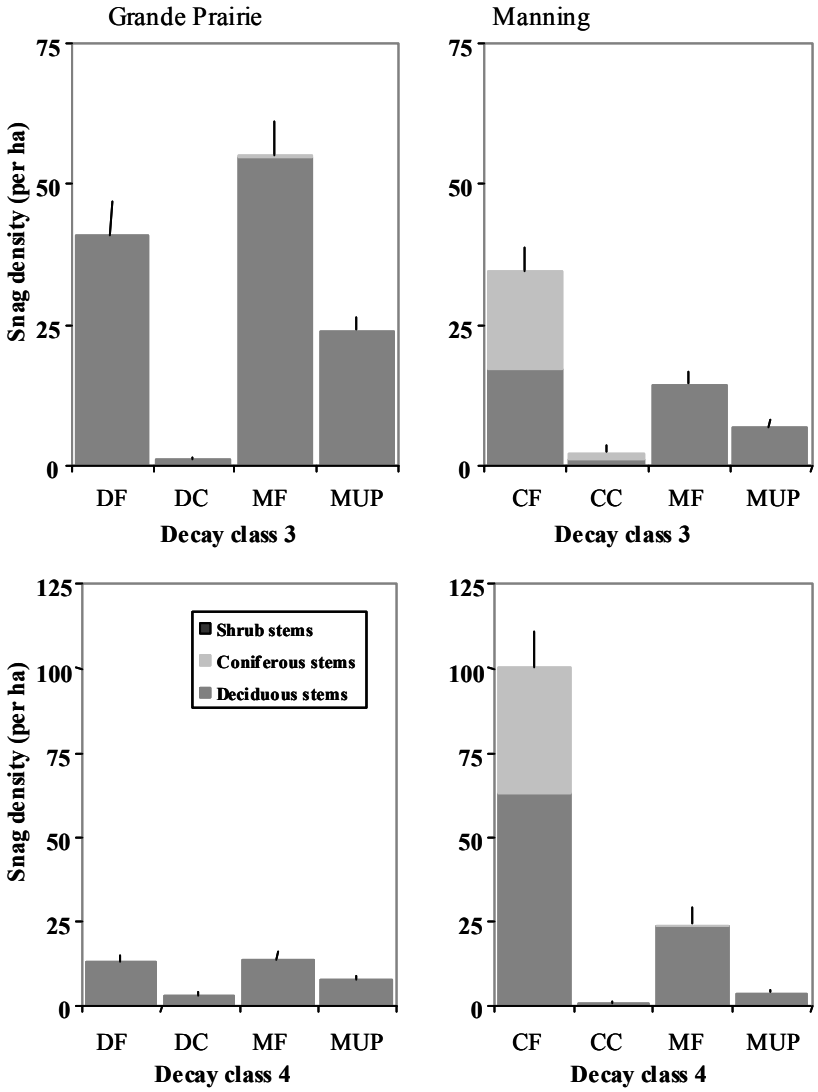


Figure 4.2 Cont. Mean snag density (stems/ha) in each of three diameter classes in the Grande Prairie (left hand graphs) and Manning (right hand graphs) study areas. Bars represent deciduous forests (DF), deciduous clearcuts (DC), mixedwood forests (MF), mixedwood understorey protection cutblocks (MUP), coniferous forests (CF) and coniferous clearcuts (CC). Error bars indicate standard error of snag density in each diameter class in each forest type.

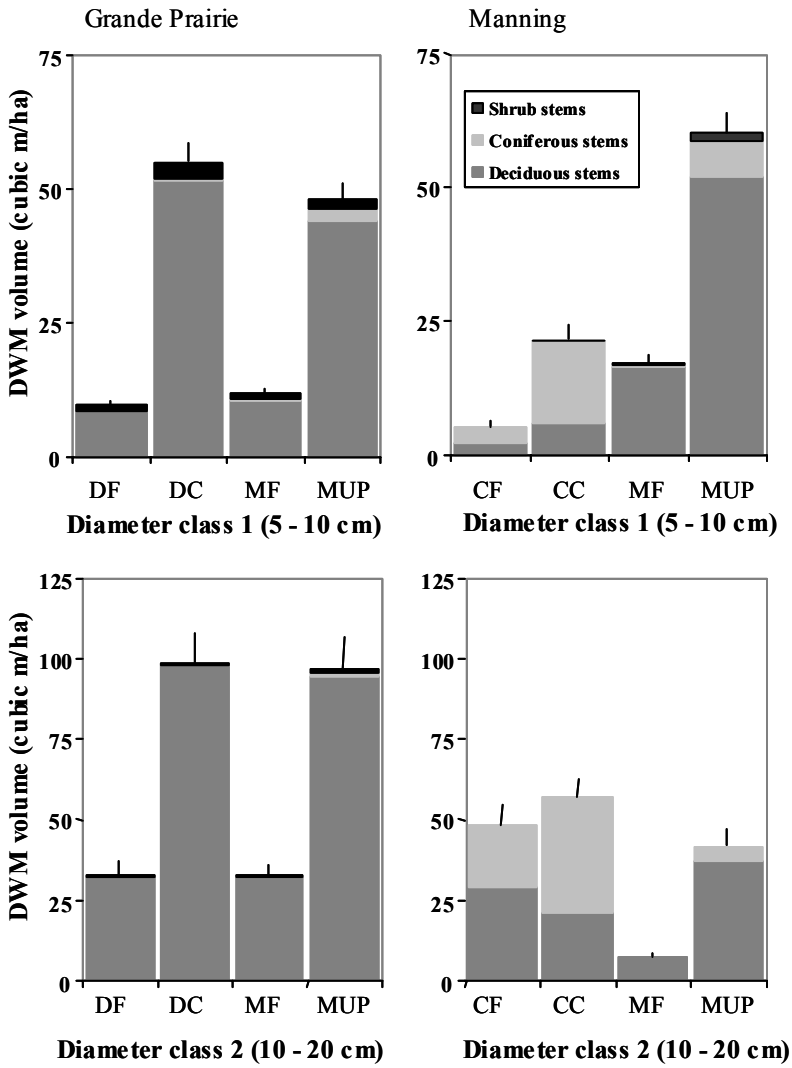


Figure 4.3. Mean DWM volume (m^3/ha) in each of two diameter classes in the Grande Prairie (left hand graphs) and Manning (right hand graphs) study areas. Bars represent deciduous forests (DF), deciduous clearcuts (DC), mixedwood forests (MF), mixedwood understorey protection cutblocks (MUP), coniferous forests (CF) and coniferous clearcuts (CC). Error bars indicate standard error of snag density in each diameter class in each forest type.

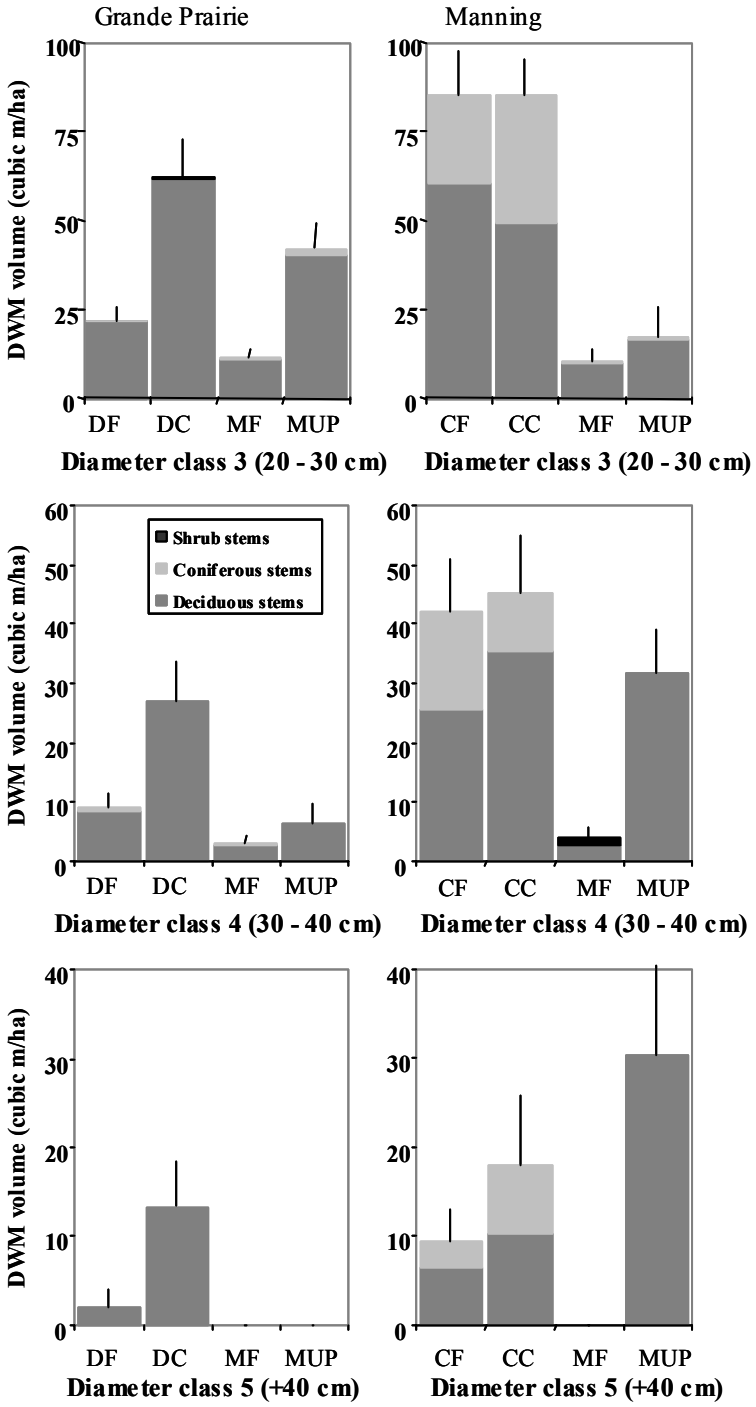


Figure 4.3 Cont. Mean DWM volume (m^3/ha) in each of three diameter classes in the Grande Prairie (left hand graphs) and Manning (right hand graphs) study areas. Bars represent deciduous forests (DF), deciduous clearcuts (DC), mixedwood forests (MF), mixedwood understorey protection cutblocks (MUP), coniferous forests (CF) and coniferous clearcuts (CC). Error bars indicate standard error of snag density in each diameter class in each forest type.

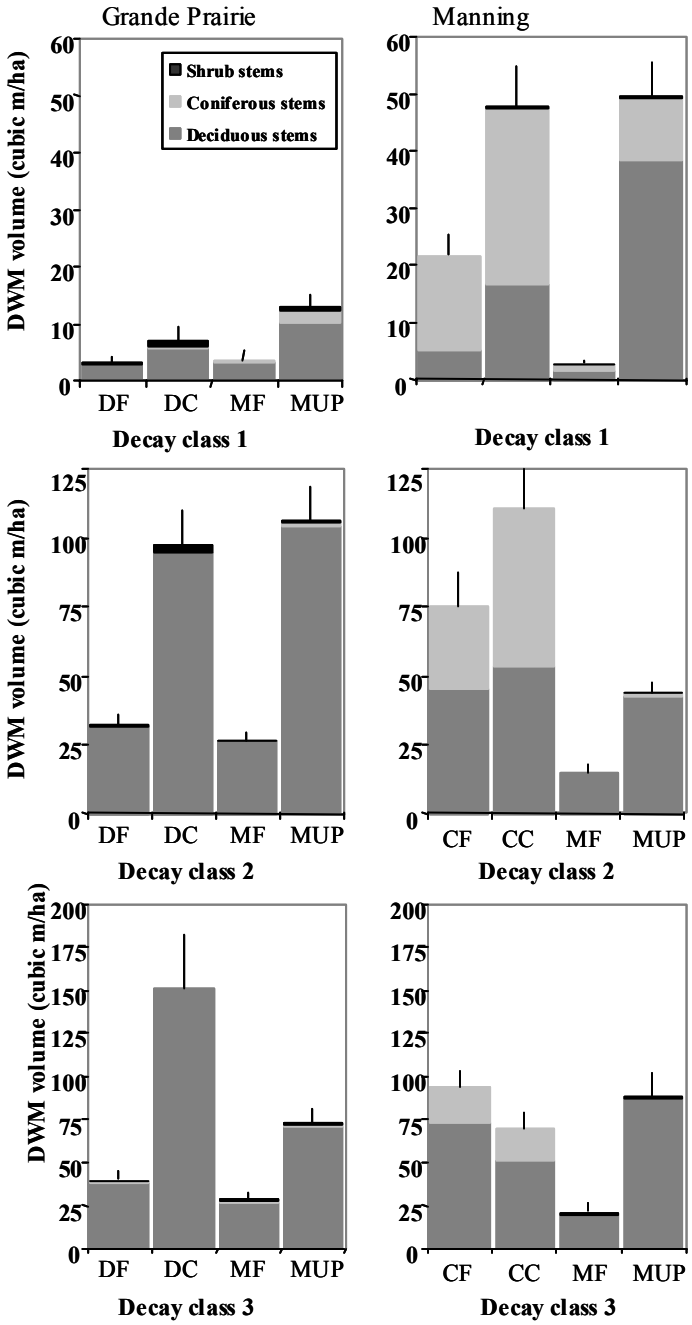


Figure 4.4. Mean DWM volume (m^3/ha) in each of three decay classes in the Grande Prairie (left hand graphs) and Manning (right hand graphs) study areas. Bars represent deciduous forests (DF), deciduous clearcuts (DC), mixedwood forests (MF), mixedwood understorey protection cutblocks (MUP), coniferous forests (CF) and coniferous clearcuts (CC). Error bars indicate standard error of snag density in each diameter class in each forest type.

CHAPTER 5: UNDERSTOREY PLANT COMMUNITIES IN DECIDUOUS, MIXEDWOOD AND CONIFEROUS FORESTS.

Steve Bradbury

Introduction

There is a growing body of research describing the plant communities found in deciduous and coniferous stands in the western boreal forest (Rowe 1956; Bradbury 2002; Frey *et al*. 2003; Rees and Juday 2002; Bradbury 2004), but few studies have examined the plant community associated with mixedwood forests (Crites 1999). Critical knowledge gaps include a basic understanding of the similarity between, and the variation within, plant communities found in boreal mixedwood forests, relative to deciduous and coniferous forests. There is increasing interest in forest development during mixedwood stages of succession. However, we are embarking on mixedwood management without an understanding of an appropriate natural mixedwood forest template, and little idea of the influence of development on mixedwood forests.

This study begins to fill these knowledge gaps by examining the understorey plant community in naturally occurring deciduous, mixedwood and coniferous stands, to determine if unique plant communities exist in mixedwood forests. Furthermore, the role of forest structural characteristics and regional variability is assessed.

Materials and Method

For a description of study areas and experimental design, see Chapter 2. To better understand factors influencing plant communities across boreal forest types, and to assess the uniqueness of plant communities found in mixedwood stands, additional stands were sampled. Thirty-three stands were sampled in addition to the 12 existing stands that comprise the Grande Prairie study area; all 45 stands were located within four adjacent townships (Twp 66, Rge 4, 5, W6M; Twp 67, Rge 4, 5, W6M). Likewise at the Manning study area, 33 stands were sampled in addition to the 12 existing stands; all 45 stands were located within six contiguous townships (Twp 92, Rge 25, W5M; Twp 93, Rge 25, W5M; Twp 94, Rge 23, 24, 25, W5M; Twp 93, Rge 01, W6M). Any reference in this chapter to the Grande Prairie and Manning study areas should be interpreted as meaning the 12 stands that comprise the main study (Figures 2.1 and 2.2); additional stands sampled in this chapter are referred to as additional stands.

Vascular plant data collection

Understorey vegetation included all forbs regardless of height, and trees and shrubs that were < 0.5 m tall. Percent of ground surface covered by leaves and stems was estimated in 5% intervals (*i.e.*, 5%, 10%, to 100%) but with a category of 1% to denote presence, and <5% to denote limited cover for understorey plants, litter (wood < 1 cm in diameter, leaves, needles and other small organic debris), bare mineral soil, wood (> 1 cm in diameter), moss, and lichen within each sample plots (0.5 m x 0.5 m). Grasses were not identified to species, but rather, percent cover was recorded for the group as a whole. Species not identified in the field were collected, pressed, and later identified in the laboratory or at the University of Alberta herbarium. Nomenclature follows Moss (1994).

In the Grande Prairie study area prior to harvest, percent cover of understorey vegetation was sampled systematically with four understorey plant plots in ten 1-ha sites in each stand (see Figure 2.3). A total of 40 understorey plots were sampled in each stand between mid-June and mid-August 2000. At the Manning study area, four understorey plant plots (0.5 m x 0.5 m) were sampled in each of seven 1-ha sites in each stand (see Figure 2.4). A total of 28 understorey plots were sampled in each pre-harvest stand between mid-June and mid-August 2000.

Additional stands in the Grande Prairie region included mixedwood stands with variable understorey conifer density and coniferous stands; additional stands in the Manning region included mixedwood stands with variable understorey conifer density and deciduous stands. Additional stands were sampled at five plot locations at four points resulting in 20 plots per stand using the same methodology for percent cover described above.

Data analysis

Vascular plant species richness (the number of species rooted within each 0.25 m^2 sampling plot) and Shannon diversity were determined for vascular plant communities found in each stand. Detrended correspondence analysis (DCA) was used to determine the relationships between forest cover types and plant communities. Sample plot data were pooled (by calculating means) into values representing mean cover of each species in each stand from both the Grande Prairie and Manning study areas and each additional stand from the different regions (a total of 90 stands were sampled). CANOCO (ter Braak and Smilauer 1998) was used to perform all ordinations. To facilitate interpretation stands were grouped into classes representing Grande Prairie deciduous, Grande Prairie mixedwood, Manning mixedwood and Manning coniferous stands, and 67% confidence ellipses were produced (SAS 2000).

Each stand was assigned to a canopy type (*i.e.*, deciduous, mixedwood and coniferous), and mixedwood stands were further categorized by understorey spruce density (*i.e.*, 100 stems/ha, 250 stems/ha, 500 stems/ha or 750 stems/ha). Linear regression was used to determine relationships between plant community variables (*i.e.*, cover, richness and diversity) and forest structural variables (*i.e.*, conifer tree understorey stem density, conifer tree overstorey stem density, deciduous tree understorey stem density, deciduous tree overstorey stem density, shrub stem density, stand age, litter cover and moss cover). Mean values were determined for each stand (n = 90), and significance was judged at $p < 0.05$. Analyses were performed using the JMP statistical package (SAS 2000).

Results

Ninety-five understorey plant species (all forbs, ferns, grasses, low shrubs, tall shrubs and trees below 0.5 m) were observed in the 90 stands sampled (Table 5.1). Of these species, 28% were only observed in mixedwood forests, and 54% occurred at their highest cover levels in mixedwood forests. Deciduous and mixedwood stands in the Grande Prairie region had 59% of plant species in common, and coniferous and mixedwood stands in the Manning region had 60% of plant species in common. Mixedwood stands between regions shared 58% of plant species. Deciduous stands in the Grande Prairie region and coniferous stands in the Manning region shared 46% of species.

Boreal deciduous, mixedwood and coniferous forests had distinct plant communities (Figure 5.1), even though mixedwood stands shared some plant species with both deciduous and coniferous stands. Detrended correspondence analysis Axis 1 (eigen value = 0.175) accounted for 11.4% of the variance in the species/stand data; Axis 2 (eigen value = 0.126) accounted for an additional 8.2% of the variance in the species/stand data.

Understorey plant communities in deciduous stands were most different from those observed in coniferous stands. In addition, plant communities in deciduous stands were the most variable, followed by mixedwood stands (in each region), and coniferous stands; mixedwood stands from both regions combined had the most variable in plant community. Overlap of treatment density ellipses is indicative of the plant species shared among the different canopy types. Dissimilarity in sample scores results from differences in cover values of shared species, and cover values of plant species unique to each sample.

The relative location of sample scores (*i.e.*, stands) along DCA Axis 1 demonstrated a transition of plant communities from deciduous through mixedwood to coniferous forests. The influence of stand structure was examined along this boreal forest continuum using linear regression (n = 90). Stand variables most

influential in structuring vascular plant cover, species richness and Shannon diversity were moss cover, coniferous overstorey stem density and, to a lesser degree, coniferous understorey stem density (Table 5.2). Plant community variables all decreased significantly as conifer density and moss cover increased: plant cover decreased from 79.3% (± 7.0%) to 50.8% (± 5.9%); species richness decreased from 25.9 plants/5m^2 (± 0.9 plants/5m^2) to 21.1 plants/5m^2 (± 1.1 plants/5m^2); and, diversity decreased from 2.9 (± 0.3) to 2.0 (± 0.2).

Plant communities within mixedwood forests exhibited regional variation (Figure 5.1). Sample scores of mixedwood stands from the Grande Prairie region were distinct from sample scores representing mixedwood stands from the Manning region. In addition, mixedwood stands from each region were more similar to the other forest type from the same region, compared to forest types from the other region (Figure 5.1). Linear regression, using the same stand structure variables as above, was used to examine within-region forest structure influences on plant community variables.

In the Grande Prairie region (n = 45), where deciduous forests dominated the sampled landscape, litter cover had the strongest influence on plant cover and diversity, and coniferous overstorey density determined species richness (Table 5.2). Moss cover contributed to plant community structure but to a lesser degree. From deciduous forests to mixedwood forests with the highest conifer density and coniferous forests, plant cover decreased from 84.7% (± 6.4%) to 64.0% (± 9.4%); species richness decreased from 27.0 plants/5m^2 (± 0.9 plants/5m^2) to 24.6 plants/5m^2 (± 0.9 plants/5m^2); and, diversity decreased from 3.1 (± 0.2) to 2.5 (± 0.3).

In the Manning region (n = 45), where coniferous forests dominated the sampled landscape, moss cover had the strongest influence on plant cover and diversity, and coniferous overstorey density determined species richness. Coniferous understorey stem density contributed to plant community structure but to a lesser degree. From deciduous forests and mixedwood forests with the lowest conifer density, to coniferous forests, plant cover decreased from 88.6% (± 5.2%) to 47.4% (± 5.6%); species richness decreased from 23.8 plants/5m^2 (± 1.6 plants/5m^2) to 19.8 plants/5m^2 (± 0.9 plants/5m^2); and, diversity decreased from 2.7 (± 0.1) to 1.8 (± 0.2).

Discussion

Understorey plant communities in mixedwood forests differed from those found in deciduous and coniferous forests both in terms of community composition and variation. Plant community differences were driven by changes in forest structure in stands along the boreal deciduous, mixedwood, and coniferous forest continuum. In this study, plant cover, species richness and diversity all decreased as overstorey coniferous stem density and moss cover increased.

Plant species are adapted to particular ecological niches, with some species having relatively broad habitat requirements and other species having narrow habitat requirements. Species with broad niches are capable of existing in a variety of forest cover types, while species with narrow niches may be restricted to particular forest cover types. Community composition, thus, is a reflection of the suite of plant species capable of growing in the microhabitat conditions created by stand structure, soil and climate (Rowe 1956; Peterson and Peterson 1992), and the competitive interactions among species present.

This study demonstrates the importance of coniferous stem density and moss cover in defining boreal forest microhabitat for understorey plants. Broad changes in coniferous stem density from deciduous stands, through mixedwood to coniferous stands, resulted in diminishing light availability at ground level along the continuum (Messier *et al.* 1998). Thus, this light gradient influenced understorey plant community composition, from species adapted to high light levels (in deciduous stands) to species adapted to low light levels (in coniferous stands). In general, mixedwood stands with

higher densities of coniferous stems and higher levels of moss cover, had plant communities with similarities to coniferous forests. In contrast, mixedwood stands with few coniferous stems and minimal moss cover had similar plant communities to deciduous forests.

Previous studies have described similar responses of plant communities to different boreal forest cover types. For example, diverse herbaceous-rich plant assemblages were found in deciduous forests, and less diverse assemblages were found in coniferous forests (Rowe 1956; Peterson and Peterson 1992).

Factors that influenced the ground layer microenvironment (light, nutrient availability, soil temperature, *etc.*) contributed to the selection of plant species found under each forest cover type. Competitive interactions among species determined relative abundance and cover of each species. These factors clearly defined plant communities found in boreal deciduous, mixedwood and coniferous stands, but they also determined variation of plant communities within each forest cover type.

Deciduous forests had highly variable plant communities because of increased light levels, nutrient rich soils, and increased soil temperatures (Rowe 1956; Peterson and Peterson 1992). Mixedwood stand plant community variability was associated with variability in mixedwood forest structure (*i.e.*, conifer overstorey and understorey stem density, and moss cover). This structural heterogeneity resulted in a highly variable microhabitat compared with deciduous forests, and thus, highly variable plant communities. In addition, mixedwood stands exhibited regional variation likely due to the influence of climatic variation associated with altitude and latitude. Coniferous forests exhibited the lowest vascular plant community variation, although, old-growth coniferous forests had increased heterogeneity due to increased canopy gap frequency (De Grandpré and Bergeron 1997).

High variation and heterogeneity is known to preserve biodiversity (Halpern and Spies 1995; Roberts and Gilliam 1995; Hartley 2002). As a result, mixedwood forests, in addition to deciduous and coniferous forests, provided unique niches for understorey plant communities and community variation.

Management Implications and Future Research

- Plant communities in mixedwood forests have unique properties compared with plant communities in deciduous and coniferous forests.
- Plant communities in mixedwood stands exhibit regional variation within and between regions.

Forest management should include provisions to manage mixedwood stands on a regional basis, with particular attention to understanding, and maintaining, mixedwood stand heterogeneity.

Additional research should be conducted to: 1) elucidate plant community dynamics in mixedwood stands as understorey conifer trees age; 2) determine the range of variation in plant communities in natural mixedwood stands to better understand a natural mixedwood forest template; and, 3) elucidate causal mechanisms of plant community variability in mixedwood stands adjacent to deciduous and coniferous forests and in different regions.

Acknowledgements

I am grateful to our technical staff for their hard work in the field with data collection. Technicians involved in data collection for this portion of the study included Cris Gray, Sharon Kendall, Dave McKinnon, Luke Nolan, Len Peleshok, Dee Ryerson, Dan Sturgess, Kelly Sturgess and Lindsay Tomyn. Phil Lee, Samantha Song, Jake Fisher and Lisa Wilkinson provided valuable insight to study design. Phil Lee, J.P. Bielech, Fred Radersma and Lisa Wilkinson provided constructive criticisms that greatly improved earlier versions of this chapter. Pat Soldan formatted the chapter.

Literature Cited

Bradbury, S. 2002. Response of understorey vascular plants to wildfire and harvesting. In: Ecological basis for stand management: a synthesis of ecological responses to wildfire and harvesting (Edited by S. Song). Alberta Research Council, Vegreville, AB.

Bradbury, S. 2004. Understorey plant communities in boreal cutblocks with different sizes and numbers of residual patches. Can. J. For. Res. *In press*.

Crites, S. 1999. A comparison of early successional understorey plant communities following fire and harvest. In: Fire and harvest residual project. Alberta Research Council, Vegreville, AB.

De Grandpré, L., and Bergeron, Y. 1997. Diversity and stability of understorey communities following disturbance in the southern boreal forest. J. Ecology. 85: 777-784.

Frey, B.R., Lieffers, V.J., Munson, A.D. and Blenis, P.V. 2003. The influence of partial harvesting and forest floor disturbance on nutrient availability and understorey vegetation in boreal mixedwoods. Can. J. For. Res. 33:1180-1188.

Halpern, C.B. and Spies, T.A. 1995. Plant species diversity in natural and managed forests of the Pacific Northwest. Ecol. Appl. 5: 913-934.

Hartley, M.J. 2002. Rationale and methods for conserving biodiversity in plantation forests. For. Ecol. Manage. 155:81-95.

Messier, C., Parent, S., and Bergeron, Y. 1998. Effect of overstorey and understorey vegetation on the understorey light environment in mixed boreal forests. J. Veg. Sci. 9:511-520.

Moss, E.H. 1994. Flora of Alberta. A manual of flowering plants, conifers, ferns and fern allies found growing without cultivation in the province of Alberta, Canada. 3rd Edition. Revised by J.G. Packer. University of Toronto Press. Toronto, ON.

Peterson, E.B. and Peterson, N.M. 1992. Ecology, management, and use of aspen and balsam poplar in the prairie provinces, Canada. For. Can., Northwest Reg., North. For. Cent., Edmonton, Alberta. Spec. Rep. 1.

Rees, D.C. and Juday, G.P. 2002. Plant species diversity on logged versus burned sites in central Alaska. For. Ecol. Manage. 155:291-302.

Roberts, M.R. and Gilliam, F.S. 1995. Patterns and mechanisms of plant diversity in forested ecosystems: implications for forest management. 5:969-977.

Rowe, J.S. 1956. Uses of undergrowth plant species in forestry. Ecology. 37:461-473.

SAS. 2000. JMP Statistics and Graphics Guide, Version 3.2.1, SAS Institute, Cary, NC.

ter Braak, C.J.F. and Smilauer, P. 1998. CANOCO: a fortran program for canonical community ordination by (partial), (detrended), (canonical), correspondence analysis, principle components analysis, and redundancy analysis, version 4 for Windows. Microcomputer Power, Ithaca, NY.

Table 5.1. Mean cover of understorey vascular plants from deciduous and mixedwood forests from the Grande Prairie region (n = 45), and mixedwood and coniferous forests from the Manning region (n = 45); stands from the Grande Prairie and Manning study areas are included. For brevity, samples are pooled into four forest types, but analyses were conducted on plant communities at the stand level using several categories of mixedwood stands based on understorey conifer density. Plant names followed by spp. and grasses were not identified to species. Understorey plant species included all forbs regardless of height, and trees and shrubs that were less than 0.5 m tall.

	Grande Prairie region		**Manning region**	
	Deciduous forest	Mixedwood forest	Mixedwood forest	Coniferous forest
Forb, grass, fern species				
Achillea millefolium	0.000	0.105	0.188	0.056
Actaea rubra	0.214	0.480	0.264	0.000
Angelica genuflexa	1.750	0.020	0.000	0.000
Aquilegia brevistyla	0.000	0.046	0.000	0.000
Aralia nudicaulis	8.214	6.197	3.208	0.583
Arenaria lateriflora	0.057	0.000	0.007	0.000
Arnica cordifolia	0.107	0.158	0.458	0.000
Aster ciliolatus	2.086	3.072	2.542	2.500
Aster conspicuous	5.464	1.724	0.500	0.500
Aster puniceus	0.429	0.217	0.014	0.000
Astragalus americanus	0.000	0.000	0.076	0.000
Carex pensylvanica	0.000	0.053	0.000	0.000
Circaea alpina	0.143	0.349	0.111	0.000
Comandra umbellate	0.000	0.000	0.007	0.000
Corallorhiza maculata	0.000	0.007	0.000	0.000
Delphinium glaucum	0.357	0.000	0.278	0.278
Disporum trachycarpum	0.179	0.099	0.000	0.000
Epilobium angustifolium	3.786	1.750	3.076	3.806
Epilobium glandulosum	0.000	0.000	0.056	0.000
Equisetum arvense	0.486	0.322	0.179	1.444
Equisetum pratense	0.157	0.026	0.000	0.000
Equisetum scirpoides	0.000	0.026	0.007	0.028
Equisetum sylvaticum	0.036	0.112	0.278	1.500
Fragaria vesca	0.357	0.000	0.007	0.000
Fragaria virginiana	2.229	3.289	2.725	1.194
Galium boreale	2.286	1.776	0.821	0.444
Galium triflorum	1.557	0.399	0.319	0.000
Geum macrophyllum	0.000	0.007	0.000	0.000
Geum rivale	0.000	0.138	0.000	0.000
Goodyera repens	0.000	0.007	0.056	0.028
Grass spp.	2.836	2.204	4.513	4.111
Gymnocarpium dryopteris	0.357	0.375	0.035	0.000
Habanaria obtusata	0.000	0.000	0.025	0.000
Habanaria orbiculata	0.000	0.020	0.000	0.000
Halenia deflexa	0.000	0.125	0.000	0.000
Heracleum lanatum	0.000	0.750	0.000	0.000
Impatiens capensis	0.000	0.033	0.007	0.000
Lathyrus ochroleucus	4.371	4.020	1.478	1.139
Listera borealis	0.000	0.000	0.000	0.028

	Grande Prairie region		Manning region	
	Deciduous forest	Mixedwood forest	Mixedwood forest	Coniferous forest
Lycopodium annotinum	0.000	0.243	0.236	0.000
Maianthemum canadense	3.107	1.875	0.961	0.806
Matteuccia struthiopteris	0.000	0.039	0.000	0.000
Mertensia paniculata	12.243	6.678	7.172	3.333
Mitella nuda	2.786	3.967	4.569	3.417
Moneses uniflora	0.000	0.000	0.021	0.000
Osmorhiza depauperata	0.000	0.086	0.000	0.000
Petasites palmatus	0.600	3.112	2.683	2.472
Pyrola asarifolia	0.407	1.171	0.818	0.278
Pyrola secunda	0.000	0.072	0.354	0.278
Scutellaria galericulata	0.000	0.020	0.000	0.000
Smilacina stellata	0.179	0.217	0.000	0.000
Smilacina trifolia	0.064	0.007	0.000	0.000
Solidago canadensis	0.750	0.099	0.000	0.000
Sonchus oleraceus	0.143	0.000	0.021	0.000
Stellaria longipes	0.000	0.020	0.000	0.000
Streptopus amplexifolius	0.000	0.053	0.000	0.000
Thalictrum venulosum	0.000	0.204	0.035	0.000
Trientalis borealis	0.000	0.007	0.153	0.306
Trifolium hybridum	0.000	0.033	0.000	0.000
Urtica dioica	0.000	0.020	0.000	0.000
Vicia americana	0.536	0.658	0.083	0.000
Viola canadensis	0.321	0.717	0.097	0.139
Viola renifolia	1.064	1.151	1.138	0.722
Low shrub species				
Cornus canadensis	14.264	15.197	15.396	11.417
Ledum groenlandicum	0.314	0.526	0.104	0.056
Linnaea borealis	3.257	4.704	4.438	5.333
Lonicera dioca	1.729	0.526	0.521	0.278
Lonicera involucrata	4.193	5.066	0.069	0.000
Ribes glandulosum	0.000	0.007	0.000	0.083
Ribes hudsonianum	0.000	0.000	0.056	0.556
Ribes lacustre	0.000	0.125	0.283	0.000
Ribes oxyacanthoides	1.657	0.309	0.160	0.028
Ribes triste	1.679	1.132	1.785	0.667
Rosa acicularis	6.779	7.822	7.118	5.611
Rubus idaeus	2.336	0.395	0.139	0.000
Rubus parviflorus	0.000	0.447	0.000	0.000
Rubus pedatus	0.000	0.053	0.000	0.000
Rubus pubescens	9.193	7.441	6.583	4.917
Shepherdia canadensis	0.286	0.526	0.549	0.667
Spiraea alba	2.286	2.322	0.000	0.000
Symphoricarpos albus	2.000	0.822	0.396	0.028
Vaccinium caespitosum	0.179	1.007	0.125	0.278
Vaccinium membranaceum	0.000	0.099	0.000	0.000
Vaccinium myrtilloides	0.343	1.020	0.000	0.000
Vaccinium vitis-idaea	0.000	0.066	0.063	0.972
Viburnum edule	4.014	4.743	3.739	2.139

	Grande Prairie region		Manning region	
	Deciduous forest	Mixedwood forest	Mixedwood forest	Coniferous forest
Tall shrub species (<0.5 m)				
Alnus crispa	0.357	0.007	0.035	0.000
Amelanchier alnifolia	0.107	0.303	0.000	0.000
Cornus stolonifera	0.250	1.000	0.368	0.000
Salix spp.	0.000	0.105	0.028	0.389
Tree species (<0.5 m)				
Abies balsamea	0.000	0.007	0.104	0.000
Betula papyrifera	0.393	0.007	0.000	0.000
Picea glauca	0.000	0.033	0.167	0.111
Populus balsamifera	0.071	0.276	0.042	0.000
Populus tremuloides	0.121	0.138	0.069	0.333

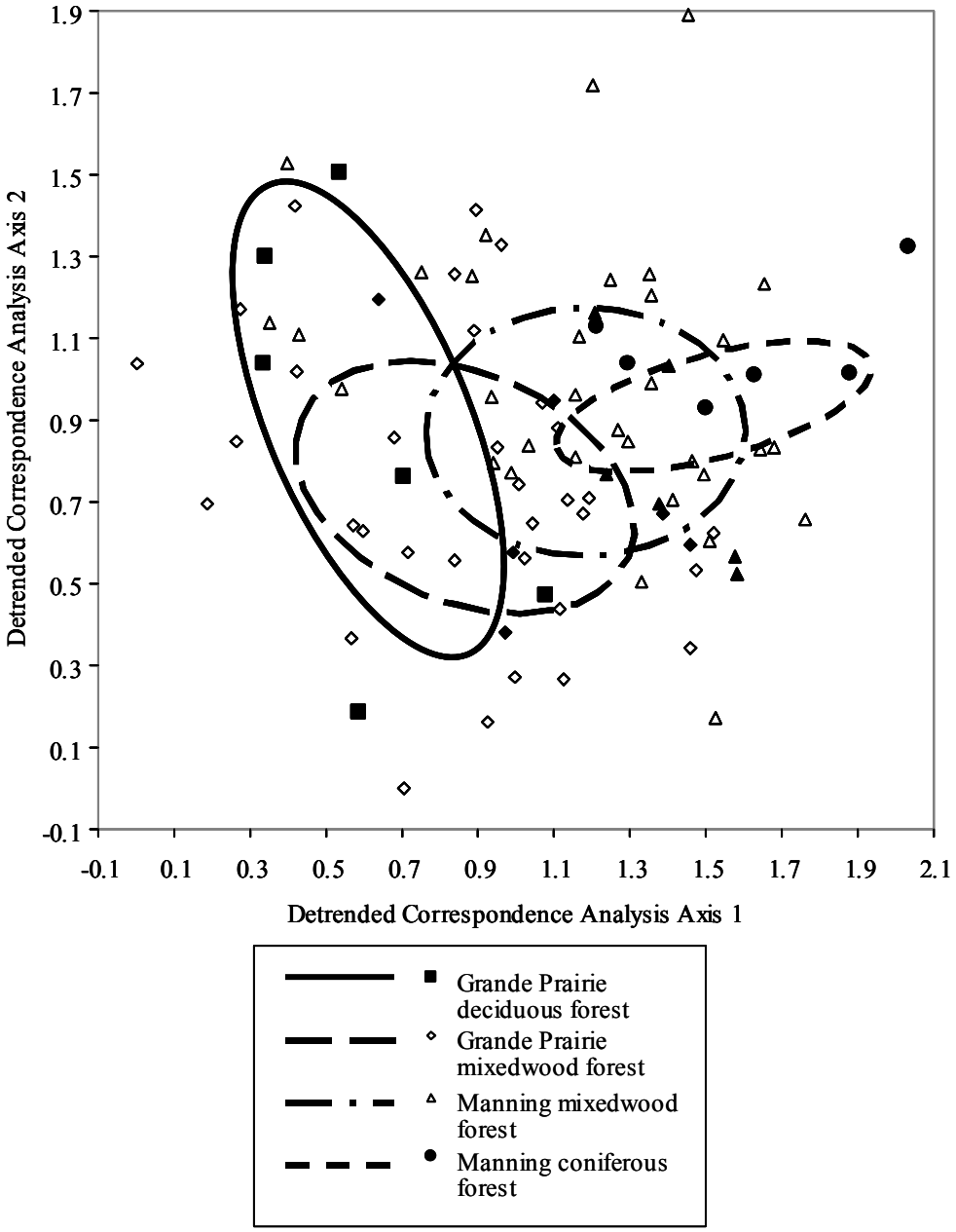


Figure 5.1. Detrended correspondence analysis of understorey vegetation in deciduous, mixedwood and coniferous stands. Filled squares and diamonds represent stands from the Grande Prairie study area, and empty diamonds represent additional mixedwood stands sampled from the surrounding landbase. Filled circles and triangles represent stands from the Manning study area, and empty triangles represent additional mixedwood stands sampled from the surrounding landbase. Confidence ellipses represent one standard deviation from the mean.

Table 5.2. Results of linear regression (adjusted-R^2) of forest structure variables with vascular plant cover (PC), species richness (SR) and Shannon diversity (D) in boreal forest stands from both the Grande Prairie (n = 45) and Manning (n = 45) study areas. Values in **boldface** combine significant slope and correlation, and represent the structural variables most influential in determining plant community response.
Note: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; n.s., not significant.

Structure variable[1]	Vascular plant cover		Species richness		Shannon diversity	
Stands from both regions (n = 90)						
Coniferous overstorey stem density	**0.32*** **	PC = 80.18 – 0.095 x variable	**0.32*** **	SR = 25.99 – 0.017 x variable	**0.33*** **	D = 2.89 – 0.003 x variable
Coniferous understorey stem density	0.12**	PC = 76.14 – 0.031 x variable	0.12**	SR = 25.28 – 0.005 x variable	0.13**	D = 2.77 – 0.001 x variable
Deciduous overstorey stem density	0.00	n.s.	0.01	n.s.	0.01	n.s.
Deciduous understorey stem density	0.05	n.s.	0.04	n.s.	0.07	n.s.
Total shrub stem density	0.06	n.s.	0.02	n.s.	0.02	n.s.
Stand age	0.03	n.s.	0.02	n.s.	0.01	n.s.
Litter cover	0.01	n.s.	0.01	n.s.	0.01	n.s.
Moss cover	**0.33*** **	PC = 79.16 – 0.982 x variable	**0.33*** **	SR = 25.81 – 0.174 x variable	**0.38*** **	D = 2.87 – 0.031 x variable
Stands from the Grande Prairie region (n = 45)						
Coniferous overstorey stem density	**0.23*** **	PC = 84.39 – 0.086 x variable	**0.43*** **	SR = 27.78 – 0.014 x variable	**0.29*** **	D = 3.14 – 0.003 x variable
Coniferous understorey stem density	0.04	n.s.	0.07*	SR = 26.91 – 0.003 x variable	0.06	n.s.
Litter cover	**0.58*** **	PC = 170.27 – 1.820 x variable	0.08*	SR = 31.21 – 0.097 x variable	**0.48*** **	D = 5.35 – 0.048 x variable
Moss cover	0.14**	PC = 83.78 – 1.523 x variable	0.18**	SR = 27.41 – 0.218 x variable	0.13**	D = 3.09 – 0.042 x variable
Stands from the Manning region (n = 45)						
Coniferous overstorey stem density	**0.34*** **	PC = 73.90 – 0.090 x variable	**0.25*** **	SR = 23.36 – 0.013 x variable	**0.36*** **	D = 2.50 – 0.002 x variable
Coniferous understorey stem density	0.15**	PC = 70.97 – 0.035 x variable	0.11*	SR = 22.93 – 0.005 x variable	0.15**	D = 2.42 – 0.001 x variable
Moss cover	**0.39*** **	PC = 75.04 – 0.841 x variable	0.18**	SR = 23.08 – 0.102 x variable	**0.41*** **	D = 2.54 – 0.022 x variable

[1] Structure variables with insignificant adjusted-R^2 values at n = 90 that also had insignificant adjusted-R^2 values at n = 45, were omitted.

CHAPTER 6: UNDERSTOREY PLANT COMMUNITIES IN DECIDUOUS, MIXEDWOOD AND CONIFEROUS STANDS BEFORE AND AFTER HARVEST, WITH SPECIFIC ATTENTION TO UNDERSTOREY PROTECTION CUTBLOCKS

Steve Bradbury

Introduction

Boreal forests in Alberta are undergoing intensive harvesting pressure. Deciduous forests are harvested for manufacture of kraft pulp and oriented strand board, and coniferous forests are harvested for dimensional lumber. Aspen is typically harvested before stands reach 100 years of age (and from stands with minimal understorey conifer density), and softwoods are typically harvested after 120 years. Mixedwood stands, until recently, were not harvested until the coniferous stems reached merchantability (Navratil *et al.* 1994).

Mixedwood understorey protection strategies aim to maximize the harvest of deciduous trees, while minimizing damage to understorey coniferous stems (Peterson and Peterson 1992; Navratil *et al.* 1994). Removal of most of the deciduous overstorey releases understorey spruce and allows access to similar, or greater, volumes of conifer sooner than if the stands were left to develop naturally. The interim between harvest phases depends on the age of the mixedwood stand, the size of the coniferous understorey when released, and the coniferous growth rate after harvest of the deciduous overstorey.

There is a growing body of research describing plant communities found in deciduous and coniferous stands in the western boreal forest before and after harvest (Rowe 1956; Bradbury 2002; Frey *et al.* 2003; Bradbury 2004), but few studies have examined the plant community associated with mixedwood forests (Crites 1999) and understorey protection cutblocks (Mourelle *et al.* 2002).

This research project was initiated because of increasing interest in forest development during mixedwood stages of succession, and the paucity of ecological knowledge from mixedwood stands in general, and understorey protection cutblocks in particular. The objectives of this study were to: 1) compare the magnitude of change in the understorey plant community found in deciduous and coniferous stands that have been clearcut with mixedwood stands that have been harvested using an understorey protection strategy; and, 2) compare the plant community in pre-harvest mixedwood forests with the plant community in different microsites established in understorey protection cutblocks.

Materials and Method

For a description of study areas and experimental design, see Chapter 2.

Vascular plant data collection

Understorey vegetation included all forbs regardless of height, and trees and shrubs that were < 0.5 m tall. Percent of ground surface covered by leaves and stems was estimated in 5% intervals (*i.e.*, 5%, 10%, to 100%) but with categories of 1% to denote presence, and <5% to denote limited cover. Cover was assessed for understorey plants, litter (wood < 1 cm in diameter, leaves, needles and other small organic debris), bare mineral soil, wood (> 1 cm in diameter), moss, and lichen within each sample plots (0.5 m x 0.5 m). Grasses were not identified to species, but rather, percent cover was recorded for the group as a whole. Species not identified in the field were collected, pressed, and later identified in the laboratory or at the University of Alberta herbarium. Nomenclature follows Moss (1994).

In the Grande Prairie study area, prior to harvest, percent cover of understorey vegetation was sampled systematically with four understorey plant plots in ten 1-ha sites in each stand (see Figure 2.3). A total of 40 understorey plots were

sampled in each pre-harvest stand between mid-June and mid-August 2000.

At the beginning of data collection in the first growing season after harvest (*i.e.*, May 2001), the 10 ha grid was relocated (from marked trees and metal pins located at the grid corners) and re-established such that all subsequent post-harvest sampling occurred in the same site locations as pre-harvest sampling.

In the second growing season after harvest (*i.e.*, July 2002), three understorey plant plots were sampled systematically with ten 1-ha sites in each deciduous clearcut (totalling 30 plots per stand). Six understorey plant plots were sampled systematically with ten 1-ha sites in each understorey protection cutblock (totalling 60 plots per stand). To investigate the influence of understorey protection harvesting on the plant community in more detail, the six sample plots per 1-ha site were separated into two plots along the skid trail, two plots along the residual strip with understorey spruce but no aspen overstorey, and two plots along the residual strip with both understorey spruce and an aspen overstorey. In total in each of the three understorey protection stands, 20 plots were measured along the skid trail, 20 plots were measured along the residual understorey strip, and 20 plots were measured along the residual overstorey strip.

Vegetation sampling in the Manning study area was similar, but with the following exceptions. Four understorey plant plots (0.5 m x 0.5 m) were sampled in each of seven 1-ha sites in each stand (see Figure 2.4). A total of 28 understorey plots were sampled in each pre-harvest stand between mid-June and mid-August 2000. Post-harvest sampling occurred in July 2003. Five understorey plant plots were sampled systematically in five 1-ha sites in each coniferous clearcut (totalling 25 plots per stand), and six understorey plant plots were sampled systematically in five 1-ha sites in each understorey protection cutblock (totalling 30 plots per stand).

Data analysis – pre-harvest versus post-harvest forest types

Vascular plant cover, species richness and Shannon diversity were determined for vascular plant communities found in each stand in the Grande Prairie and Manning study areas. One-way ANOVA, with a *post hoc* Student's t-test, was used to investigate differences between pre-harvest and post-harvest deciduous and mixedwood stands in the Grande Prairie study area. The same approach was used to test coniferous and mixedwood stands in the Manning study area. Differences were judged as significant if $p < 0.05$. Analyses were performed using the JMP statistical package (SAS 2000).

Detrended correspondence analysis (DCA) was used to determine the relationships between forest canopy types and plant communities; DCA was used because of the presumed gradient length separating plant communities found in deciduous forests compared to coniferous forests (see Chapter 5). Sample site data were pooled (by calculating means) into values representing each stand (n = 3) from both the Grande Prairie and Manning study areas. CANOCO (ter Braak and Smilauer 1998) was used to perform all ordinations.

Stand sample scores, from the DCA, were used to calculated two-dimensional orthogonal distances (using the Pythagorean theorem) between a pre-harvest stand and its subsequent post-harvest location in ordination space; the distance between a pre-harvest stand sample score and its post-harvest stand sample score in ordination space was assumed to represent the magnitude of change to the sampled community due to the harvesting strategy. Mean distance in ordination space between stands before and after harvest was calculated for deciduous clearcuts and understorey protection cutblocks in the Grande Prairie study area and coniferous clearcuts and understorey protection cutblocks in the Manning study area.

Data analysis – understorey protection harvest

Three habitat types (microsites) were designated within mixedwood understorey protection cutblocks: 1) residual strips with both an aspen overstorey and a spruce understorey; 2) residual strips with a spruce understorey; and, 3) skid trails. Principal components analysis (PCA) was used to determine the relationships between habitat types (including mixedwood forests and the three understorey protection cutblock microsites) and plant communities; PCA was used because of the relatively short gradient identified among treatments. CANOCO (ter Braak and Smilauer 1998) was used to perform all ordinations. To facilitate interpretation, density ellipses (67%) were plotted using PCA sample scores grouped by treatment (SAS 2000).

Results

Comparison of pre-harvest and post-harvest forest cover types

At the Grande Prairie study area, 97 understorey plant species were found in all deciduous and mixedwood stands combined before and after harvest (Table 6.1). Sixty-eight herbaceous species (*i.e.*, forbs, grasses and ferns), 19 low shrub species, 6 tall shrub species, and 4 tree species were recorded. Beta diversity (*i.e.*, species richness from all stands per treatment) increased after harvest in both deciduous (from 64 to 70 species) and mixedwood (from 58 to 68 species) stands.

At the Manning study area, 75 understorey plant species were found in coniferous and mixedwood stands combined before and after harvest (Table 6.1). Forty-nine herbaceous species, 21 low shrub species, 2 tall shrub species, and 3 tree species were recorded. Beta diversity decreased after harvest in coniferous stands (from 46 to 39 species) and increased after harvest in mixedwood stands (from 36 to 50 species).

At the Grande Prairie study area, total vascular plant cover (*i.e.*, percent of ground covered by vascular vegetation within each plot regardless of species) was greater ($F = 5.80$; $p = 0.001$) in deciduous forests (45.7% ± 2.1) compared to mixedwood forests (38.5% ± 2.2), and this difference was maintained after harvesting both forest types (deciduous clearcut: 46.8% ± 1.8; mixedwood understorey protection: 38.2% ± 1.5).

At the Manning study area, total vascular plant cover in coniferous and mixedwood forests was lower than that observed in Grande Prairie. Vascular plant cover in coniferous forests (23.27% ± 1.7) decreased ($F = 6.77$; $p < 0.001$) after harvest (18.8% ± 2.2). In contrast, vascular plant cover in mixedwood forests (17.5% ± 1.2) increased in understorey protection cutblocks (28.1% ± 2.2). Lower pre-harvest plant cover in the Manning study area was likely due to a higher coniferous stem density (Chapter 3) and a concomitant reduction in light availability to understorey vegetation (Chapter 5). The increase in plant cover in understorey protection cutblocks was a plant growth response to increased light availability.

At both the Grande Prairie and Manning study areas, average understorey plant species richness increased in the mixedwood understorey protection stands (Grande Prairie study area: $F = 20.9$; $p < 0.0001$; Manning study area: $F = 18.0$; $p < 0.0001$) compared to pre-harvest mixedwood stands (Table 6.1). This increase was likely a result of the heterogeneity of habitat created in understorey protection cutblocks. For example, early seral species emerged along skid trails, but the residual strips continued to support the vascular species found before harvest. Average species richness did not change after clearcutting deciduous or coniferous forests, because forest plant species not found in clearcut habitat were replaced by vascular plant species capable of growth in the newly created high-light environment.

Shannon diversity increased in understorey protection cutblocks at the Manning study area compared to mixedwood forests ($F = 4.87$; $p < 0.05$), but this result was not observed in the Grande Prairie study area ($F = 1.72$; $p = 0.240$). Increased diversity in the Manning study area

resulted from the combination of increased species richness and plant cover. Removal of 53% of conifer stem density in Manning study area understorey protection cutblocks (Chapter 3) created light conditions that significantly increase plant growth (*i.e.*, cover). Plant cover was already high in Grande Prairie study area mixedwood stands (due to a lower pre-harvest conifer stem density – Chapter 3). As a result, increased light levels did not alter plant vigour or competitive interactions among mixedwood forest species to the same degree as observed in the Manning study area. Shannon diversity did not change after clearcutting, in either the Grande Prairie or Manning study areas, because of minimal changes to plant cover and species richness after harvest.

Understorey plant communities were compared using detrended correspondence analysis (DCA) in deciduous, coniferous and mixedwood stands before and after harvest (Figure 6.1). Axis 1 (eigen value = 0.222) accounted for 24% of the variance in the species/stand data; Axis 2 (eigen value = 0.142) accounted for an additional 15% of the variance in the species/stand data. Axis 1 separated deciduous, mixedwood and coniferous stands based on distinct understorey plant communities; the slight overlap in deciduous and mixedwood stands in the Grande Prairie study area suggests a greater similarity in understorey plant communities found between these forest cover types. In contrast at the Manning study area, mixedwood stands and coniferous forests were more dissimilar because nonvascular plants had such a dominant influence in coniferous stands. Axis 2 separated deciduous stands, but had little influence on mixedwood and coniferous stands.

Mean distance between individual stands before and after harvest was measured in ordination space, and was assumed to represent the magnitude of the disturbance on the understorey plant community (Table 6.2). Changes to plant communities after deciduous and coniferous clearcutting were greater than after understorey protection harvesting. Clearcutting coniferous forests resulted in the greatest distance (0.42 ± 0.13) between individual stands, followed by clearcutting deciduous forest (0.22 ± 0.02). Harvesting of mixedwood stands using an understorey protection strategy resulted in the least distance between stands before and after harvest; distance was similar between mixedwood stands in the Grande Prairie (0.11 ± 0.06) and Manning (0.10 ± 0.04) study areas. These results indicate that clearcutting resulted in a greater change to the plant community than did understorey protection harvesting.

The high level of variation in plant communities found in deciduous forests increased slightly in deciduous clearcuts due to increased microsite variability. Similarly, variation in plant communities in mixedwood stands increased after understorey protection harvest. In contrast, clearcutting coniferous stands substantially reduced plant community variation. Furthermore, the plant community found in coniferous clearcuts had fewer similarities to plant communities in other stand types, including coniferous forests. The direction of change (in ordination space) was consistently unidirectional for coniferous clearcuts, but variable for deciduous clearcuts and understorey protection cutblocks (Figure 6.1). Unidirectional change resulted in reduced plant community variation, and variable directional change increased plant community variation.

Comparison of mixedwood stands and understorey protection cutblock habitat types

Overall, plant communities in mixedwood stands and their response to understorey protection harvesting, strongly indicated regional differences between the Grande Prairie and Manning study areas.

High species richness and cover, in Grande Prairie study area mixedwood stands, suggested that the plant community was highly competitive and saturated with species (Table 6.3). In contrast at the Manning study area, mixedwood forests had lower initial cover and fewer species. Furthermore, individual mixedwood stands at the Manning study area, were less likely to have complete representation of plant species, because average richness was much lower than Beta diversity (*i.e.*, total species counts across all mixedwood stands).

The establishment of skid trails (relative to the other two habitat types) had the greatest influence on mixedwood plant communities (Table 6.3). In both study areas, species richness was reduced, but plant cover increased. The increase was most significant at the Manning study area, where plant cover along skid trails was more than double the level observed in mixedwood stands before harvest (Table 6.3). In addition, skid trails supported fewer species in both study areas. At the Grande Prairie study area, the combination of fewer species and limited increase in plant cover resulted in no change to Shannon diversity. Shannon diversity increased along skid trails in the Manning study area largely due to the substantial increase in plant cover.

Plant communities found along the residual understorey strips responded similarly at the Grande Prairie and Manning study areas (Table 6.3). At the Grande Prairie study area, plant cover did not change after harvest, but species richness decreased. This suggests that a few species dominated in the increased light environment along the understorey residual strips. At the Manning study area, the same response occurred, but with considerably more vigour (*i.e.*, cover). Fewer species accounted for a 150% increase in plant cover in the increased light environment. Shannon diversity did not change along understorey residual strips relative to pre-harvest mixedwood forests in either study area.

In both study areas, a similar plant community response was observed along overstorey residual strips, where microenvironmental conditions after harvest were most similar to mixedwoods forests before harvest (Table 6.3). In both study areas, plant cover did not change but species richness decreased after harvest. These results suggest that fewer species dominated in the overstorey strips relative to mixedwood forests. Shannon diversity did not change along overstorey residual strips relative to pre-harvest mixedwood forests in either study area.

Plant communities in pre-harvest mixedwood stands, post-harvest residual overstorey strips, residual understorey strips, and skid trails were compared using principal components analysis (PCA). Plant communities in the four habitat types overlapped. At the Grande Prairie study area (Figure 6.2), Axis 1 (eigen value = 0.161) accounted for 16.1% of the variance in the species/stand data, and Axis 2 (eigen value = 0.153) accounted for an additional 15.2% of the variance in the species/stand data. At the Manning study area (Figure 6.3), Axis 1 (eigen value = 0.235) accounted for 23.5% of the variance in the species/stand data, and Axis 2 (eigen value = 0.176) accounted for an additional 17.6% of the variance in the species/stand data.

At the Grande Prairie study area, plant communities in understorey protection cutblocks were similar to pre-harvest mixedwood forests (Figure 6.2). Plant communities in overstorey and understorey residual strips had the least amount of variation and the most overlap. Plant communities along skid trails had similar variation to mixedwood stands, and only limited dissimilarity. PCA results supported the theory of a highly competitive and species saturated plant community with few differences after harvest.

At the Manning study area, PCA results supported the theory of limited representation of plant species in each mixedwood stand. Differences in plant communities in mixedwood forests before harvest were magnified after harvest. As a result, plant community variation increased with disturbance intensity from overstorey residual strips, to understorey residual strips, to skid trails.

Discussion

Comparison of pre-harvest and post-harvest forest cover types

Clearcutting deciduous and coniferous forests resulted in a greater change to the understorey plant community compared with an understorey protection harvesting strategy. Previous studies from the boreal forest (Rees and Juday 2002; Roberts and Zhu 2002; Frey *et al.* 2003), the

Pacific Northwest (Halpern *et al.*, 1999), northern California (Battles *et al.* 2001), and Scandinavia (Jalonen and Vanha-Majamaa 2001) have reported a link between the intensity of the disturbance (clearcutting, site preparation, herbicide application, *etc.*) and the magnitude of change to the plant community.

Clearcutting coniferous forests caused a greater change to plant communities than clearcutting deciduous forests. Furthermore, clearcutting coniferous stands produced a more homogeneous plant community, whereas, clearcutting deciduous stands increased plant community variation. Previous studies have indicated that the response of the plant community to harvest depends on community composition before harvest, and the resiliency of that plant community to microclimatic change (Halpern and Spies 1995; De Grandpré and Bergeron 1997; Roberts and Zhu 2002).

Deciduous forest plant communities are highly competitive, species rich, and more resilient to microclimatic change compared to coniferous forests. After harvest, the deciduous forest plant community was dominated by a few species that responded with vigorous growth. Microsite variation, and its influence on plant species competitive interactions resulted in increased plant community variation (Ehnes and Shay 1995; Johnston and Elliot 1996; Peltzer *et al.* 2000). In contrast, the vascular plant community in coniferous forests was relatively species poor, and less dominant than the nonvascular plant vegetation. After clearcutting, the plant community responded slowly to the altered microclimate due to the lack of vigorous, competitive herbaceous species (Bradbury 2004). Furthermore, plant communities in coniferous forests were distinct from mixedwood and deciduous forests, and clearcutting these coniferous forests produced plant communities that were even more dissimilar. This supports the theory that clearcutting coniferous forests had a greater influence on the vascular plant community than clearcutting deciduous forests.

The plant community in mixedwood forests changed the least (relative to deciduous and coniferous forests) after understorey protection harvesting. The extent to which microclimate changes with different retention levels influences the magnitude of change to the plant community (North *et al.* 1996; Halpern *et al.* 1999; Thomas *et al.* 1999; Vanha-Majamaa and Jalonen 2001). Different levels of partial cutting in boreal spruce forests in Finland resulted in a greater change in post-harvest understorey plant communities with decreasing residual retention (Vanha-Majamaa and Jalonen 2001). Harvested stands with 35% residual retention, or greater, showed few changes relative to the unharvested control plant community; lower levels of retention caused changes to the plant community. Similar trends were observed here, with 30% of canopy stems retained in mixedwood understorey cutblocks. These results were likely driven by the microclimatic conditions created after mixedwood understorey protection harvest and the resiliency of the plant community. While it is true that removal of 70% of the deciduous canopy, and roughly 40% of coniferous stems, increased light availability (Prévost and Pothier 2003), the magnitude of this change did little to alter the overall composition of mixedwood plant communities after harvest.

Partial harvesting, and understorey protection harvesting, provides silivicultural alternatives that leave abundant residuals on a managed landbase. Abundant residuals in cutblocks are expected to create old-growth characteristics as cutblocks age, and thus, may provide habitat for old-growth dependent species later in rotation (Meier *et al.* 1995; Roberts and Gilliam 1995; Hartley 2002).

Comparison of mixedwood stands and understorey protection cutblock habitat types

Plant communities in mixedwood forests, and in understorey protection cutblocks, exhibited regional variation. At the Grande Prairie study area, mixedwood stands had a species-saturated, and highly competitive plant community. At the Manning study area, each mixedwood stand had a lower representation of all plant species capable of existing in mixedwood forests. Variation in plant communities at the Manning

study area resulted from individual stands having different plant species assemblages. Variation in plant communities at the Grande Prairie study area resulted from competitive interactions between species producing different individual species cover values. Other studies of plant community response to understorey protection harvesting in northwest and central Alberta have reported regional variation (Mourelle *et al.* 2002). Mourelle *et al.* (2002) reported an increase in species richness after understorey protection harvesting in 9 of 17 stands examined (Navratil *et al*. 1994).

After harvest at the Grande Prairie study area, the plant community along the understorey and overstorey residual strips responded by maintaining pre-harvest cover levels, but this cover was dominated by fewer species. In mixedwood stands with a highly competitive and species-saturated plant community, the increased in available light after harvest, and the absence of an increase in cover, suggests that light availability did not limit plant growth.

At the Manning study area, mixedwood stands had lower representation of all plant species capable of existing in mixedwood forests. After harvest, increased light levels along the understorey residual strips resulted in a substantial increase in vigour (*i.e.*, cover) despite a further decrease in species richness. Unlike the Grande Prairie study area, the vigorous response to harvesting at the Manning study area was likely due to increased light availability. Pre-harvest mixedwood stands in the Manning study area had a higher density of coniferous stems compared to pre-harvest mixedwood stands in the Grande Prairie study area (Chapter 3), and this would have resulted in lower light availability at the forest floor (Messier *et al.* 1998; Prévost and Pothier 2003). The plant community growing under the lower light conditions would have favoured shade tolerant species. At the Manning study area, harvesting removed the limitations due to light and forest generalist species responded.

Plant communities in both study areas had a similar response along skid trails. In both regions, a few species dominated and responded vigorously by increasing plant cover. The high intensity of disturbance removed some forest species, but those species were replaced by fast growing, high light adapted, early seral stage species and aspen suckers. These species were capable of responding to increased light along skid trails. Despite the similar plant community response, regional differences in plant communities were maintained. At the Manning study area, plant communities along skid trails had the greatest amount of variation, while at the Grande Prairie study area, plant communities along skid trails had similar variation to pre-harvest mixedwood stands. These differences were linked to differences in pre-harvest mixedwood plant communities. In particular, harvesting aggravated the differences in plant communities among pre-harvest mixedwood stands in the Manning study area.

In conclusion, understorey protection cutblocks provided environmental conditions that supported plant communities similar to pre-harvest mixedwood forests. In addition, regional variation in pre-harvest mixedwood plant communities was maintained after harvest. Within understorey protection cutblocks, environmental conditions along skid trails produced the greatest changes to vascular plant communities, although only limited differences were observed in the Grande Prairie study area. Understorey protection cutblocks had plant communities that were unlike plant communities found in both deciduous and coniferous clearcuts, and provided no habitat where clearcut conditions could be reproduced.

Management Implications and Future Research

- Plant communities in mixedwood stands exhibited regional variation.

Management of mixedwood forests should occur with regional objectives.

- Plant communities found in understorey protection cutblocks were similar to those found in pre-harvest mixedwood forests; any

regional differences were maintained after harvest.

Understorey protection harvesting resulted in increased variation in different habitat types within the cutblock. These differences were linked to the plant community found in pre-harvest mixedwood stands, and thus, were linked to regional differences.

- Understorey protection cutblocks provide a silvicultural option for leaving high densities of residuals in cutblocks.

On a managed landbase, silvicultural options for leaving high levels of residuals allows for management of stand level variation. This has implications for biodiversity objectives. However, understorey protection strategies provide high retention cutblocks for mixedwood stands but not for deciduous or coniferous stands. High retention cutblocks from these forest cover types must be considered independently.

Acknowledgements

I am grateful to our technical staff for their hard work in the field with data collection. Technicians over the course of the study included Gavin Berg, Cris Gray, Sharon Kendall, Dave McKinnon, Luke Nolan, Len Peleshok, Dee Ryerson, Dan Sturgess, Kelly Sturgess and Lindsay Tomyn. Phil Lee, Samantha Song, Jason Fisher and Lisa Wilkinson provided valuable insight to study design and analysis. Phil Lee, J.P. Bielech, Fred Radersma and Lisa Wilkinson provided advice on improving this chapter.

Literature Cited

Battles, J.J., Shlisky, A.J., Barrett, R.H., Heald, R.C. and Allen-Diaz, B.H. 2001. The effects of forest management on plant species diversity in a Sierran conifer forest. For. Ecol. Manage. 146:211-222.

Bradbury, S. 2002. Response of understorey vascular plants to wildfire and harvesting. In: Ecological basis for stand management: a synthesis of ecological responses to wildfire and harvesting (Edited by S. Song). Alberta Research Council, Vegreville, AB.

Bradbury, S. 2004. Understorey plant communities in boreal cutblocks with different sizes and numbers of residual patches. Can. J. For. Res. *In press*.

Crites, S. 1999. A comparison of early successional understorey plant communities following fire and harvest. In: Fire and harvest residual project. Alberta Research Council, Vegreville, AB.

De Grandpré, L., and Bergeron, Y. 1997. Diversity and stability of understorey communities following disturbance in the southern boreal forest. J. Ecology. 85: 777-784.

Ehnes, J.W., and Shay, J.M. 1995. Natural recovery of logged and burned plant communities in the Lake Winnipeg East Forest Section, Manitoba. Canada-Manitoba Partnership Agreement in Forestry. Winnipeg, MB.

Frey, B.R., Lieffers, V.J., Munson, A.D. and Blenis, P.V. 2003. The influence of partial harvesting and forest floor disturbance on nutrient availability and understorey vegetation in boreal mixedwoods. Can. J. For. Res. 33:1180-1188.

Halpern, C.B. and Spies, T.A. 1995. Plant species diversity in natural and managed forests of the Pacific Northwest. Ecol. Appl. 5: 913-934.

Halpern, C.B., Evans, S.A., Nelson, C.R., McKenzie, D., Liguori, D.A., Hibbs, D.E. and Halaj, M.G. 1999. Response of forest vegetation to varying levels and patterns of green-tree retention: an overview of a long-term experiment. Northwest Sci. 73:27-44.

Hartley, M.J. 2002. Rationale and methods for conserving biodiversity in plantation forests. For. Ecol. Manage. 155:81-95.

Jalonen, J. and Vanha-Majamaa, I. 2001. Immediate effects of four different felling methods on mature boreal spruce forest understorey vegetation in southern Finland. For. Ecol. Manage. 146:25-34.

Johnston, M.H., and Elliot, J.A. 1996. Impacts of logging and wildfire on an upland black spruce community in northwestern Ontario. Env. Mon. Assess. 39:283-297.

Meier, A.J., Bratton, S.P. and Duffy, D.C. 1995. Possible ecological mechanisms for loss of vernal-herb diversity in logged eastern deciduous forests. Ecol. Appl. 5:935-946.

Messier, C., Parent, S., and Bergeron, Y. 1998. Effect of overstorey and understorey vegetation on the understorey light environment in mixed boreal forests. J. Veg. Sci. 9:511-520.

Moss, E.H. 1994. Flora of Alberta. A manual of flowering plants, conifers, ferns and fern allies found growing without cultivation in the province of Alberta, Canada. 3rd Edition. Revised by J.G. Packer. University of Toronto Press. Toronto, ON.

Mourelle, C., Macdonald, E., Dankert, B., and Major, M. 2002. Stand structure and plant diversity under two forest management practices: salvage thinning and understorey protection in the Canadian western boreal. In: Proceedings from Sustainable Forest Management Network Conference "Advances in forest management: from knowledge to practice", Edmonton 2002. pp 154-159.

Navratil, S., Brace, L.G., Sauder, E.A., and Lux, S. 1994. Silvicultural and harvesting options to favor immature white spruce and aspen regeneration in boreal mixedwoods. Nat. Resour. Can., Can. For. Serv., Northwest Reg., North. For. Cent., Edmonton, Alberta. Inf. Rep. NOR-X-327.

North, M., Chen, J., Smith, G., Krakowiak, L, and Franklin, J. 1996. Initial response of understorey plant diversity and overstorey tree diameter growth to a green tree retention harvest. Northwest Sci. 70:24-35.

Peltzer, D.A., Blast, M.L., Wilson, S.D., and Gerry, A.K. 2000. Plant diversity and tree responses following contrasting disturbances in boreal forests. For. Ecol. Manage. 127:191-203.

Peterson, E.B. and Peterson, N.M. 1992. Ecology, management, and use of aspen and balsam poplar in the prairie provinces, Canada. For. Can., Northwest Reg., North. For. Cent., Edmonton, Alberta. Spec. Rep. 1.

Prévost, M. and Pothier, D. 2003. Partial cuts in a trembling aspen-conifer stand: effects on microenvironmental conditions and regeneration dynamics. Can. J. For. Res. 33: 1-15.

Rees, D.C. and Juday, G.P. 2002. Plant species diversity on logged versus burned sites in central Alaska. For. Ecol. Manage. 155:291-302.

Roberts, M.R. and Gilliam, F.S. 1995. Patterns and mechanisms of plant diversity in forested ecosystems: implications for forest management. 5:969-977.

Roberts, M.R. and Zhu, L. 2002. Early response of the herbaceous layer to harvesting in a mixed coniferous-deciduous forest in New Brunswick, Canada. For. Ecol. Manage. 155:17-31.

Rowe, J.S. 1956. Uses of undergrowth plant species in forestry. Ecology. 37:461-473.

SAS. 2000. JMP Statistics and Graphics Guide, Version 3.2.1, SAS Institute, Cary, NC.

ter Braak, C.J.F. and Smilauer, P. 1998. CANOCO: a fortran program for canonical community ordination by (partial), (detrended), (canonical), correspondence analysis, principle components analysis, and redundancy analysis, version 4 for Windows. Microcomputer Power, Ithaca, NY.

Thomas, S.C., Halpern, C.B., Falk, D.A., Liguori, D.A., Austin, K.A. 1999. Plant diversity in managed forests: understorey responses to thinning and fertilization. Ecol. Appl. 9:864-879.

Vanha-Majamaa, I., and Jalonen, J. 2001. Green tree retention in Fennoscandian forestry. Scand. J. For. Res. Suppl. 3:79-90.

Table 6.1. Mean percent cover of recorded plant species, plant group species richness, total species richness per treatment (Beta diversity), average species richness, and Shannon diversity of understorey vascular plants recorded in the Grande Prairie and Manning study areas before and after harvest. Plant names followed by sp. and grasses were not identified to species. Understorey plant species included all forbs regardless of height, and trees and shrubs that were less than 0.5 m tall.

	Grande Prairie study area				**Manning study area**			
	Pre-harvest deciduous forests	Post-harvest deciduous clearcuts	Pre-harvest mixedwood forests	Post-harvest mixedwood understorey protection cutblocks	Pre-harvest mixedwood forests	Post-harvest mixedwood understorey protection cutblocks	Pre-harvest coniferous forests	Post-harvest coniferous clearcuts
Forb, grass, fern species								
Achillea millefolium	0.01	0.00	0.13	0.08	0.06	0.02	0.01	0.00
Actaea rubra	0.00	0.15	0.18	0.17	0.24	0.16	0.04	0.00
Adoxa moschatellina	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00
Angelica genuflexa	0.36	0.56	0.00	0.03	0.00	0.00	0.00	0.00
Aquilegia canadensis	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00
Aralia nudicaulis	3.50	1.37	3.07	1.63	0.00	0.00	0.00	0.00
Arenaria lateriflora	0.05	0.06	0.01	0.00	0.00	0.00	0.00	0.00
Arnica cordifolia	0.00	0.01	0.26	0.31	0.00	0.00	0.06	0.00
Aster ciliolatus	0.98	1.73	1.74	2.69	0.90	2.29	0.01	0.07
Aster conspicuous	1.83	2.26	0.20	0.17	0.00	0.11	0.00	0.00
Aster puniceus	0.03	0.21	0.06	0.13	0.05	0.07	0.00	0.00
Aster sp.	0.00	0.00	0.02	0.00	0.00	0.03	0.00	0.00
Astragalus americanus	0.00	0.00	0.00	0.00	0.00	0.14	0.00	0.01
Carex pensylvanica	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Castilleja miniata	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00
Chrysanthemum leucanthemum	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00
Chrysoplenium tetrandrum	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00
Circaea alpina	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Corallorhiza striata	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00
Corallorhiza trifida	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00
Disporum trachycarpum	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Dracocephalum parviflorum	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.15
Epilobium angustifolium	2.58	2.47	1.54	0.90	0.98	0.93	3.65	6.28
Epilobium ciliatum	0.00	0.44	0.00	0.00	0.00	0.08	0.00	0.45
Epilobium glandulosum	0.00	0.00	0.00	0.01	0.00	0.09	0.00	0.60
Equisetum arvense	0.25	0.29	0.04	0.00	0.00	0.06	1.13	1.00
Equisetum hyemale	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00
Equisetum pratense	0.08	0.01	0.01	0.00	0.00	0.00	0.00	0.00

	Grande Prairie study area				Manning study area			
	Pre-harvest deciduous forests	Post-harvest deciduous clearcuts	Pre-harvest mixedwood forests	Post-harvest mixedwood understorey protection cutblocks	Pre-harvest mixedwood forests	Post-harvest mixedwood understorey protection cutblocks	Pre-harvest coniferous forests	Post-harvest coniferous clearcuts
Equisetum scirpoides	0.03	0.00	0.01	0.02	0.00	0.00	0.00	0.00
Equisetum sylvaticum	0.00	0.00	0.02	0.45	0.01	0.00	0.76	0.53
Erigeron philadelphicus	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Fragaria vesca	0.01	0.68	0.01	0.03	0.00	0.06	0.00	0.00
Fragaria virginiana	1.51	2.04	2.40	2.79	1.61	2.72	0.23	0.13
Galium boreale	1.06	1.59	1.06	1.28	0.52	0.79	0.12	0.04
Galium triflorum	0.54	1.10	0.18	0.22	0.02	0.00	0.00	0.00
Geocaulon lividum	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00
Geranium bicknellii	0.00	0.01	0.00	0.01	0.00	0.10	0.00	0.24
Geum aleppicum	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Geum macrophyllum	0.04	0.05	0.00	0.03	0.00	0.00	0.00	0.00
Geum rivale	0.00	0.43	0.00	0.08	0.00	0.00	0.00	0.00
Goodyera repens	0.00	0.00	0.00	0.00	0.01	0.00	0.01	0.00
Grass spp.	2.24	2.61	1.21	0.92	1.57	1.91	1.75	2.41
Gymnocarpium dryopteris	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.01
Habanaria obtusata	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00
Habanaria orbiculata	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00
Halenia deflexa	0.00	0.13	0.02	0.15	0.00	0.00	0.00	0.01
Heracleum lanatum	0.00	0.21	0.15	0.28	0.00	0.00	0.00	0.00
Hieracium umbellatum	0.00	0.01	0.00	0.01	0.00	0.01	0.00	0.00
Impatiens capensis	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00
Lathyrus ochroleucus	3.12	2.68	2.16	3.07	0.49	0.34	0.33	0.05
Lilium philadelphicum	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Listera cordata	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00
Lycopodium annotinum	0.00	0.00	0.09	0.03	0.00	0.00	0.00	0.00
Lycopodium complanatum	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00
Maianthemum canadense	2.32	1.33	1.01	0.69	0.18	0.42	0.23	0.15
Matteuccia struthiopteris	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00
Mertensia paniculata	5.09	5.96	4.62	3.57	1.46	2.48	0.75	1.43
Mitella nuda	1.66	0.83	1.41	2.09	0.69	0.54	0.77	0.37
Moehringia lateriflora	0.00	0.00	0.00	0.00	0.01	0.00	0.01	0.00
Moneses uniflora	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.00
Osmorhiza depauperata	0.04	0.07	0.03	0.06	0.00	0.00	0.00	0.00
Petasites palmatus	1.26	1.10	2.25	2.62	0.57	0.94	2.06	1.65

	Grande Prairie study area				Manning study area			
	Pre-harvest deciduous forests	Post-harvest deciduous clearcuts	Pre-harvest mixedwood forests	Post-harvest mixedwood understorey protection cutblocks	Pre-harvest mixedwood forests	Post-harvest mixedwood understorey protection cutblocks	Pre-harvest coniferous forests	Post-harvest coniferous clearcuts
Petasites vitifolius	0.00	0.00	0.00	0.00	0.00	0.00	0.12	0.00
Potentilla norvegica	0.00	0.00	0.00	0.00	0.00	0.06	0.00	0.01
Prunella vulgaris	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Pyrola asarifolia	0.34	0.17	0.49	0.72	0.18	0.14	0.10	0.00
Pyrola secunda	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.00
Ranunculus sceleratus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07
Smilacina racemosa	0.00	0.10	0.00	0.08	0.00	0.00	0.00	0.00
Smilacina stellata	0.17	0.32	0.00	0.02	0.00	0.00	0.00	0.00
Smilacina trifolia	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Solidago canadensis	0.00	0.11	0.07	0.00	0.00	0.00	0.00	0.00
Solidago gigantea	0.39	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sonchus arvensis	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.08
Sonchus oleraceus	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00
Stellaria calycantha	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00
Stellaria longifolia	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Streptopus streptopoides	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00
Taraxacum officinale	0.04	0.02	0.00	0.02	0.00	0.29	0.04	0.00
Thalictrum venulosum	0.12	0.11	0.00	0.00	0.00	0.00	0.00	0.00
Trientalis borealis	0.00	0.00	0.00	0.00	0.08	0.08	0.00	0.19
Trifolium hybridum	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.00
Vicia americana	0.41	0.47	0.18	0.43	0.01	0.04	0.00	0.00
Viola adunca	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00
Viola canadensis	0.22	0.36	0.00	0.19	0.10	0.00	0.05	0.00
Viola renifolia	0.74	0.22	0.76	0.54	0.20	0.33	0.30	0.27
Forb, grass, fern species richness	**41**	**45**	**33**	**42**	**23**	**34**	**26**	**24**
Low shrub species								
Arctostaphylos uva-ursi	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.00
Cornus canadensis	10.31	6.03	9.74	8.14	5.51	6.62	5.15	1.48
Ledum groenlandicum	0.18	0.14	0.12	0.02	0.00	0.13	0.36	0.21
Linnaea borealis	2.23	0.58	2.90	2.24	1.38	1.70	3.05	0.99
Lonicera dioca	1.34	0.56	0.23	0.21	0.10	0.24	0.00	0.04
Lonicera involucrata	3.16	2.77	3.24	2.31	0.04	0.11	0.00	0.00

	Grande Prairie study area				Manning study area			
	Pre-harvest deciduous forests	Post-harvest deciduous clearcuts	Pre-harvest mixedwood forests	Post-harvest mixedwood understorey protection cutblocks	Pre-harvest mixedwood forests	Post-harvest mixedwood understorey protection cutblocks	Pre-harvest coniferous forests	Post-harvest coniferous clearcuts
Ribes americanus	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00
Ribes glandulosum	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00
Ribes hudsonianum	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00
Ribes lacustre	0.00	0.00	0.03	0.04	0.00	0.00	0.00	0.00
Ribes oxyacanthoides	0.64	0.62	0.12	0.30	0.01	0.00	0.13	0.00
Ribes triste	1.15	0.55	0.22	0.53	0.63	0.07	0.32	0.08
Rosa acicularis	4.33	4.31	5.31	3.92	3.42	5.69	3.93	2.99
Rubus acaulis	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08
Rubus chamaemorus	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00
Rubus idaeus	0.93	1.54	0.08	0.35	0.00	0.00	0.00	0.01
Rubus pubescens	6.12	6.19	5.25	4.24	1.26	2.14	2.17	0.89
Shepherdia canadensis	0.29	0.06	0.76	0.52	0.21	1.02	0.27	0.01
Spiraea alba	2.37	0.91	0.97	0.91	0.00	0.00	0.00	0.00
Symphoricarpos albus	1.60	0.71	0.54	0.45	0.12	0.29	0.00	0.00
Vaccinium caespitosum	0.00	0.08	0.68	0.72	0.00	0.09	0.12	0.00
Vaccinium myrtilloides	0.45	0.96	0.10	0.06	0.00	0.00	0.06	0.01
Vaccinium vitis-idaea	0.00	0.01	0.02	0.02	0.00	0.06	1.92	0.08
Viburnum edule	1.47	0.93	1.84	1.79	1.65	2.20	1.73	0.48
Low shrub species richness	**15**	**17**	**18**	**19**	**11**	**13**	**16**	**13**
Tall shrub species (<0.5 m)								
Alnus tenuifolia	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Amelanchier alnifolia	0.39	0.64	0.10	0.11	0.01	0.00	0.00	0.00
Cornus stolonifera	0.20	0.20	0.18	0.18	0.00	0.00	0.00	0.00
Corylus cornuta	0.21	0.71	0.00	0.00	0.00	0.00	0.00	0.00
Prunus pensylvanica	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.00
Salix spp.	0.42	0.33	0.08	0.10	0.00	0.04	0.13	0.00
Tall shrub species richness	**5**	**4**	**4**	**3**	**1**	**1**	**1**	**0**
Tree species (<0.5 m)								
Betula papyrifera	0.04	0.03	0.01	0.02	0.00	0.00	0.00	0.00
Picea glauca	0.00	0.01	0.10	0.03	0.07	0.12	0.08	0.07
Populus balsamifera	0.04	0.20	0.00	0.17	0.00	0.00	0.04	0.00
Populus tremuloides	0.07	2.28	0.05	1.16	0.00	1.87	0.05	0.28

	Grande Prairie study area				Manning study area			
	Pre-harvest deciduous forests	Post-harvest deciduous clearcuts	Pre-harvest mixedwood forests	Post-harvest mixedwood understorey protection cutblocks	Pre-harvest mixedwood forests	Post-harvest mixedwood understorey protection cutblocks	Pre-harvest coniferous forests	Post-harvest coniferous clearcuts
Tree species richness	**3**	**4**	**3**	**4**	**1**	**2**	**3**	**2**
Plant species richness (Beta diversity)	**64**	**70**	**58**	**68**	**36**	**50**	**46**	**39**
Average plant species richness[1]	**21.9[a] (0.6)**	**20.6 [a] (0.6)**	**21.5 [a] (0.4)**	**25.8 [b] (0.4)**	**15.7 [a] (0.5)**	**18.5 [b] (0.8)**	**14.1 [a] (0.7)**	**13.1 [a] (0.9)**
Shannon diversity[2]	**2.4[a] (0.2)**	**2.2 [a] (0.1)**	**2.0 [a] (0.1)**	**2.0 [a] (0.01)**	**1.0 [a] (0.1)**	**1.4 [b] (0.1)**	**1.2 [a] (0.2)**	**1.0 [a] (0.1)**

[1] Mean (standard error) species richness per 1-ha site; Grande Prairie and Manning study area treatments analyzed separately; treatments followed by the same letter (within a study area) are not significantly different at $p < 0.05$.

[2] Mean (standard error) Shannon diversity per 1-ha site; Grande Prairie and Manning study area treatments analyzed separately; treatments followed by the same letter (within a study area) are not significantly different at $p < 0.05$.

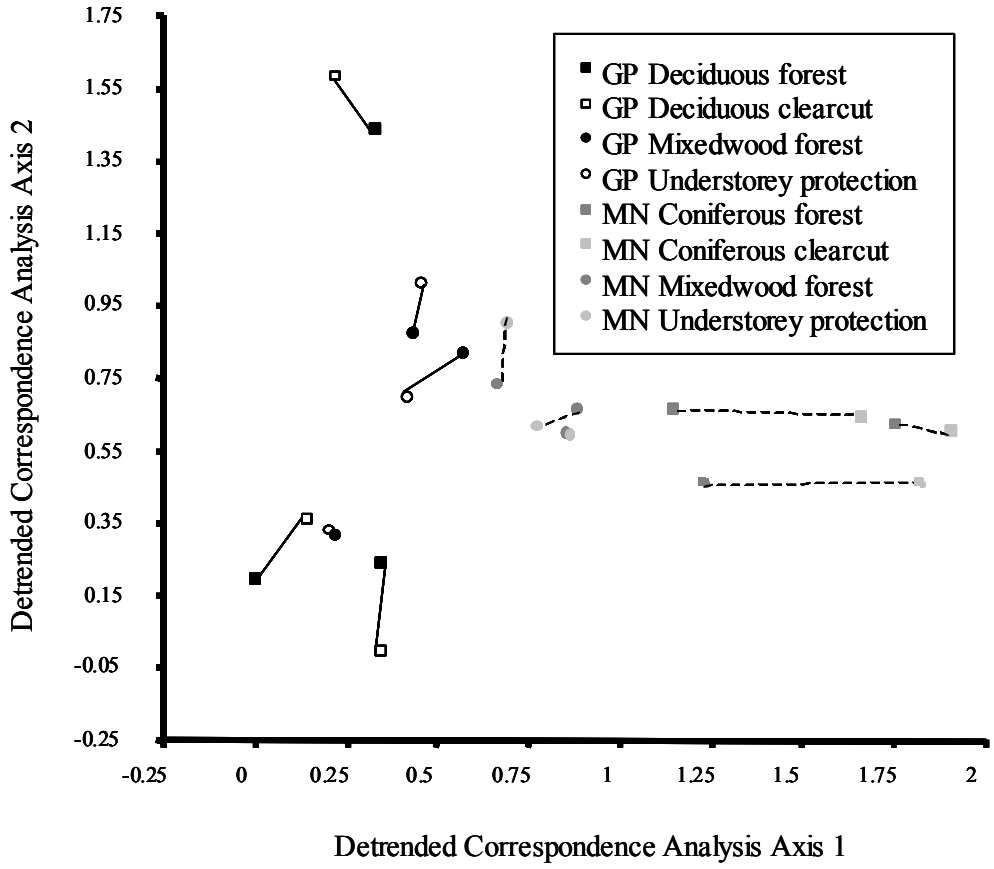


Figure 6.1. Detrended correspondence analysis of understorey vegetation in pre-harvest and post-harvest stands in the Grande Prairie (GP) and Manning (MN) study areas. Lines connect a pre-harvest stand with the same stand after harvest; the length of the connecting line represents distance in ordination space that a stand has moved due to changes in the understorey plant community resulting from the harvesting activity. Mean distance within the deciduous, mixedwood and coniferous stand types represents the magnitude of disturbance to the understorey plant community relative to harvesting type (clearcutting versus understorey protection harvest).

Table 6.2. Mean orthogonal distances (standard error) in DCA ordination space between pre-harvest stands and the same stand after harvest.

	Grande Prairie study area		**Manning study area**	
	Deciduous clearcut	Mixedwood understorey protection cutblock	Coniferous clearcut	Mixedwood understorey protection cutblock
Distance[1]	0.22 (0.02)	0.11 (0.06)	0.42 (0.13)	0.10 (0.04)

[1] Three distance values for each forest type were derived as follows: plot stand locations in ordination space (Figure 6.1); determine distance in ordination space between stand (*e.g.*, DC1) before and after harvest; repeat for remaining stands in each forest type and determine mean.

Table 6.3. Mean (standard error) understorey vascular plant cover, species richness and Shannon diversity per 1-ha site in the Grande Prairie and Manning study areas in mixedwood forest stands and three habitat types found in understorey protection cutblocks (*i.e.*, understorey protection cutblock residual overstorey strips, understorey protection cutblock residual understorey strips, and understorey protection cutblock skid trails). Treatments followed by the same letter are not significantly different at $p < 0.05$.

	Grande Prairie study area					
	Pre-harvest mixedwood forest	Understorey protection residual overstorey strips	Understorey protection residual understorey strips	Understorey protection skid trails	F statistic	*p* value
Plant cover	38.5^{ab} (2.2)	37.6^{ab} (2.2)	33.3^{a} (1.6)	43.6^{b} (3.7)	2.8	<0.05
Species richness	21.5^{a} (0.4)	17.2^{b} (0.4)	17.1^{b} (0.5)	16.8^{b} (0.6)	20.9	<0.0001
Shannon diversity	1.8^{a} (0.1)	1.7^{a} (0.1)	1.6^{a} (0.1)	1.7^{a} (0.1)	1.4	0.24

	Manning study area					
	Pre-harvest mixedwood forest	Understorey protection residual overstorey strips	Understorey protection residual understorey strips	Understorey protection skid trails	F statistic	*p* value
Plant cover	17.5^{c} (1.2)	18.0^{c} (1.6)	26.5^{b} (2.8)	39.9^{a} (4.1)	17.4	<0.0001
Species richness	15.7^{a} (0.5)	10.1^{c} (0.8)	10.6^{c} (0.7)	13.5^{b} (0.6)	18.0	<0.0001
Shannon diversity	0.9^{b} (0.1)	0.9^{b} (0.1)	1.1^{b} (0.1)	1.4^{a} (0.1)	10.6	<0.0001

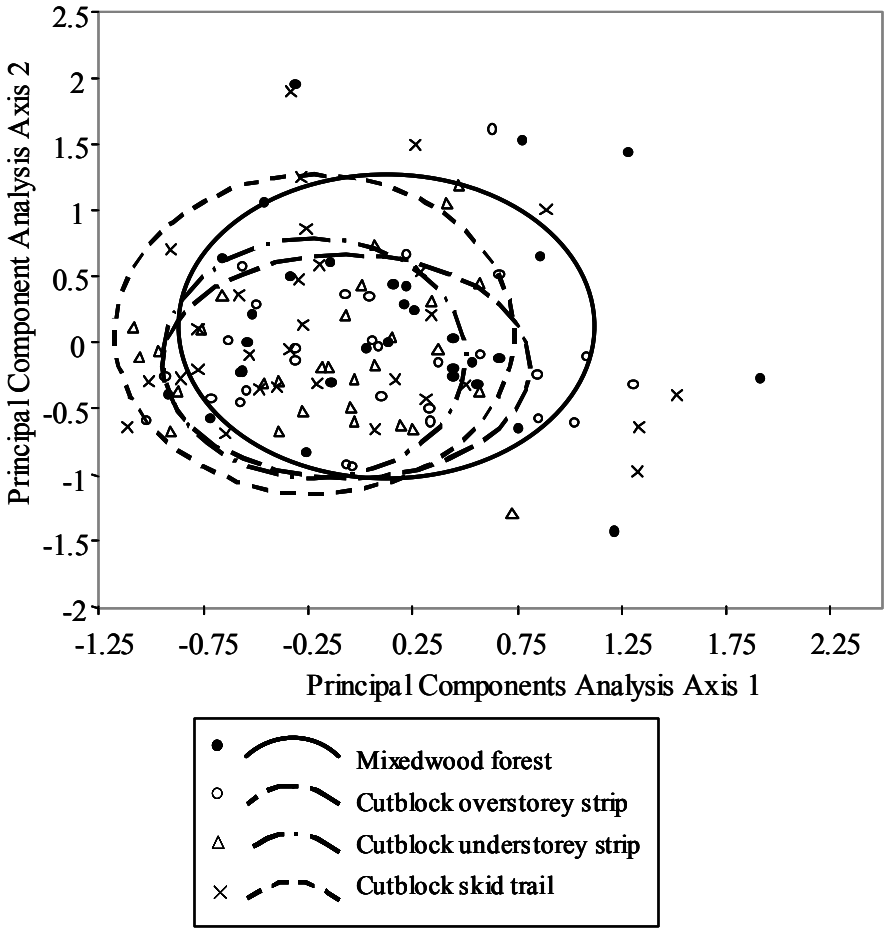


Figure 6.2. Principal components analysis of understorey vegetation in pre-harvest mixedwood stands and post-harvest understorey protection stands in the Grande Prairie study area. Sixty-seven percent confidence ellipses are shown to clarify treatment locations.

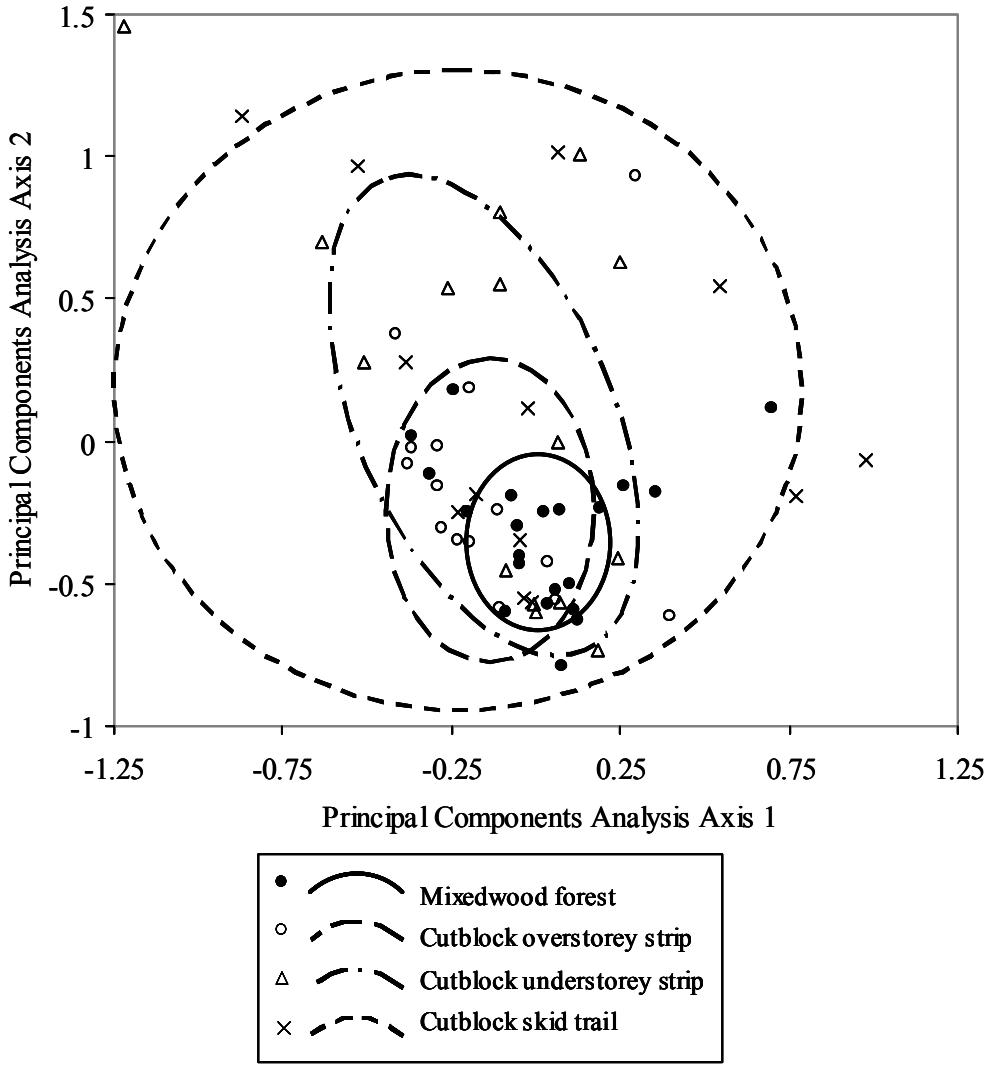


Figure 6.3. Principal components analysis of understorey vegetation in pre-harvest mixedwood stands and post-harvest understorey protection stands in the Manning study area. Sixty-seven percent confidence ellipses are shown to clarify treatment locations.

CHAPTER 7: EFFECT OF UNDERSTOREY PROTECTION ON BOREAL SONGBIRDS

Samantha J. Song

Introduction

Within the boreal forest landscape in Canada, mixedwood stands represent a unique habitat for songbird species (Pojar 1995; Song 1998; Hobson and Bayne 2000). Mixedwood stands can provide habitat for some bird species that are associated with both deciduous or coniferous stands and a number of boreal birds attain their highest densities within mixedwood stands (Hobson and Bayne 2000), particularly in older mixedwood stands that are very structurally complex (Schieck and Song 2002).

Traditional forestry has not focused on the management of mixedwood stands. Landbases are allocated based on a simple coniferous or deciduous classification. Stands are subsequently managed for single tree species and on a short rotation length that can result in an "unmixing" of the mixedwood forest as succession is truncated (Bayne and Hobson 2000).

Understorey protection is a silvicultural technique that intends to maximize the yield of deciduous and coniferous timber from mixedwood stands. Stands conducive to understorey protection are characterised by a deciduous overstorey and a coniferous understorey or sub-canopy. Candidate stands are usually 75 years or older (see Chapter 3). The practice may also provide ecological services, such as the maintenance of forest bird species in harvest blocks, but this has not been well investigated.

Forest structure, that is, the physical structure that a forest possesses from the configuration of trees, standing or downed trees, tall shrubs and other plants within it, has a strong effect on the composition and density of songbird communities found within a forest (MacArthur & MacArthur 1961; Karr 1968; Recher 1969; Willson 1974). Clearcut harvesting of mixedwood or other forest stands, by removing most of the forest structure, usually removes most of the forest birds (Schieck and Song 2002). Understorey protection removes a portion of the overstorey aspen and leaves understorey white spruce intact. (For a detailed description, see Chapter 3.) It could provide more structure and thus habitat for forest bird species than conventional clearcuts or harvesting with low levels of retention, especially in the years immediately following harvest. Although some canopy trees are retained, understorey protection presents a shift to an "open" habitat with many shrubs, as well as clearings for machine corridors and decking of logs. Species that utilise shrubby habitat with some mature trees, or younger coniferous areas, or generalist species that are very plastic in their habitat choices could benefit from the retention of understorey cover. It is not clear how forest bird species will respond to understorey protection.

This paper presents a summary of songbird responses to understorey protection in mixedwood stands, with both a spatial and temporal control and focusing on the two years immediately post-harvest. The study was conducted on forested lands in 2 locations in north-western Alberta with two forest companies, one, a user of deciduous forests and the other, a user of coniferous forests. Songbird communities were studied in these forests (either deciduous or coniferous depending on the operator) and after business-as-usual harvesting practices (*i.e.*, clearcutting with tree retention from 0-5%). Biodiversity impact of understorey protection is a little-studied technique in the western boreal forest; there is currently more focus on silvicultural effects (*e.g.,* Mixedwood Management Association 2004). Northwestern Alberta has also been subject to less study on boreal birds, particularly in mixedwood and conifer forests (but see Harrison 2002). With these factors in combination, this study aims to address an important knowledge gap.

Methods

Songbird surveys

A description of the overall study areas and experimental harvesting is presented in Chapter 2.

The study design focused on effects at the stand level and on territorial songbird species. I chose a spotmapping technique over a more rapid survey technique such as point counts because I had a small spatial scale to survey and spotmapping provides (1) stronger evidence that birds are holding territories, (2) clearer information about territory location and (3) better estimates of density (Bibby *et al.* 1992). Survey timing was designed to focus sampling effort during the breeding season of migrant species although many resident species were also recorded.

In the Grande Prairie study area, grids were 10-ha in size and centred in the stand with at least 50 m buffer from the edge. Grids were 500 m by 200 m and 2 survey transects set parallel with the length of the grid: 50 m in from the edge and 100 m apart from each other. In the Manning study area, grid size was limited by a smaller minimum stand size and here, 7 ha grids were set in a single line, 100 m by 700 m.

Grids were surveyed by slowly walking the transects and recording the species and location of singing males up to a distance of approximately 50 m on either side of the transect. Dawn surveys were conducted in fine weather (no rain and wind speed <25 km/h) between 05:00 and 10:00, during peak songbird activity. Both study areas were sampled simultaneously 6 times between late May and late June, when nesting activity is highest, and with a minimum of 3 days between visits. Route direction and observers were alternated each visit. To help define territories, we recorded additional information about songbird activity such as counter-singing, calling, aggressive encounters, nest locations, carrying nest material or food. All bird observations were recorded on pre-drawn maps of the grid and new maps were used for each observation day.

In the last week of June of each year, a playback of chickadee mobbing calls was used to increase the chance of visual observations of birds and thus sighting reproductive behaviours on the grids (Gunn *et al*. 2000). Playbacks were conducted once at 2 points in each grid, at least 400 m apart. Mobbing calls were played for 6 minutes and observations of species and activities recorded during this time and for 5 minutes afterwards. Evidence of breeding activity, *e.g*., presence of pairs or young, copulatory activity, carrying of nesting material, food or faecal sacs, was used as an additional measure to help confirm territory presence of species on spotmapping grids.

Seven observers worked on this study over the 3 years in Grande Prairie and 4 years in Manning. In Grande Prairie, 2 observers were constant for all 3 years and 2 observers were constant for 2 years. In Manning, 1 observer was constant for all 4 years, 1 observer was constant for 3 years and 3 observers were constant for 2 years.

Individual territory maps of each species were compiled from survey maps so that there was one species per map per grid. Territories were defined using clustered records of singing males where a cluster had at least 2 records 10 days apart (Bibby *et al*. 1992). Territories that lay over a grid boundary and had equal registrations in and out of the grid were counted as half territories but no further subdivisions of territories took place. Within Manning sites, having a single 100 m wide transect strongly limited the rigour of delimiting territory boundaries. Reported results of territory densities should be interpreted as relative rather than absolute estimates between stand types and treatments within the Manning location.

Statistical analysis

All analyses were conducted separately for Grande Prairie and Manning because of differences in grid size and year of harvesting (between Year 1 and 2 for Grande Prairie and between Year 2 and 3 for Manning).

The effect of treatment on the total density and species richness of songbird communities was calculated using a repeated measures analysis of variance (RMANOVA) with contrasts to compare effects of treatment and treatment by year interaction. All data were tested for normality and sphericity to ensure that assumptions of the RMANOVA were not violated. Data were log (x+1)-transformed or square-root transformed as appropriate. Means are reported with standard error.

Songbird community composition for each site, using density of individual songbird species, was compared between stand types and treatments using ordination analysis in Canoco for Windows 4.5 (ter Braak and Smilauer 2002). Because there was a known environmental gradient to the data, I used detrended correspondence analysis (DCA) to determine how the variance within communities at each site was affected by stand type and treatment. Rare species were downweighted. A DCA was performed for the entire data set in both Grande Prairie and Manning but results for comparisons of treatment effects were graphed separately to facilitate interpretation.

To test for differences between songbird community composition between specific treatments (intact vs. clearcut, intact mixedwood vs. understorey protection), individual songbird densities were entered into a canonical correspondence analysis against a dummy variable representing treatment types. This provided a relative 'weighting' or association of a songbird species with one treatment relative to another. To facilitate accurate interpretation, rare species were downweighted and as a further measure, species with only 1 territory in the compared treatments were removed from the analysis. Songbird communities were graphed relative to centroids of the treatments. The effect of the treatment on songbird community pattern was tested against a randomized distribution of relationships between species and environmental variables using a Monte-Carlo test (McCune and Grace 2002). Comparisons were based on the first axis and tests were performed with 499 randomizations (permutations).

Results

Density and species richness of songbird communities

In both Grande Prairie & Manning, density and species richness of songbird communities varied depending on the stand type and treatment and the year. There was a significant interaction between stand treatment and year for both density (birds/ha) and species richness (# of species) of songbird communities (Table 7.1). A better understanding is achieved by looking at the contrast of harvested and unharvested stands within a stand type and over the years.

Table 7.1 Comparison of effect of year and stand treatment on density and species richness of songbird communities in Grande Prairie and in Manning.

Factor	P (Density)	P (Species Richness)
Grande Prairie		
Stand treatment	0.003	0.019
Year	0.005	0.223
Stand treatment x year	0.004	0.014
Manning		
Stand treatment	0.002	0.011
Year	0.004	0.001
Stand treatment x year	<0.001	<0.001

In Grande Prairie, deciduous retention (DR) stands had significantly higher density of birds than mixedwood retention (MR) stands ($\bar{x}$ (DR) = 5.6 ± 0.4/ha vs. $\bar{x}$ (MR) = 4.3 ± 0.4/ha; p=0.047). Richness was not significantly different between these two stand types (p=0.866). In Manning, density of birds was not different between coniferous retention (CR) and mixedwood reserve stands (p=0.314); however, CR stands were significantly richer than MR stands ($\bar{x}$ (CR) = 13.6 ± 0.8 species/grid vs. $\bar{x}$ (MR) = 8.8 ± 0.8 species/grid; p=0.003).

In Grande Prairie, songbird community density and richness was significantly decreased after clearcut harvesting in the deciduous stands (p(density) = 0.001; p(richness) = 0.008; Figure 7.1, 7.2). There was no effect of understorey protection on density or richness relative to intact mixedwood stands (p(density) = 0.565; p(richness) = 0.732; Figures 7.1 and 7.3).

In Manning, songbird community density and richness was also significantly decreased after clearcut harvesting in conifer stands (p(density) =<0.001; p(richness) = 0.017; Figure 7.4 and 7.5). However, there was a significant difference between the 2 years of data before harvesting in the coniferous clearcut stands, where both density and richness was significantly lower in the first year (p(density) = 0.012; p(richness)=0.005). Patterns of density and species richness in mixedwood reserve and mixedwood understorey protection stands were not significantly different (p(density) = 1.00; p(richness) = 1.00; Figures 7.4 and 7.6).

Songbird community composition pre- and post-harvest

In Grande Prairie, songbird community composition, based on density of individual species, remained similar between all years in stands that were unharvested, as demonstrated by strongly clustered DCA scores in both graphs of deciduous reserve and mixedwood reserve sites (Figure 7.7). In both deciduous clearcuts and understorey protection stands, the harvesting treatment changed the community from the pre-harvest state. This turnover is demonstrated in Figure 7.7 where site scores for pre- and post-harvest states do not overlap, for either mixedwood understorey protection or deciduous clearcut sites.

In the 2 years post-harvest in the deciduous clearcut stands, community composition differed between years, as demonstrated by the lack of overlap between sites measured in both post-harvest years. In the post-harvest understorey protection stands, community composition was similar in both post-harvest years, as demonstrated by the clustering of sites in both those years.

In Manning, similar results were found (Figure 7.8). Songbird community composition was similar between years in both conifer and mixedwood reserve stands. With harvesting treatments, both conifer clearcuts and understorey protection changed the community composition from the pre-harvest state. Here again, community composition changes in the two years post-harvest in the coniferous clearcut while staying similar between years in the mixedwood understorey protection stands.

Variation explained by the first 2 axes of the DCA was 37% in Grande Prairie and 24% in Manning. There were distinct songbird communities composing stands before and after clearcutting, in both Grande Prairie and Manning. The differences in these communities were confirmed by a Monte-Carlo test after running the canonical correspondence analysis (Grande Prairie: p=0.002; Manning: p=0.002). The turnover of species is explained by the loss of forest species in clearcut stands, the appearance of open country species such as Tree Swallows and Lincoln's Sparrows, shorebirds such as Solitary Sandpipers, Killdeer and Common Snipe, and the increase of generalist species such as Dark-eyed Juncos and White-throated Sparrows (Figure 7.9 and 7.10). Many forest species were excluded from the clearcut sites, including species of ecological concern such as Brown Creeper, Black-throated Green Warbler, Bay-breasted Warbler, Canada Warbler, Cape May Warbler and Western Tanager, among others.

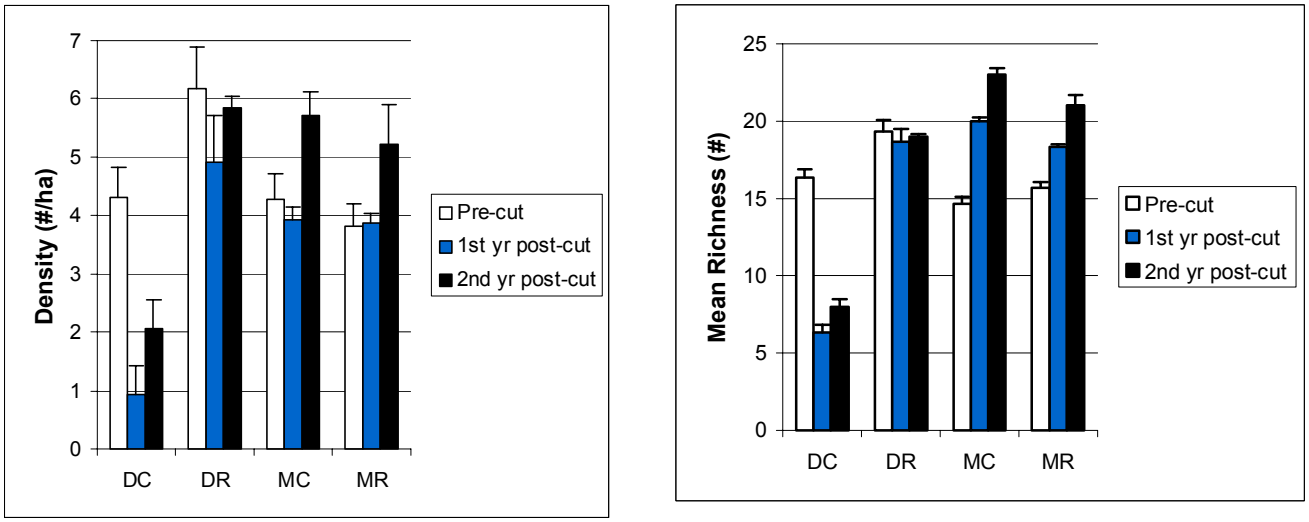


Figure 7.1. Mean density (birds/ha) and richness (# species) of songbird communities in Grande Prairie. Treatments are deciduous clearcut (DC), deciduous retention (DR), mixedwood understorey protection (MC), and mixedwood retention (MR).

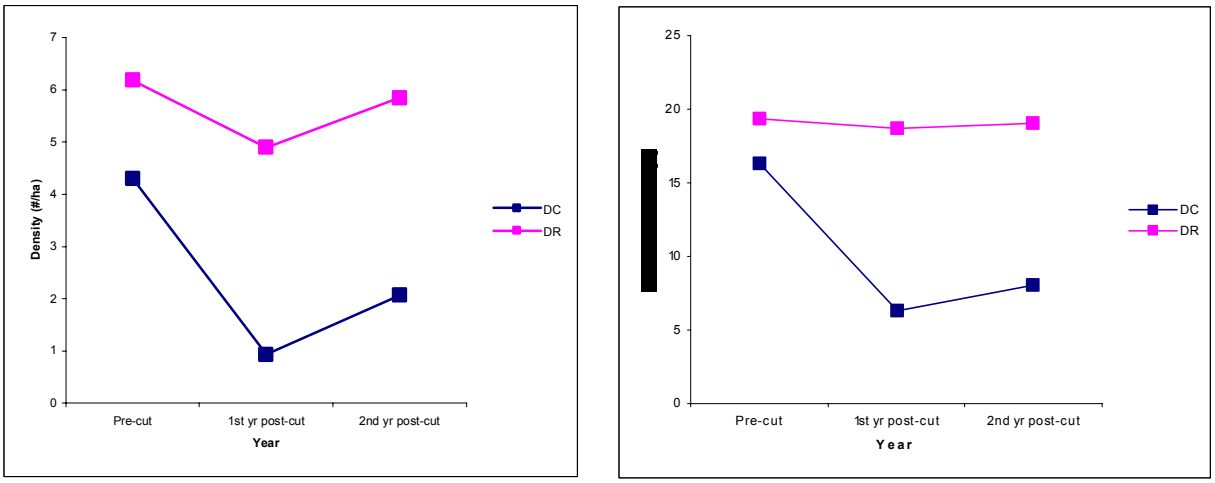


Figure 7.2. Comparison of deciduous reserve (DR) and deciduous clearcut stands (DC) showing a significant decrease in both territory density and species richness of songbird communities after harvesting in DC stands in Grande Prairie. Harvesting occurred in DC stands between year 1 and 2.

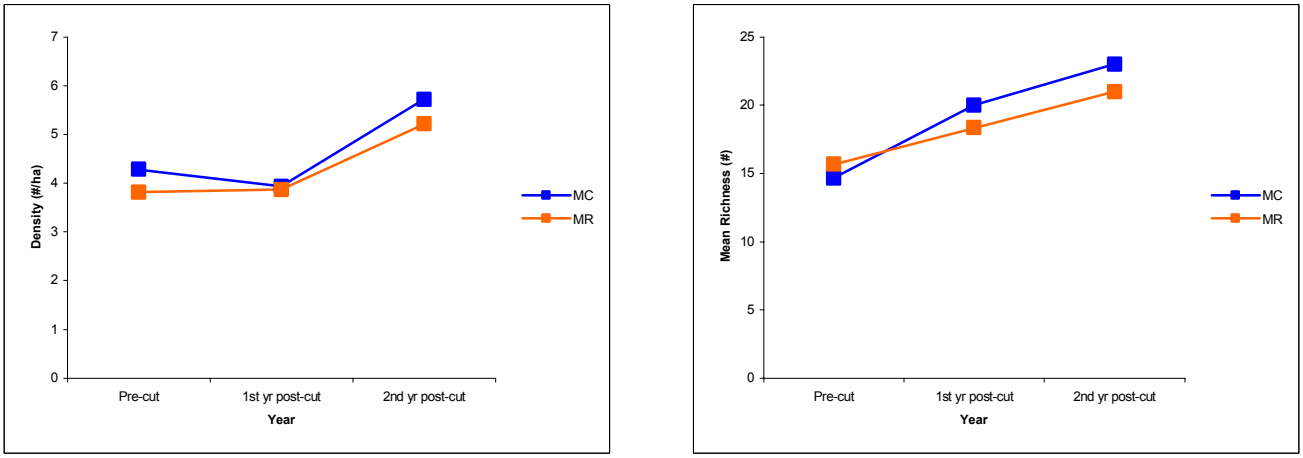


Figure 7.3. Comparison of mixedwood reserve (MR) and mixedwood understorey protection (MC) stands showing that songbird community densities and species richness are similar before and after harvesting in MC stands in Grande Prairie. Harvesting occurred in MC stands between year 1 and 2.

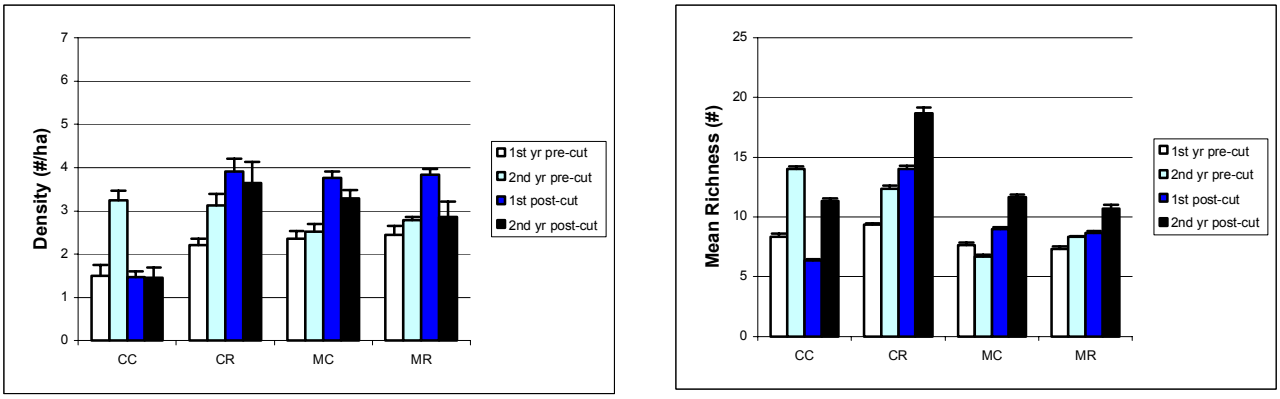


Figure 7.4. Mean density (birds/ha) and richness (# species) of songbird communities in Manning. Treatments are conifer clearcut (CC), conifer reserve (CR), mixedwood understorey protection (MC), and mixedwood reserve (MR),.

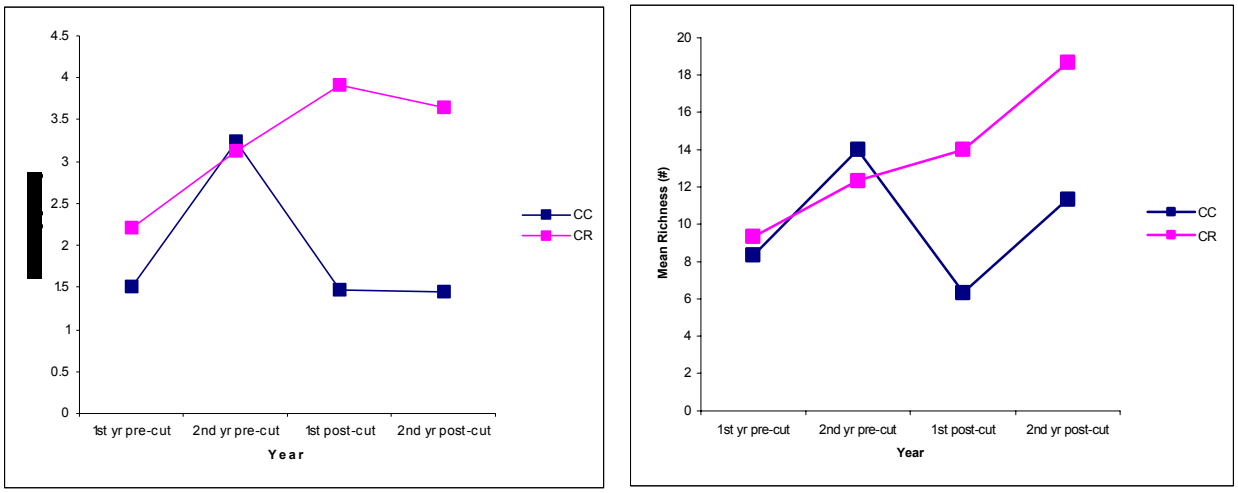


Figure 7.5. Comparison of coniferous reserve (CR) and coniferous clearcut stands (CC) showing a significant decrease in both territory density and species richness of songbird communities after harvesting in CC stands in Grande Prairie. Harvesting occurred in CC stands between years 2 and 3.

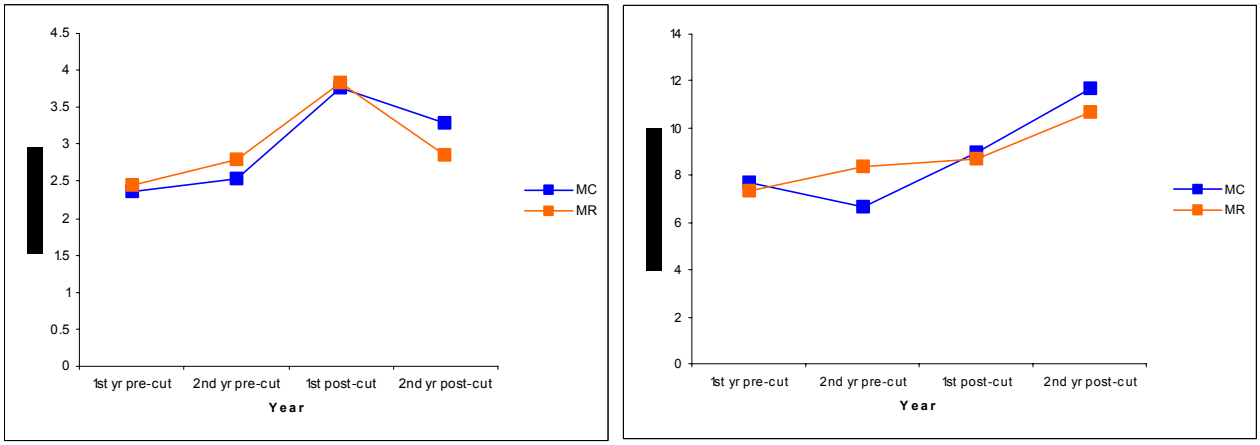


Figure 7.6. Comparison of mixedwood reserve and mixedwood understorey protection stands showing that songbird community densities and species richness are similar before and after harvesting in MC stands in Manning. Harvesting occurred in MC stands between year 2 and 3.

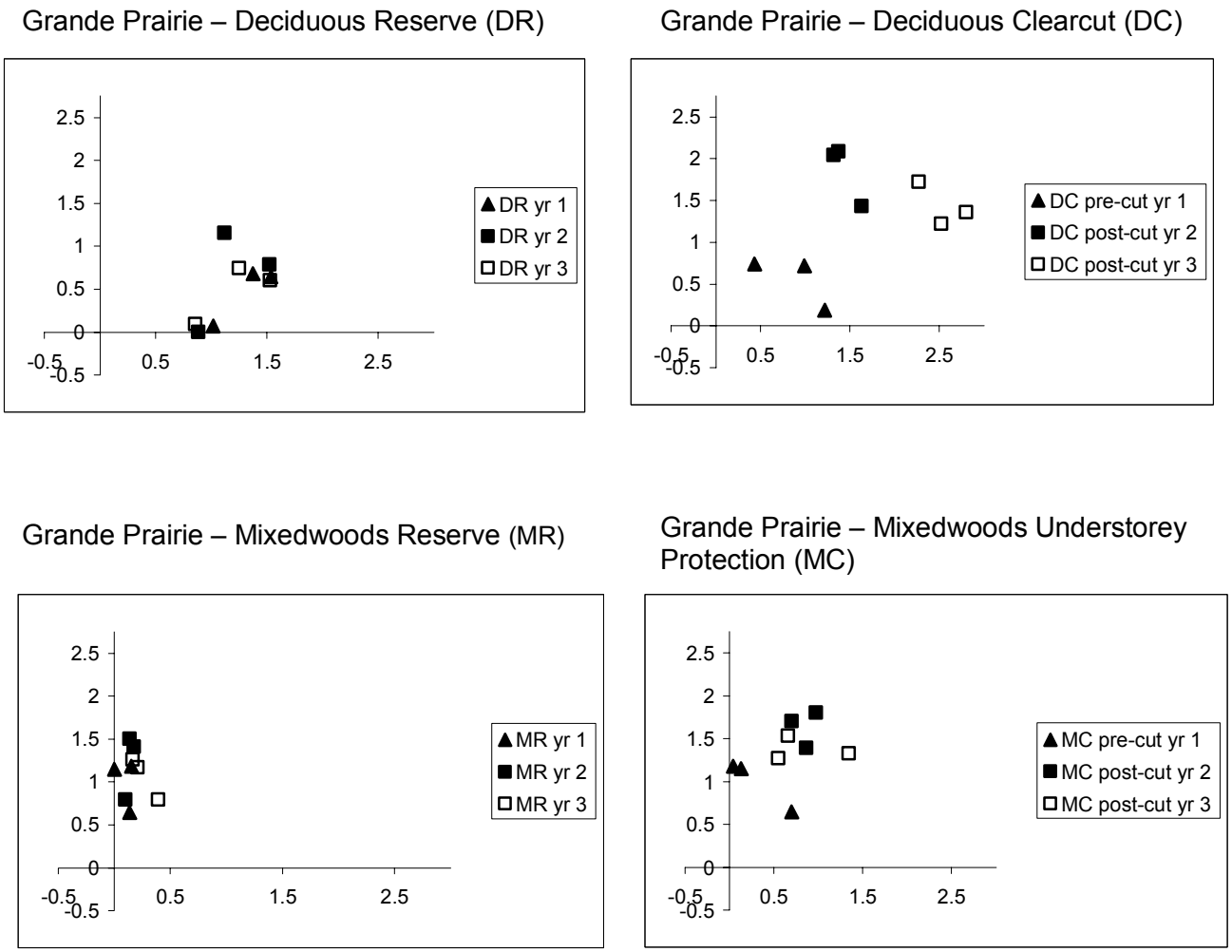
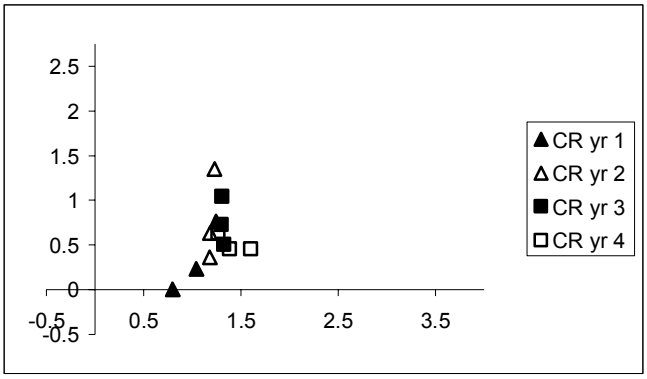
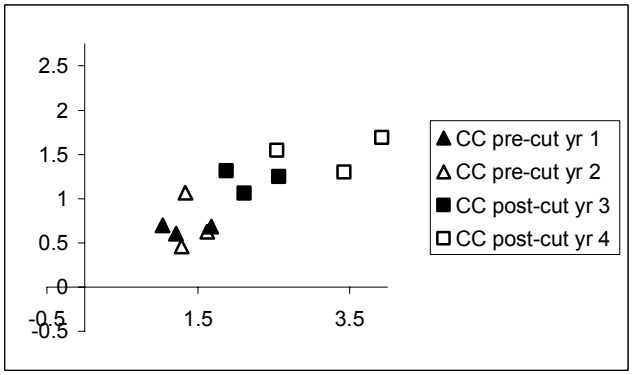


Figure 7.7. Comparison of community composition, based on densities of avian species through time and across treatments in Grande Prairie. Points represent community composition in individual stands. Points that are closer to one another represent bird communities that are more similar than points that are farther apart. Lack of overlap of circles and squares in both DC and MC stands demonstrates a turnover in species composing the communities pre-harvest (triangles) and post-harvest (squares) years. Stands that remained unharvested (Reserve) have very similar songbird communities over the years, as indicated by the clustering of sites over the years.

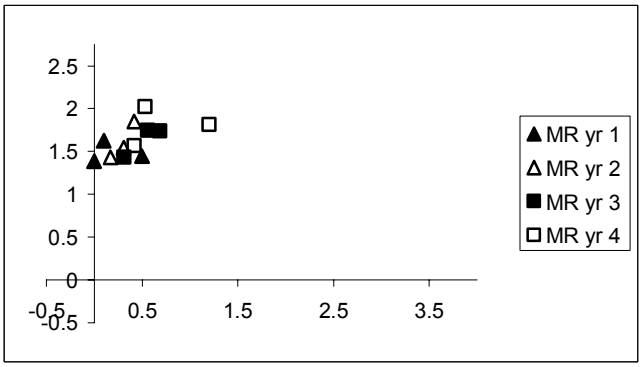
Manning – Coniferous Reserve (CR)



Manning – Coniferous Clearcut (CC)



Manning – Mixedwoods Reserve (MR)



Manning – Mixedwoods Understorey Protection (MC)

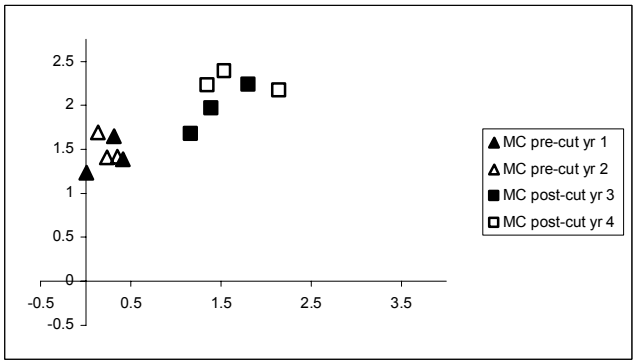


Figure 7.8. Comparison of community composition, based on densities of avian species through time and across treatments in Manning. Points represent community composition in individual stands. Points that are closer to one another represent bird communities that are more similar than points that are farther apart. Lack of overlap of circles and squares in both CC and MC stands demonstrates a turnover in species composing the communities pre-harvest (triangles) and post-harvest (squares) years. Stands that remained unharvested (Reserve) have very similar songbird communities over the years, as indicated by the clustering of sites over the years.

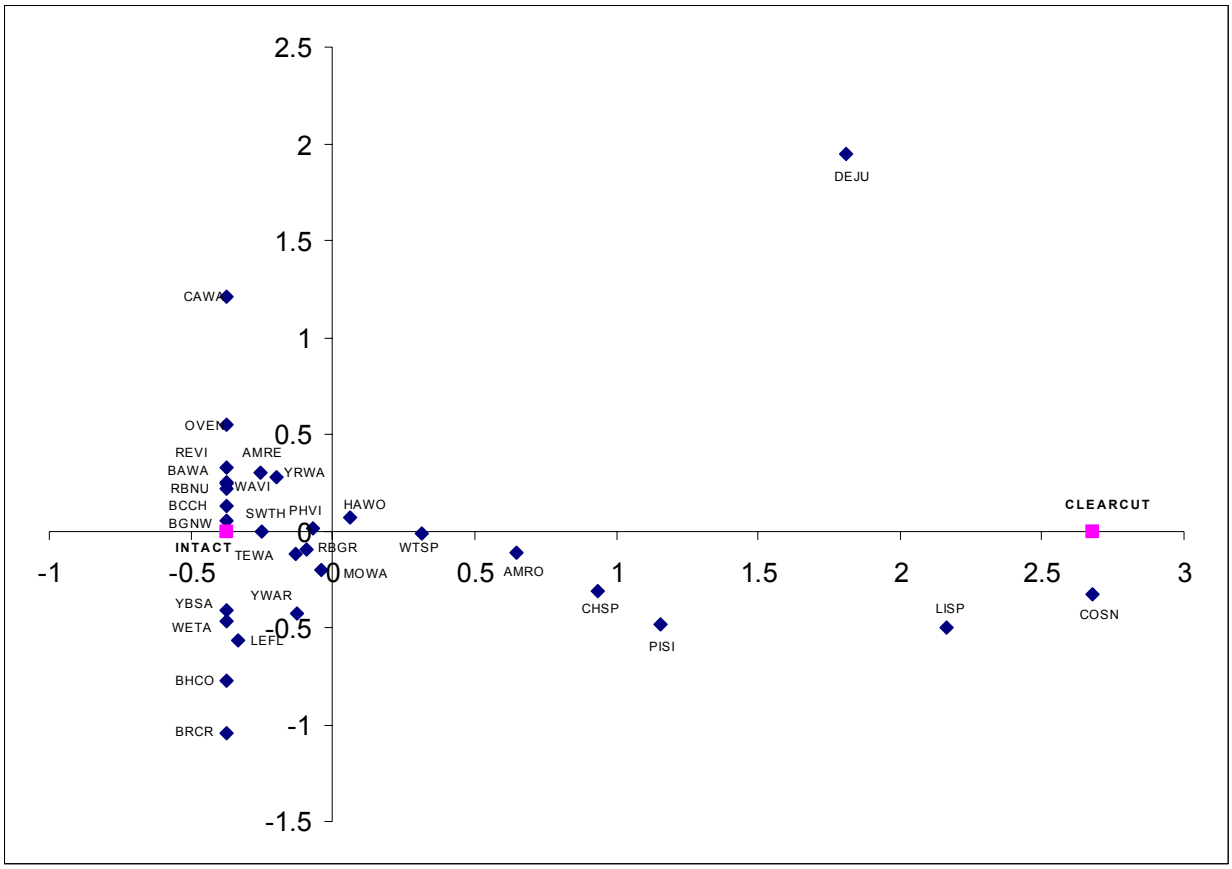


Figure 7.9. Distribution of densities of songbird species in intact and clearcut deciduous stands in Grande Prairie. The closer a species score (blue diamonds) is to a treatment centroid (pink squares), the more closely associated the species is with that treatment.

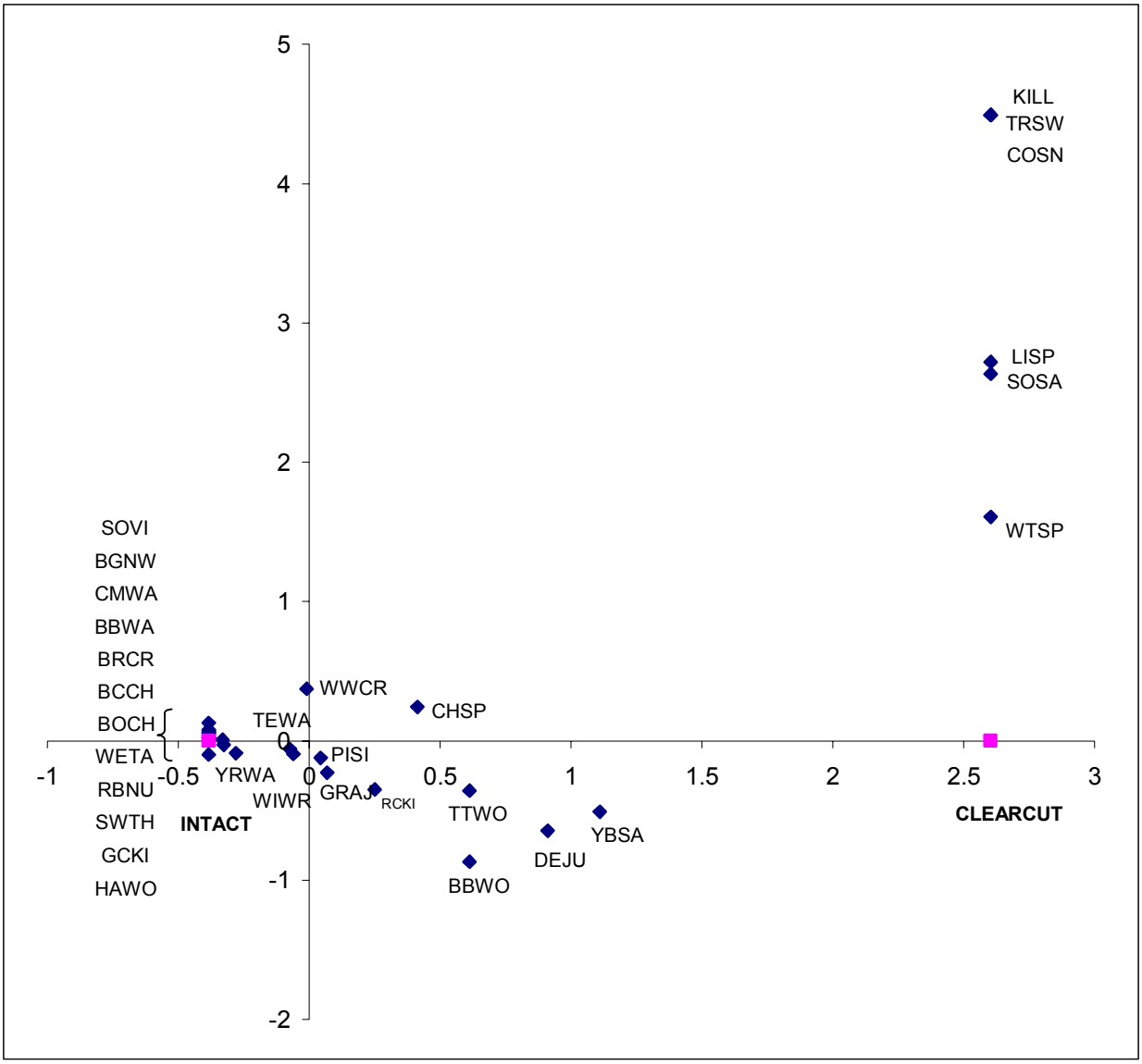


Figure 7.10. Distribution of densities of songbird species in intact and clearcut coniferous stands in Manning. The closer a species score (blue diamonds) is to a treatment centroid (pink squares), the more closely associated the species is with that treatment.

The composition of songbird communities in intact mixedwood stands was distinct from those found in understorey protection stands, but the turnover was not nearly as severe as seen in the clearcutting scenario. This result was consistent in both Grande Prairie and Manning (Grande Prairie: p=0.002; Manning: p=0.002).

In Grande Prairie, understorey protection stands were characterised by increases in generalist species (White-throated Sparrow, Chipping Sparrow), and open country species (Brown-head Cowbird, American Robin, Lincoln's Sparrow) and species that utilise shrubby habitats with some mature trees (Mourning Warbler, Western Wood Peewee, Least Flycatcher) (Figure 7.11). There were also species more often associated with forests including Purple Finch and Three-toed Woodpecker. Species that were strongly associated with intact mixedwood stands (rather than understorey protection) were Brown Creeper, Golden-crowned Kinglet, Ovenbird, Connecticut Warbler, Canada Warbler, and Black-throated Green Warbler.

In Manning, mixedwood understorey protection were characterised by increases in generalist or open country species, *i.e.,* Chipping Sparrow, White-throated Sparrow, Dark-eyed Junco, Lincoln's Sparrow and American Robin (Figure 7.12). Species that were strongly associated with intact mixedwood stands (rather than understorey protection) were Red-breasted Nuthatch, Red-eyed Vireo, Warbling Vireo, Ovenbird, Bay-breasted Warbler, and Black and White Warbler.

A complete listing of territorial bird species, their species codes and record of presence or absence is contained in Appendix 7.1.

Discussion

Birds and understorey protection stands

In both Grande Prairie and Manning, clearcutting had the strongest effect on songbird communities, with significant decreases in density and number of bird species relative to intact stands and an almost complete turnover in community composition for both coniferous and deciduous sites. This result mirrors those found in many other studies of clearcutting in Alberta and the rest of the boreal forest (see Schieck and Song 2002 for a review).

Understorey protection does not have as dramatic an effect on forest songbird communities as clearcutting, based on our results here and for the short term. In both sites, this silvicultural treatment maintained species density and richness at the community level. In partial cutting studies with up to 46% retention, Norton and Hannon (1997) found decreasing abundance of birds relative to the intact state. Conversely, King and DeGraaf (2000) found increasing diversity and richness in shelterwood cuts compared with intact eastern forest. Results might be explained by the structural complexity of the stands and the habitat niches here from harvesting. Partial cutting leaves patches of trees with little focus on understorey retention while shelterwood cuts can have many trees at a variety of ages and heights, creating a diverse array of habitats. In a study of retention levels from 0-75%, Harrison (2002) reports different results for richness depending on stand type: in deciduous overstorey/coniferous understorey sites, richness does not change while in mixedwoods stands, there is a trend of increasing richness with increasing retention. Mixedwood study sites in Grande Prairie and Manning fit more closely with his deciduous overstorey/coniferous understorey description.

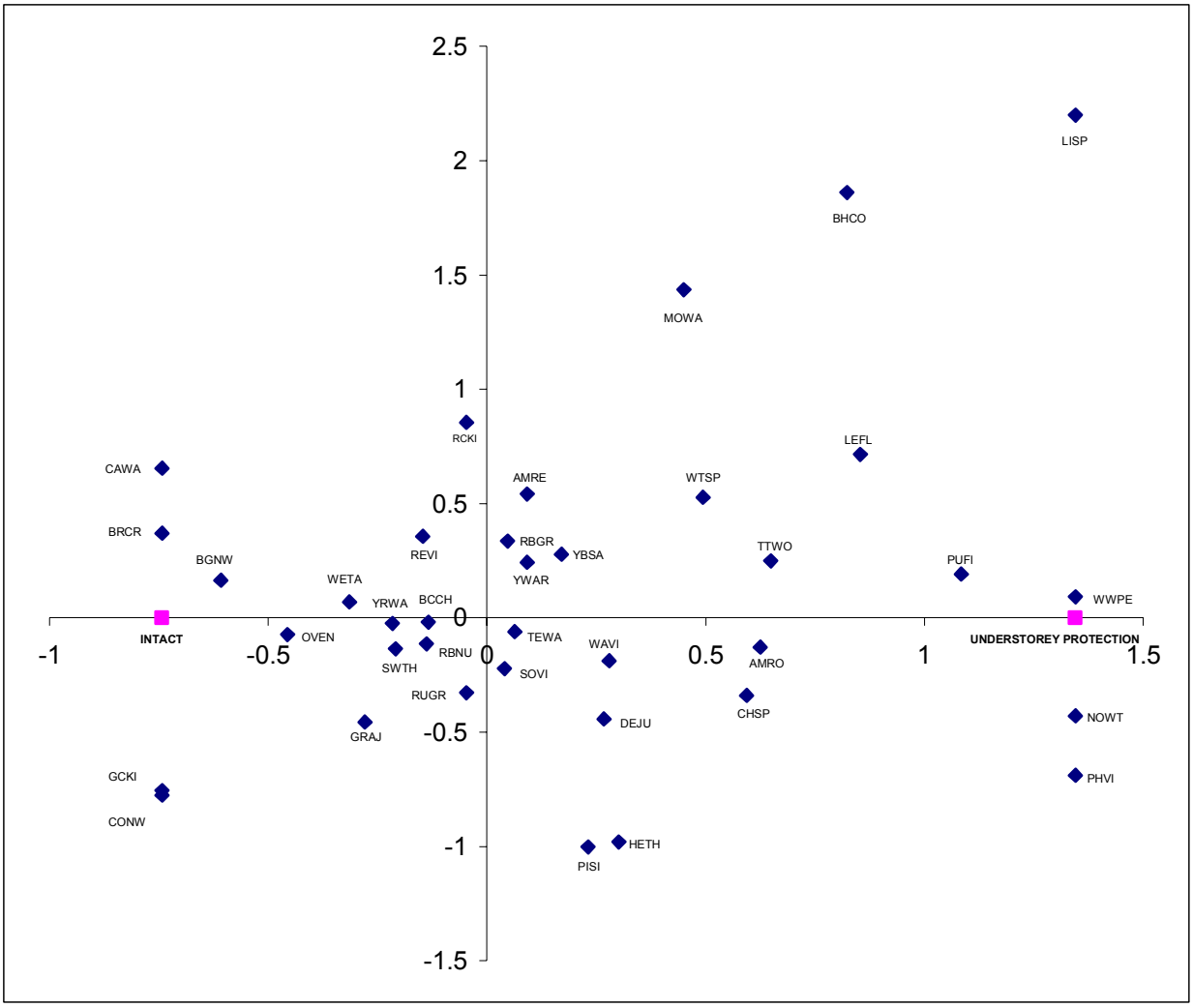


Figure 7.11. Distribution of densities of songbird species in intact mixedwoods and mixedwoods with understorey protection harvesting treatment in Grande Prairie. The closer a species score (blue diamonds) is to a treatment centroid (pink squares), the more closely associated the species is with that treatment.

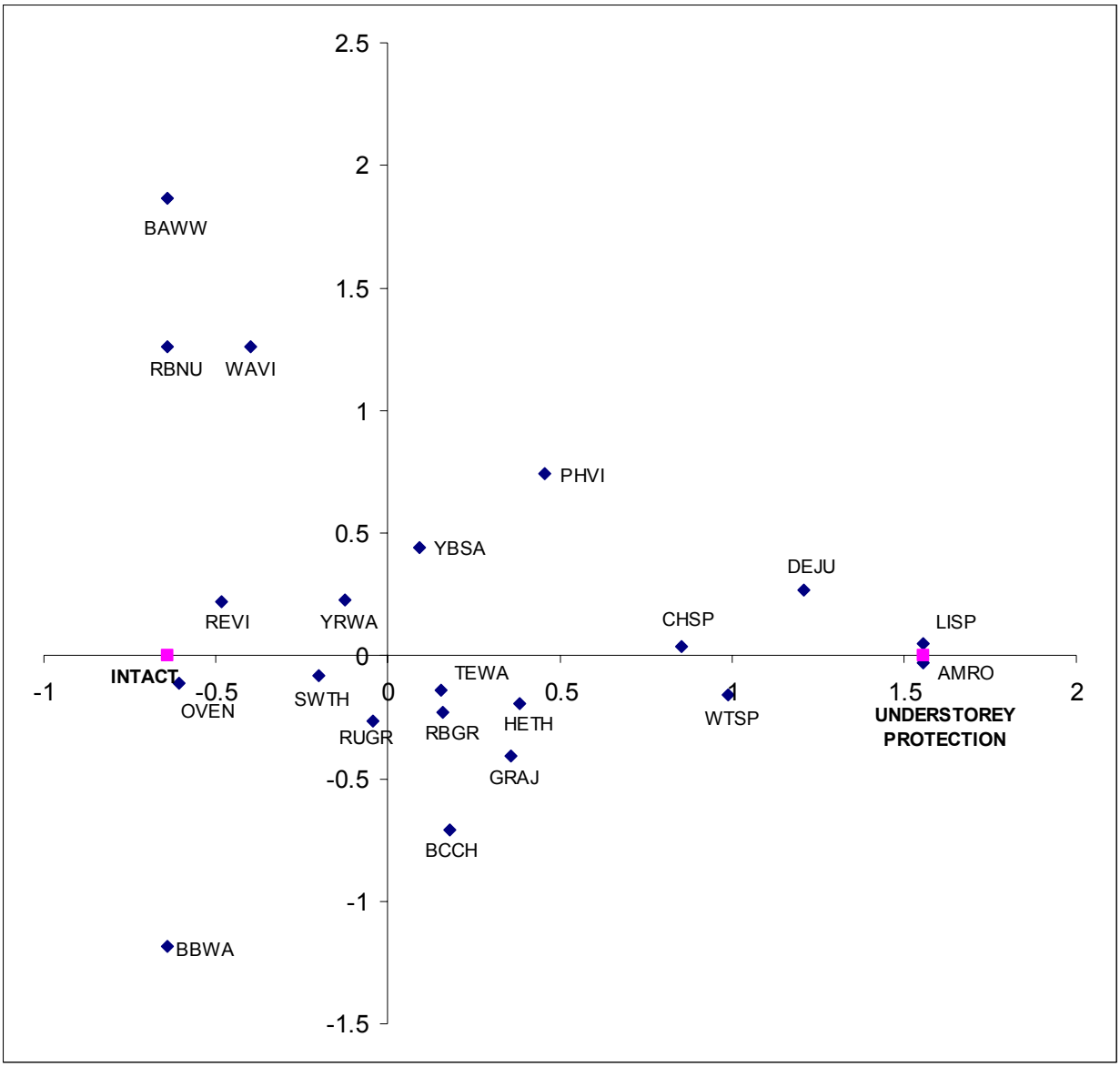


Figure 7.12. Distribution of densities of songbird species in intact mixedwoods and mixedwoods with understorey protection harvesting treatment in Manning. The closer a species score (blue diamonds) is to a treatment centroid (pink squares), the more closely associated the species is with that treatment.

Understorey protection harvesting did change the composition of birds using the stands from the pre-harvest state in this study: communities were dominated by species associated with early successional, open or shrubby habitats but there were also some forest species present. Many studies of partial harvesting techniques mirror my results and demonstrate decreased abundances or densities of forest species and increases in early-successional species (*e.g.,* Norton and Hannon 1997; King and DeGraaf 2000; Rodewald and Yahner 2000; Harrison 2002). In this study, most forest species were more closely associated with intact stands but Purple Finch, a forest species, was found only in the understorey protection sites in Grande Prairie albeit in low numbers.

Retention of original forest structure within cutblocks generally seems to be effective for increasing the presence of forest bird species relative to clearcut techniques. Tittler *et al*. (2001) found some forest species responded positively to increasing levels of retention in mixedwood forest cutblocks in Alberta. Larger patches of trees dispersed close to intact forest will also increase the presence of many forest species (Schieck and Hobson 2000; Schieck *et al*. 2000) and these conditions are created by understorey protection.

As has been noted in other studies of avian responses to tree retention (review in Schieck and Song 2002), breeding success for birds holding territories associated with understorey protection habitats is unknown. Nest searches were conducted in addition to the spotmapping surveys in 2004 in the Manning understorey protection stands: there were confirmed nesting records in understorey protection of American Robin, Tennessee Warbler, Dark-eyed Junco, White-throated Sparrow, and Chipping Sparrow. There was insufficient sample size (11 nests in 3 cutblocks) to draw any conclusions about nesting success, however. Hannah's (2000) study of nesting success of White-throated Sparrow demonstrated decreased reproductive success in clearcuts despite similar densities to intact forests. It would be revealing to study this species in understorey protection blocks to know whether this effect is repeated or mitigated.

Although analysis for individual species is not presented, Ovenbird was the most common species in intact mixedwood forests in both Grande Prairie and Manning sites and this species declines sharply in understorey protection. This result reflects other spotmapping-based studies of harvesting and cumulative effects that show a strong requirement for intact forests for Ovenbirds to establish territories (Lambert and Hannon 2000; Bayne and Hobson 2001; Bayne *et al*. submitted). Other forest species of ecological concern, as noted by the Alberta Fish and Wildlife (2000, 2004), were not maintained in either clearcut or understorey protection stands. Cape May Warbler, a recommended species of special concern, held territories only in old seral stage conifer forests in Manning. Bay-breasted Warbler, also a recommended species of special concern, held territories only in intact mixedwood and coniferous stands in Manning. Black-throated Green Warbler, a species of special concern, held territories only in intact deciduous and mixedwoods forests of Grande Prairie, and in intact coniferous forests in Manning. Intact mixedwoods forests in Manning, with a stand origin of 1950's are likely too young to possess the large conifer trees required by these birds (Robichaud and Villard 1999). Brown Creeper and Canada Warbler, both with the general status of Sensitive, are found only in intact deciduous and mixedwoods stand in Grande Prairie. In Manning, Brown Creeper is only found in intact coniferous stands. Western Tanager, also designated Sensitive, is the only species in this category that is found in the understorey protection stands in Grande Prairie, although in low numbers. It is more strongly associated with the intact mixedwood, deciduous and coniferous stands. Generally, understorey protection harvesting will not conserve any of these species; older, intact forests are necessary for them to prosper in this landscape (Norton 1999, 2001a, 2001b; Hannah 2002).

Birds in mixedwood vs. deciduous or coniferous stands

For intact stands, songbird community density and species richness was not consistently higher in mixedwood stands than their deciduous or coniferous counterparts. In Grande Prairie, the understorey of deciduous stands was much more developed than mixedwoods (see stem density means for 3-5m and 5-10 m trees in Chapter 3). This added structural complexity of the understorey may explain increased densities found here (Song 1998; Machtans and Latour 2003). In Manning, mixedwood stands were younger and less structurally complex than the old seral stage coniferous forests and may explain the higher species richness found in the conifer stands. These conifer stands possessed many large trees, and dead standing and downed trees, creating a niche for cavity nesters such as Black-backed and Three-toed Woodpeckers and old growth specialists such as the Cape May Warbler.

These results are not consistent with other studies comparing mixedwood, deciduous and coniferous stands in western boreal forests. In central Saskatchewan, mixedwood stands supported more species than deciduous or coniferous counterparts (Hobson and Bayne 2000). In southern Northwest Territories, mixedwood stands supported marginally higher richness than coniferous stands and higher richness than deciduous stands (Machtans and Latour 2003). In both these cases, the higher structural heterogeneity in mixedwood stands was offered as an explanation for the higher richness found there.

Management Implications

Overall, it is difficult to assess the ecological contribution of understorey protection stands. These cutblocks maintain more species than a clearcut block in the short term, but they do not maintain all forest species and importantly, do not maintain sensitive species such as Brown Creeper, Cape May Warbler, Bay-breasted Warbler, and Black-throated Green Warbler. For management of forest bird species, provisions, preferably through landscape-scale planning, must be made to maintain old seral stage forests across the range of forest types, from deciduous through mixedwood to coniferous forests.

Understorey protection blocks may have value for some of the generalist and shrub species. They could make an important short-term contribution for species such as the White-throated Sparrow which have demonstrated continental population declines (Blancher 2003). However, given the cautions that cutblocks can act as population “sinks”, further research on reproductive success of species here is needed to confirm whether birds nesting here benefit from this habitat.

Tree retention in cutblocks managed within a natural disturbance regime is thought to provide ecological benefits in the longer term by providing patches of old growth structure as a stand regenerates. Therefore the ecological benefit is viewed as a legacy for the future rather than a lifeboat to maintain old-growth species on the landbase (*sensu* Franklin *et al*. 1997). Understorey protection could be viewed similarly. The remaining aspen trees will age and die, likely providing increased habitat in the maturing spruce stands. However, if stands are harvested used standard clearing practices as soon as the conifer trees are at a merchantable age, that timing will be before these stands can provide the maximum ecological benefit of the old seral stage forest.

For management of forests and boreal songbirds, understorey protection may provide best value as a silvicultural technique. A broader view to the landscape and the management of forest at a natural range of seral stages and stand compositions is necessary for maintenance of all forest species.

Acknowledgements

Many thanks to Cris Gray, David McKinnon, Len Peleshok, Gavin Berg, Sharon Kendall and Lindsay Tomyn who provided excellent technical assistance. Pat Soldan efficiently formatted this chapter. My thanks to Mike

Norton, J.P. Bielech and Fred Radersma whose comments improved this chapter. Funding for this study was provided by Ainsworth Lumber Co., Manning Diversified Forest Products, Alberta Research Council and Environment Canada under the Western Boreal Conservation Initiative.

Literature Cited

Alberta Fish and Wildlife Divison. 2000. The general status of Alberta wild species 2000. Alberta Sustainable Resource Development, Edmonton, AB. Available online: http://www.gov.ab.ca/env/fw/status/index.html.

Alberta Fish and Wildlife Division. 2004. Report of Alberta's Endanger ed Species Conservation Committee: June 2002. Alberta Sustainable Resource Development, Fish and Wildlife Division, Edmonton, AB. 40 pp.

Bayne, E.M. and K.A. Hobson. 2001. Effects of habitat fragmentation on pairing success of Ovenbirds: Importance of male age and floater behaviour. Auk 118: 380-388.

Bayne, E.M, S.L. Van Wilgenburg, S. Boutin and K.A. Hobson. Modeling and field-testing of Ovenbird (*Seiurus aurocapillus*) responses to boreal forest dissection by energy sector development at multiple spatial scales. Submitted to Landscape Ecology, 14 February 2004.

Bibby, C.J., N.D. Burgess and D.A. Hill. 1992. Bird census techniques. Academic Press, Toronto.

Blancher, P. 2003. Importance of Canada's boreal forest to landbirds. Canadian Boreal Initiative and Boreal Songbird Initiative. Ottawa, ON.

Franklin, J.F., D.R. Berg, D.A. Thornburg and J.C. Tappeiner. 1997.Alternative silvicultural approaches to timber harvesting: Variable retention harvest systems. Pages 113-149 in K.A. Kohm and J.F. Franklin, editors. Creating a forestry for the 21st century. The science of ecosystem management. Island Press, Washington, DC.

Gunn, J.S., A. Desrochers, M-A Villard, J. Bourque & J. Ibarzabal. 2000. Playbacks of mobbing calls of black-capped chickadees as a method to estimate reproductive activity of forest birds. J. Field Ornithol. 71(3): 472-483.

Hannah, K.C. 2000. Patterns of habitat quality for the White-throated Sparrow (*Zonotrichia albicollis*) in a recently logged landscape. M.Sc. thesis. Department of Renewable Resources, University of Alberta, Edmonton, AB.

Hannah, K.C. 2002. The Status of the Brown Creeper (*Certhia americana*) in Alberta. Alberta Wildlife Status Report No. 49. Alberta Sustainable Resource Development and Alberta Conservation Association. Edmonton, AB.

Harrison, R.B. 2002. Stand-level response of boreal forest songbirds to experimental partial-cut harvest in northwestern Alberta. M.Sc. Thesis, Dept. of Renewable Resources, University of Alberta, Edmonton, AB.

Hobson, K.A. and E. Bayne. 2000. Breeding bird communities in boreal forest of western Canada: Consequences of "unmixing" the mixedwoods. Condor 102: 759-769.

Karr, J.R. 1968. Habitat and avian diversity on strip-mined land in east-central Illinois. Condor **70**:348-357.

King, D.I. and R.M DeGraaf. 2000. Bird species diversity and nesting success in mature, clearcut and shelterwood forest in northern New Hampshire, USA. Forest Ecology and Management 129: 227-235.

Lambert, J.D. and S.J. Hannon. 2000. Short-term effects of upland timber harvest on ovenbird abundance, territory characteristics, and pairing success in riparian buffer strips. Auk **117**: 687-698.

MacArthur, R.H. and J.W. MacArthur. 1961. On bird species diversity. Ecology **42(3)**:594-598.

Machtans, C.S. and P.B. Latour. 2003. Boreal forest songbird communities of the Liard Valley, Northwest Territories. Condor 105: 27-44.

McCune, B. and J.B. Grace. 2002. Analysis of ecological communities. MjM Software, Gleneden Beach, Oregon.

Mixedwood Management Association. 2004. Research webpage: http://www.mwma.rr.ualberta.ca/Research.asp Last accessed 3 March 2004.

Norton, M.R. 1999. Status of the Black-throated Green Warbler (Dendroica tigrina) in Alberta. Alberta Wildlife Status Report No. 23. Alberta Sustainable Resource Development and Alberta Conservation Association. Edmonton, AB.

Norton, M.R. 2001a. Status of the Bay-breasted Warbler (Dendroica castanea) in Alberta. Alberta Wildlife Status Report No. 32. Alberta Sustainable Resource Development and Alberta Conservation Association. Edmonton, AB.

Norton, M.R. 2001b. Status of the Cape May Warbler (Dendroica virens) in Alberta. Alberta Wildlife Status Report No. 33. Alberta Sustainable Resource Development and Alberta Conservation Association. Edmonton, AB.

Norton, M.R. and S.J. Hannon. 1997. Songbird response to partial-cut logging in the boreal mixedwood forest of Alberta. Canadian Journal of Forest Research **27**:44-53.

Pojar, R.A. 1995. Breeding bird communities in aspen forests of the sub-boreal spruce (dk Subzone) in the Prince Rupert forest region. Province of British Columbia, Ministry of Forests Research Program, Victoria, BC.

Recher, H.F. 1969. Bird species diversity and habitat diversity in Australia and North America. American Naturalist **103**:75-80.

Rodewald, A.D. and R.H. Yahner. 2000. Bird communities associated with harvested hardwood stands containing residual trees. Journal of Wildlife Management 64: 924-932.

Robichaud, I. And M-A. Villard. 1999. Do Black-throated Green Warblers prefer conifers? Meso- and microhabitat use in a mixedwood forest. Condor 101: 262-271.

Schieck. J. and K.A. Hobson. 2000. Bird communities associated with live residual tree patches within cut blocks and burned habitat in mixedwood boreal forests. Canadian Journal of Forest Research 30:1281-1295.

Schieck, J., K. Stuart-Smith and M. Norton. 2000. Bird communities are affected by amount and dispersion of vegetation retained in mixedwood boreal forest harvest areas. Forest Ecology and Management 126: 239-254.

Schieck, J. and S.J. Song. 2002. Responses of boreal birds to wildfire and harvesting. Chapter 9 in S.J. Song. Ecological Basis for Stand Management: A summary and synthesis of ecological responses to wilfire and harvesting in boreal forests. Alberta Research Council, Vegreville, AB.

Song, S.J. 1998. Effects of natural and anthropogenic forest edge on songbirds breeding in the boreal mixed-wood forest of northern Alberta. Ph.D. Thesis, University of Alberta, Edmonton, Alberta.

ter Braak, C.J.F. and P. Smilauer. 2002. CANOCO reference manual and CanoDraw for Windows User's guide: Software for canonical community ordination (version 4.5). Microcomputer Power. Ithaca, NY.

Tittler, R., M. Norton and S.J. Hannon. 2001. Residual tree retention ameliorates negative effects of clearcutting some boreal songbirds. Ecological Applications **11(6)**:1656-1666.

Willson, M.F. 1974. Avian community organization and habitat structure. Ecology **55**:1017-1029.

Appendix 7.1. Listing of territorial bird species with species codes in Grande Prairie and Manning and with presence/absence record for each stand type. Presence is indicated by an X.

Common name	Scientific Name	Species Code	Grande Prairie				Manning			
			Intact deciduous	Clearcut deciduous	Intact mixed-woods	Under-storey protection	Intact conifer	Clearcut conifer	Intact mixed-woods	Under-storey protection
Northern Goshawk	*Accipiter gentilis*	NOGO					X			
Ruffed Grouse	*Bonasa umbellus*	RUGR	X		X	X			X	X
Killdeer	*Charadrius vociferus*	KILL						X		
Solitary Sandpiper	*Tringa solitaria*	SOSA						X		
Common Snipe	*Gallinago gallinago*	COSN		X				X		
Yellow-bellied Sapsucker	*Sphyrapicus varius*	YBSA	X		X	X	X	X	X	X
Hairy Woodpecker	*Picoides villosus*	HAWO	X	X		X	X			
Three-toed Woodpecker	*Picoides tridactylus*	TTWO				X	X	X		
Black-backed Woodpecker	*Picoides arcticus*	BBWO					X	X		
Northern Flicker	*Colaptes auratus*	NOFL		X						
Pileated Woodpecker	*Dryocopus pileatus*	PIWO					X			
Olive-sided Flycatcher	*Contopus cooperi*	OSFL						X		
Western Wood-Pewee	*Contopus sordidulus*	WWPE			X	X				
Alder Flycatcher	*Empidonax alnorum*	ALFL						X		
Yellow-bellied Flycatcher	*Empidonax flaviventris*	YBFL					X			
Least Flycatcher	*Empidonax minimus*	LEFL	X	X	X	X		X	X	
Blue-headed Vireo	*Vireo solitarius*	SOVI			X	X	X			
Warbling Vireo	*Vireo gilvus*	WAVI	X		X	X			X	X
Philadelphia Vireo	*Vireo philadelphicus*	PHVI	X			X			X	X
Red-eyed Vireo	*Vireo olivaceus*	REVI	X		X	X			X	X
Gray Jay	*Perisoreus canadensis*	GRAJ	X		X	X	X	X	X	X
Blue Jay	*Cyanocitta cristata*	BLJA	X							
Common Raven	*Corvus corax*	CORA				X				
Tree Swallow	*Tachycineta bicolor*	TRSW						X		
Black-capped Chickadee	*Poecile atricapilla*	BCCH	X		X	X	X		X	X
Boreal Chickadee	*Poecile hudsonica*	BOCH			X	X	X			
Red-breasted Nuthatch	*Sitta canadensis*	RBNU	X		X	X	X		X	
Brown Creeper	*Certhia americana*	BRCR	X		X		X			
Winter Wren	*Troglodytes troglodytes*	WIWR					X	X		
Golden-crowned Kinglet	*Regulus satrapa*	GCKI			X		X	X		
Ruby-crowned Kinglet	*Regulus calendula*	RCKI	X		X	X	X	X		
Swainson's Thrush	*Catharus ustulatus*	SWTH	X		X	X	X		X	X
Hermit Thrush	*Catharus guttatus*	HETH			X	X			X	X
American Robin	*Turdus migratorius*	AMRO	X	X	X	X				X
Varied Thrush	*Ixoreus naevius*	VATH			X					
Cedar Waxwing	*Bombycilla cedrorum*	CEWA				X				
Tennessee Warbler	*Vermivora peregrina*	TEWA	X	X	X	X	X	X	X	X
Yellow Warbler	*Dendroica petechia*	YWAR	X	X	X	X				
Magnolia Warbler	*Dendroica magnolia*	MNWA					X			
Cape May Warbler	*Dendroica tigrina*	CMWA					X			
Yellow-rumped Warbler	*Dendroica coronata*	YRWA	X	X	X	X	X	X	X	X
Black-throated Green Warbler	*Dendroica virens*	BGNW	X		X		X		X	
Bay-breasted Warbler	*Dendroica castanea*	BBWA					X		X	

Blackpoll Warbler	*Dendroica striata*	BPWA					X			
Black-and-white Warbler	*Mniotilta varia*	BAWW	X						X	
American Redstart	*Setophaga ruticilla*	AMRE	X	X	X	X				
Ovenbird	*Seiurus aurocapillus*	OVEN	X		X	X			X	X
Northern Waterthrush	*Seiurus noveboracensis*	NOWT				X				
Connecticut Warbler	*Oporornis agilis*	CONW	X		X					X
Mourning Warbler	*Oporornis philadelphia*	MOWA	X	X	X	X				
Common Yellowthroat	*Geothlypis trichas*	COYE		X						
Canada Warbler	*Wilsonia canadensis*	CAWA	X		X					
Western Tanager	*Piranga ludoviciana*	WETA	X		X	X	X		X	
Chipping Sparrow	*Spizella passerina*	CHSP	X	X	X	X	X	X	X	X
Clay-colored Sparrow	*Spizella pallida*	CCSP						X		
Fox Sparrow	*Passerella iliaca*	FOSP	X							
Lincoln's Sparrow	*Melospiza lincolnii*	LISP	X	X		X		X		X
White-throated Sparrow	*Zonotrichia albicollis*	WTSP	X	X	X	X		X	X	X
Dark-eyed Junco	*Junco hyemalis*	DEJU	X	X	X	X	X	X	X	X
Brown-headed Cowbird	*Molothrus ater*	BHCO	X			X				
Rose-breasted Grosbeak	*Pheucticus ludovicianus*	RBGR	X	X	X	X			X	X
Purple Finch	*Carpodacus purpureus*	PUFI				X				
White-winged Crossbill	*Loxia leucoptera*	WWCR				X	X	X		
Pine Siskin	*Carduelis pinus*	PISI	X	X	X	X	X	X		
Evening Grosbeak	*Coccothraustes vespertinus*	EVGR			X					

CHAPTER 8: FUNGAL COMMUNITIES IN BOREAL FORESTS BEFORE AND AFTER HARVEST, WITH PARTICULAR EMPHASIS ON UNDERSTOREY PROTECTION HARVEST

Steve Bradbury

Introduction

Fungi play a critical role in plant growth, canopy tree senescence, and decomposition of deadwood in all forest types. In general, conspicuous boreal forest fungi (*i.e.*, macrofungi) can be separated into two general groups based on the manner in which they acquire carbohydrates (*i.e.*, decomposers and mycorrhizal species). Decomposer species acquire carbohydrates by breaking down dead organisms or other organic matter. Organic matter decomposition is critical for carbon and nutrient cycling in forest ecosystems, and the role of decomposer fungi in these cycles is more extensive than just breaking down the organic matter. For example, decomposer sporocarps (fungal fruit bodies) growing on downed woody material (DWM) have been shown to accumulate nutrients from dead wood (Edmonds and Lebo 1998). Nutrients accumulated by these fungi can be consumed by organisms feeding on sporocarps (small mammals, ungulates, invertebrates, *etc.*), or released into the soil and made available for uptake by plants (Edmonds and Lebo 1998).

Mycorrhizal species acquire carbon through symbiotic relationships with woody plants. Plants with mycorrhizal associations have improved access to soil moisture and nutrients (via uptake from the fungal mycelial network), and the mycorrhizal fungus in return, receives photosynthetic carbohydrates from the host plant. All boreal tree and shrub species form mycorrhizal associations with many conspicuous fungal species (Trappe 1962; Lumley *et al.* 1995; Bradbury 1997; Bradbury *et al.* 1998).

While many studies of macrofungal communities have been conducted in a variety of stand types and forested systems (Mason *et al.* 1982; Dighton *et al.* 1986; Last *et al.* 1987; Edmonds and Lebo 1998; Hintikka 1988; Senn-Irlet and Bieri 1999; O'Dell *et al.* 1999; Allen *et al.* 2000), few have been conducted in Alberta (Danielson 1984; Bradbury 1998; Bradbury *et al.* 1998), and fewer still in Alberta's northern boreal forests (Lumley *et al.* 1995; Crites and Dale 1998). Existing fungal community studies from other ecosystems have found differences in species abundance, species composition, and diversity among stand types and stand ages, but have typically concentrated on only one guild of fungi (*i.e.*, decomposer or mycorrhizal).

Traditional forest harvesting is known to alter the fungal community (Lumley *et al.* 1995; Bradbury 1997; Bradbury 1998; Bradbury *et al.* 1998), however, it is currently unknown to what extent an understorey protection strategy may influence the fungal communities found in mixedwood forests. The objectives of this study were to: 1) compare macrofungal communities in boreal deciduous, mixedwood and coniferous forests, 2) determine the response of the fungal community to understorey protection harvesting in boreal mixedwood stands, and 3) compare the response of the fungal community after understorey protection harvesting to clearcut harvesting of deciduous and coniferous stands.

Materials and Method

For a description of study areas and experimental design, see Chapter 2.

Fungal data collection

Due to time limitations only epigeous (above ground) macrofungal sporocarps were sampled. A 500 m x 2 m belt transect (Figures 2.3 and 2.4) was sampled in each stand in each study area at various times during the growing season in 2000, 2001, and 2002; only the Manning study area was sampled in 2003 (see Table 8.1). All sporocarps found within the belt transect were identified and counted, yielding sporocarp abundance values. Relative abundance of fruiting species was determined for each stand on a yearly basis; square-root transformed

sporocarp relative abundance was used for all subsequent analyses. Specimens not identified in the field were collected, spore prints were made and samples were dried to assist in later identification. Species were separated by carbohydrate acquisition strategy (*i.e.*, mycorrhizal species and decomposer species) to facilitate analysis; decomposer species in this study included both saprotrophic and parasitic species. Nomenclature followed Arora (1986), Schalkwijk-Barendsen (1991) and Allen *et al.* (1996).

Data analysis

One year of data (2000) was used to compare fungal communities in deciduous, mixedwood and coniferous forests from both study areas. In the Grande Prairie study area, two years of data (2001 and 2002) were pooled and used to compare deciduous forests with clearcuts and mixedwood forests with understorey protection cutblocks. In the Manning study area, two years of data (2002 and 2003) were pooled and used to compare coniferous forests with clearcuts and mixedwood forests with understorey protection cutblocks. One-way ANOVA, with a *post hoc* Student's t-test, was used to investigate differences in sporocarp species richness and Shannon diversity between stand types. Differences were judged as significant if $p < 0.05$. Analyses were performed using the JMP statistical package (SAS 2000).

Detrended correspondence analysis (DCA) was used to determine the relationships between forest cover treatments and fungal communities. CANOCO (ter Braak and Smilauer 1998) was used to perform all ordinations. To identify differences between treatments, sample scores along DCA Axis 1 and Axis 2 were subjected to ANOVA (SAS 2000). Confidence ellipses were determined based on algorithms from the JMP statistical package (SAS 2000).

To compare the magnitude of disturbance on fungal communities (*i.e.*, between understorey protection harvesting and clearcutting), sample scores from the DCA were used to calculated two-dimensional orthogonal distances (using the Pythagorean theorem) between a forest reserve stand and a post-harvest stand in ordination space; the distance between pre-harvest sample scores and post-harvest sample scores was assumed to represent the magnitude of change to the sampled fungal community due to the harvesting strategy. To determine whether clearcutting or understorey protection harvesting had a different magnitude of influence, distance values were subjected to ANOVA (using the same criteria to determine significance as above).

Results

Comparison of deciduous, mixedwood and coniferous stands

In total, 124 fungal species were found fruiting in the Grande Prairie and Manning study areas between June and August of 2000. Sixty-five fungal species were found in deciduous stands and 63 species were found in mixedwood stands in the Grande Prairie study area (Table 8.2). Deciduous stands had 50 decomposer species and 15 mycorrhizal species; mixedwood stands had 41 decomposer species and 22 mycorrhizal species. Deciduous and mixedwood stands shared 49% of decomposer species and 44% of mycorrhizal species. Overall, 48% of fungal species were common between forest types in the Grande Prairie study area.

Sixty fungal species were observed fruiting in both coniferous and mixedwood stands in the Manning study area (Table 8.2). Coniferous stands had 45 decomposer species and 15 mycorrhizal species; mixedwood stands had 36 decomposer species and 24 mycorrhizal species. Coniferous and mixedwood stands shared 33% of decomposer species and 26% of mycorrhizal species. Overall, 30% of species were common between forest types in the Manning study area.

Between study areas, mixedwood stands shared 45% of all fungal species (48% of decomposer species and 39% of mycorrhizal species), and deciduous stands (from the Grande Prairie study area) and coniferous stands (from the Manning study area) shared 25% of all fungal species

(26% of decomposer species and 20% of mycorrhizal species).

In undisturbed forests, average fungal species richness did not differ significantly (F = 1.63; p = 0.214) between treatments (Table 8.2), although, mixedwood stands in the Manning study area tended to have more species. Fungal Shannon diversity was highest (F = 3.58; $p < 0.05$) in deciduous stands, lowest in coniferous stands and intermediate in mixedwood stands (Table 8.2).

Neither average decomposer species richness (F = 0.78; p = 0.517), nor decomposer diversity differed significantly (F = 1.56; p = 0.230) between forest cover types. However, decomposer diversity tended to be higher in the Grande Prairie study area.

More mycorrhizal species (F = 5.05; $p < 0.01$) were found in mixedwood stands compared with deciduous and coniferous stands (Table 8.2). Mycorrhizal diversity differed (F = 7.29; $p < 0.01$), with higher diversity in deciduous and mixedwood stands and lower diversity in coniferous stands (Table 8.2). Low diversity of mycorrhizal species in coniferous stands was a result of very low abundance values of fruiting species.

Detrended correspondence analysis revealed significant differences in fungal communities between deciduous, mixedwood and coniferous stands (Figure 8.1). Axis 1 separated fungal communities along a gradient representing forest cover type (*i.e.*, deciduous – mixedwood – coniferous). Axis 2 dispersed sample scores revealing relative variation within treatments. The first ordination axis was significant (F = 19.79; $p < 0.0001$) and accounted for 14.3% of the variance in the overall species-treatment relationship. Axis 2 accounted for an additional 7.5% of the variation. Axes 1 and 2 had eigen values of 0.79 and 0.42, respectively.

The fungal community in coniferous stands had the highest level of variation (as evidenced by the greatest dispersal of sample scores in ordination space - Figure 8.1), and this community was distinct from that observed in mixedwood stands. In addition, fungal communities observed in mixedwood stands from both study areas were distinct, with mixedwood stands in the Manning study area having a more variable fungal community than mixedwood stands in the Grande Prairie study area. The fungal community found in deciduous stands differed from the community found in mixedwood stands, despite some overlap. The fungal community in deciduous stands was more variable than the fungal community in mixedwood stands (Figure 8.1). Distinct regional variation in fungal communities found in mixedwood stands was observed.

Decomposer and mycorrhizal species groups were equally and evenly dispersed throughout ordination space with no definitive associations of either group with forest type or DCA axes (data not shown). However, specific species (decomposer and/or mycorrhizal) that combined a high relative abundance with a high frequency of occurrence carried the most weight in determining species-sample relationships. The location of species scores, in ordination space, indicated the forest cover type wherein each species occurred in higher than average relative abundance.

Decomposer species most diagnostic of deciduous stands included *Phellinus tremulae* and *Collybia dryophila*, where *P. tremulae* dominated aspen boles and *C. dryophila* dominated decaying organic matter on the forest floor. Mixedwood stands, at the Grande Prairie study area, were dominated by *C. acervata* and *Tubaria furfuracea*. In addition, decaying wood in both deciduous and mixedwood stands in the Grande Prairie study area was commonly populated by *Cerrena unicolor* and *Pleurotus ostreatus*, and *Mycena pectinata* was abundant on the floor of each forest type. At the Manning study area, coniferous stands were dominated by *Chondrostereum purpureum* on dead wood, and by *Marasmius epiphyllus, Phaeocollybia similis* and *Psathyrella hydrophila* on the forest floor. Mixedwood stands had abundant *Tremella mesentarica* and *Polyporus pargamenus* on dead wood, and *Marasmius pallidocephalus* on the forest floor.

The mycorrhizal species most strongly associated with deciduous stands included *Russula laurocerasi* and *R. paludosa*, but *R. chamaeoleontina, R. borealis* and *R. nigricans* were representative of both deciduous and mixedwood stands in the Grande Prairie study area; *Cortinarius mucosus* dominated mixedwood stands. At the Manning study area, mixedwood stands were dominated by *C. alboviolaceous, C. castaneus* and *Leccinum boreale.* Coniferous stands had strong associations with mycorrhizal species that included *Boletus edulis, Hebeloma crustuliniforme* and *Tricholoma flavovirens*.

Comparison of deciduous clearcutting and understorey protection harvesting

At the Grande Prairie study area, 67 fungal species were found fruiting in the deciduous stands, deciduous clearcuts, mixedwood stands and understorey protection cutblocks during the summers of 2001 and 2002. Forty-five fungal species (30 decomposer and 15 mycorrhizal species) were found in deciduous stands and 17 fungal species (15 decomposer and 2 mycorrhizal species) were found in deciduous clearcuts (Table 8.3). Of these species, 26% were common between deciduous stands and clearcuts. Deciduous stands and clearcuts shared 32% of decomposer species and 13% of mycorrhizal species. Forty-eight fungal species (29 decomposer and 19 mycorrhizal species) were found in mixedwood stands and 28 fungal species (20 decomposer and 8 mycorrhizal species) were found in understorey protection cutblocks (Table 8.3). Of these species, 36% were common between mixedwood stands and understorey protection cutblocks. Mixedwood stands and understorey protection cutblocks shared 36% of decomposer species and 35% of mycorrhizal species.

At the Grande Prairie study area, average fungal species richness differed significantly ($F = 11.65$; $p < 0.001$) between stand types (Table 8.3), with harvested stands having fewer species than forested stands. Average fungal Shannon diversity decreased ($F = 7.78$; $p < 0.01$) after harvest in deciduous stands, but did not change statistically after understorey protection harvesting (Table 8.3).

On average, fewer decomposer species ($F = 0.78$; $p = 0.517$) and fewer mycorrhizal species ($F = 5.05$; $p < 0.01$) were found in harvested stands compared to forested stands, and the least number of species were observed in deciduous clearcuts (Table 8.3). The same trend was observed for both decomposer ($F = 3.24$; $p < 0.05$) and mycorrhizal Shannon diversity ($F = 2.50$; $p = 0.089$) (Table 8.3).

Detrended CA revealed differences ($F = 4.75$; $p < 0.05$) in fungal communities between deciduous stands and clearcuts, and between mixedwood stands and understorey protection cutblocks (Figure 8.2). Axis 1 distinguished between pre-harvest and post-harvest stand fungal communities. In addition, the fungal communities observed in deciduous clearcuts over the two-year period differed completely. Axis 2 distinguished different fungal communities between deciduous clearcuts and mixedwood understorey protection cutblocks. The first ordination axis accounted for 13.1% of the variance in the overall species-treatment relationship. Axis 2 accounted for an additional 8.4% of the variation. Axes 1 and 2 had eigen values of 0.64 and 0.42, respectively.

The fungal community in deciduous and mixedwood stands shared many similarities, but deciduous stands produced the most variable community (Table 8.2). Fruiting species, in deciduous clearcuts, were completely different from one year (2001) to the next (2002) resulting in the highest level of variation. Fungal communities observed in mixedwood stands and understorey protection cutblocks were different, with the fungal community in understorey protection cutblocks being more variable (Table 8.2).

Decomposer and mycorrhizal species groups were dispersed differently throughout ordination space, with decomposers being dispersed along Axis1 (data not shown). As a result, the decomposer community was most important in structuring differences between deciduous stands and clearcuts. Decomposer species most

diagnostic of deciduous stands (and the aspen canopy of mixedwood stands) included *Phellinus tremulae, Cerrena unicolor* and *Fometopsis pinicola*. *Collybia acevata* and *Psathyrella hydrophila* were associated with decaying litter and wood in deciduous stands. Deciduous clearcuts were dominated by *Scutellinia scutellata* in the first year after harvest, and *Peziza badia* in the second year after harvest.

Mixedwood stands were dominated by *Tremella mesentarica,* and understorey protection cutblocks were dominated by *Tubaria furfuracea* (on the forest floor) and *Pleurotus ostreatus* (on dead wood). *Collybia dryophila* commonly occurred in both types of harvested stands.

Mycorrhizal species were dispersed along Axis 2 (data not shown), and thus, were most important in structuring differences between mixedwood stands and understorey protection cutblocks. *Hydnum repandum* and *Hygrocybe laeta* dominated mixedwood stands. Understorey protection cutblocks were dominated by *Leccinum boreale, Inocybe fastigiata* and *R. fragilis*.

The mycorrhizal species most strongly associated with deciduous stands included *Russula laurocerasi, R. paludosa*, and *R. borealis*, but *R. xerampelina* was representative of both deciduous and mixedwood stands. Only two mycorrhizal species fruited in deciduous clearcuts: *Tricholoma populinum* and *I. fastigiata*.

Orthogonal distance was determined from sample scores in ordination space to determine if clearcut harvesting had a greater influence on deciduous stand fungal communities compared to understorey protection harvesting on mixedwood stand fungal communities. Average distance between deciduous stands and deciduous clearcuts was marginally greater ($F = 3.81$; $p < 0.05$) than the distance between understorey protection cutblocks and mixedwood stands (Table 8.4). This difference suggests that understorey protection harvesting resulted in a smaller change in the fungal community after harvest, compared to clearcutting.

Comparison of coniferous clearcutting and understorey protection harvesting

At the Manning study area, 55 fungal species were found fruiting in the coniferous stands, coniferous clearcuts, mixedwood stands and understorey protection cutblocks during the summers of 2002 and 2003. Thirty-three fungal species (30 decomposer and 3 mycorrhizal species) were found in coniferous stands and 12 fungal species (11 decomposer and 1 mycorrhizal species) were found in coniferous clearcuts (Table 8.3). Of these species, 15% were common between coniferous stands and clearcuts. Coniferous stands and clearcuts shared 14% of decomposer species and 33% of mycorrhizal species. Eighteen fungal species (15 decomposer and 3 mycorrhizal species) were found in mixedwood stands and 27 fungal species (21 decomposer and 6 mycorrhizal species) were found in understorey protection cutblocks (Table 8.3). Of these species, 45% were common between mixedwood stands and understorey protection cutblocks. Mixedwood stands and understorey protection cutblocks shared 50% of decomposer species and 29% of mycorrhizal species. These differences, particularly the low number of mycorrhizal species found in the Manning study area, exemplify regional differences in plant communities.

At the Manning study area, average fungal species richness differed significantly ($F = 6.24$; $p < 0.001$) between stand types (Table 8.3), with clearcut stands having fewer species than coniferous stands. Average fungal diversity decreased ($F = 8.21$; $p < 0.001$) after harvest in coniferous forests, but did not change statistically after understorey protection harvesting (Table 8.3).

On average, fewer decomposer species ($F = 5.24$; $p < 0.01$) were found in clearcuts compared to coniferous stands, but richness was higher in understorey protection cutblocks compared to mixedwood stands (Table 8.3).

However, decomposer diversity (F = 6.60; $p < 0.01$) was only lower in coniferous clearcuts.

Fewer mycorrhizal species (F = 3.02; $p = 0.05$) were found in clearcuts compared to coniferous stands, but richness did not change statistically in understorey protection cutblocks (Table 8.3). Fungal diversity was highest in mixedwood stands and understorey protection cutblocks, and lowest in coniferous stands and clearcuts (F = 6.60; $p < 0.01$); harvested stands did not differ from their pre-harvest forest types (Table 8.3).

Detrended CA revealed differences (F = 39.86; $p < 0.0001$) in fungal communities between coniferous stands and clearcuts, and between mixedwood stands and understorey protection cutblocks (Figure 8.3). Axis 1 distinguished fungal communities between forest cover types and harvest treatments; Axis 2 dispersed sample scores based on community variation within treatments. The first ordination axis accounted for 11.9% of the variance in the overall species-treatment relationship. Axis 2 accounted for an additional 8.8% of the variation. Axes 1 and 2 had eigen values of 0.87 and 0.64, respectively.

The fungal community in coniferous stands had the most variability and was distinct from both mixedwood treatments and coniferous clearcuts. Fungal communities observed in mixedwood stands and understorey protection cutblocks were different, with the fungal community in understorey protection cutblocks being more variable, possible as a result of an increase in species richness. Strong year-to-year relationships were observed with more variation existing between years compared to within years.

Decomposer and mycorrhizal species groups were dispersed evenly throughout ordination space, with no strong relationships identified between decomposer and mycorrhizal species with either DCA Axes (data not shown). Decomposer species had slightly more variation.

Decomposer species most diagnostic of coniferous forests, and the aspen canopy of mixedwood stands, included *Phellinus tremulae* and *Fometopsis pinicola. Morchella elata* was common on the forest floor of both forest types.

Collybia acevata and *Tremella mesentarica* dominated mixedwood forests. Mixedwood understorey protection cutblocks were dominated by *Tubaria furfuracea* and *Collybia dryophila. Pleurotus ostreatus* (on dead wood) and *Psathyrella hydrophila* (on the forest floor) commonly occurred in mixedwood forests and understorey protection cutblocks.

Coniferous clearcuts were dominated by *Peziza badia* the first year after harvest, and *Scutellinia scutellata* the second year after harvest (the reverse of deciduous clearcuts in Grande Prairie).

The mycorrhizal species most strongly associated with coniferous forests included *Russula chaemaeoleontina, Boletus edulis, Cortinarius castaneus*, and *Inocybe fastigiata*; only *C. multiformis* was observed in coniferous clearcuts, but it dominated mixedwood understorey protection cutblocks with *Leccinum boreale* and *Tricholoma populinum*. Mixedwood forests were dominated by *Boletus piperatus* and *Hygrocybe ceracea*.

Clearcutting coniferous stands had a greater influence on the fungal community than implementing and understorey protection strategy on mixedwood stands. Orthogonal distance between coniferous reserve stands and coniferous clearcuts was significantly greater (F = 182.80; $p < 0.0001$) than the distance between understorey protection cutblocks and mixedwood stands (Table 8.4). Clearcutting coniferous stands had the greatest influence on plant communities among all harvest treatments in both study areas.

Discussion

Over the four years of data collection in this study annual variation in sporocarp production and abundance was observed. Fluctuations in temperature and moisture (O'Dell *et al.* 1999) regulate which fungal species fruit in any given year (Senn-Irlet and Bieri 1999), and within any

given season. As a result, collections over a number of years are considered essential to more accurately describe treatment effects. The number of growing seasons in which fungal sporocarps were sampled in this project represents the minimum study length, but the consistent area sampled, both before and after harvest, reduced sampling error due to variation in sporocarp presence and abundance.

Comparison of deciduous, mixedwood and coniferous stands

Fungal communities in deciduous, mixedwood and coniferous forest cover types differed. Similar differences have been associated with fungal-substrate relationships and successional changes over time. For example, decomposer fungi and mycorrhizal fungi have substrate-specific limitations. Some decomposer species are highly deadwood species-specific, while others have broad deadwood species specifications. In addition, as DWM progresses through the various decay stages, chemical changes to the deadwood influences substrate specificity (Hintikka 1988; Crites and Dale 1998; Senn-Irlet and Bieri 1999; Allen *et al.* 2000). The availability of deadwood and litter resources was different in each forest cover type, in terms of wood and litter species, volume and stage of decay (Chapter 4). This variation and the regulating influences of ambient temperature and precipitation determined fungal species presence and decomposer sporocarp production.

Mycorrhizal fungi have similar host-specific limitations. Some species are highly host species-specific, while others have broad host species requirements (Trappe 1962). In addition, as host trees age, physiological changes to the host tree influence mycorrhizal community dynamics (Mason *et al.* 1982; Hintikka 1988; Lumley *et al.* 1995; Senn-Irlet and Bieri 1999). Deciduous, mixedwood and coniferous forests had a different canopy tree species composition (Chapter 3) and consisted of different aged trees. Thus, different forest cover types supported different communities of mycorrhizal fungi.

Decomposer and mycorrhizal species both contributed to fungal community variation. Variation in fungal communities was greatest in coniferous stands, followed by variation in deciduous stands. The high variation in fungal communities in coniferous stands was likely a result of patchy distribution of fungal species within each stand. This patchy distribution was associated with availability and distribution of appropriate substrate for decomposer species (Allen *et al.* 2000) and host trees or shrubs for mycorrhizal species (Bradbury 1996). Being older, the coniferous stands were more variable in deadwood resources (both in terms of decay stages and size classes – Chapter 4), and in age and size cohorts of suitable mycorrhizal host trees and shrubs (Chapter 3).

Regional differences were observed in fungal communities found in mixedwood stands. Fungal community variation was lowest in mixedwood stands within each region. However, overall variation in mixedwood stands from both regions was greater than that observed in deciduous stands. Regional differences were a result of different decomposer communities fruiting on different types of available deadwood resources (Chapter 4), and the regulating influence of regional climate (temperature and precipitation).

Comparison of clearcutting and understorey protection harvesting

Understorey protection harvesting influenced decomposer fungi to a lesser degree than traditional clearcutting of both deciduous and coniferous stands. Clearcuts have been described previously as poor habitat for decomposer sporocarp production, due to inappropriate microclimatic conditions (Lumley *et al.* 1995). In all cutblock scenarios, some proportion of the previously colonized deadwood resource was removed or damaged (*i.e.,* crushed in harvesting or piled and burned), but the proportion damaged in clearcuts was greater than in understorey protection cutblocks. In addition, the dessicated condition of exposed DWM and duff in clearcuts limited fungal growth and sporocarp production. Furthermore, mechanical site preparation in the coniferous clearcuts buried some DWM and disrupted mycelial networks within duff. This likely further

contributed to limited sporocarp production, and may explain the extensive differences observed in decomposer communities after clearcutting coniferous stands compared to deciduous stands.

Compared with clearcuts, understorey protection cutblocks retained abundant mixedwood stand substrates for decomposer fungi. In understorey protection cutblocks, most of the cutblock area was undisturbed by harvest machinery, and thus, cutblocks did not lose as much existing DWM to crushing or to burn piles compared to clearcuts. Furthermore, changes to the microclimatic conditions in understorey protection cutblocks were not as dramatic as those changes found in clearcuts. Despite these similar structural characteristics, the response of the decomposer community to understorey protection harvesting resulted in regional differences. At the Grande Prairie study area, decomposer species abundance decreased in the first year after harvest, but recovered during the second year after harvest. In contrast, at the Manning study area, decomposer species abundance and richness increased after harvest.

Climate data (Environment Canada 2004) from the Manning study area, indicated that 2002 and 2003 had average precipitation, but below average temperatures during the summer season. As a result, partial harvesting in the understorey protection cutblocks may have improved sporocarp production conditions by increasing ground layer temperatures (via increased radiant heating). This response was not observed at the Grande Prairie study area because summer climatic conditions were normal, and any microclimatic changes that occurred due to harvesting did not improve sporocarp production conditions further.

Mycorrhizal communities are known to change after logging in both coniferous and deciduous forest types (Lumley *et al.* 1995; Bradbury 1996). The biggest difference between deciduous and coniferous clearcuts was the availability of suitable refuge hosts for mycorrhizal fungi after harvest (Bradbury 1997); deciduous clearcuts had extensive and vigorous woody species growth and as a result likely maintained a vigorous mycorrhizal community. On the other hand, most woody host species were removed or damaged in coniferous clearcuts. The potential for loss of viable mycorrhizal inoculum in these stands is greater if new mycorrhizal hosts do not re-establish quickly after harvest. Ambient conditions may still limit sporocarp production despite a functional symbiosis, but this pattern may be short-lived, as the microenvironment stabilizes in regenerating clearcuts.

Clearcutting caused a greater change to the mycorrhizal community than did understorey protection harvesting. The high density of live residuals provided a stable host root system in the understorey protection cutblocks. Observed differences in mycorrhizal communities in understorey protection cutblocks compared with mixedwood stands likely resulted from the change in microenvironment resulting from harvest. Very few mycorrhizal species produced sporocarps in the first year after harvest in both study areas. However, sporocarp production during the second growing season after harvest increased dramatically in understorey protection cutblocks in both study areas, and surpassed mixedwood forests at the Manning study area. This response was probably due to improved sporocarp production conditions as described above.

Management Implications and Future Research

High annual variation in fungal fruiting patterns points out the need for long-term studies so that we can better understand community structure and habitat preferences. The fact that fungal species richness and community structure varies greatly within and between forest types, led O'Dell *et al.* (1999) to suggest that conserving fungal diversity may require protecting more area than required to conserve understorey plants.

- To maintain decomposer communities manage deadwood resources such that all size classes and decay stage classes are available.

Decomposer fungal species require deadwood resources in a variety of sizes, decay stages and tree species. Previous studies have identified reductions of deadwood resources in harvested stands (Lee 2002), and suggest that these losses may represent one of the most identifiable and long term effects on a managed landbase (Freedman *et al.* 1996). While these consequences may be of concern after traditional clearcutting, it is unlikely that changes in understorey protection cutblocks will be as dramatic. Abundant live residuals, and only limited mechanical disruption of DWM in understorey protection cutblocks, results in abundant DWM immediately after harvest and provides for future inputs.

- To maintain mycorrhizal communities provide a suitable suite of host tree species.

While many mycorrhizal species are capable of forming associations with hardwood and softwood trees, many other mycorrhizal species are far more host-specific. As a result, mixedwood forests with active aspen and coniferous root growth support a diverse and abundant mycorrhizal community. Understorey protection cutblocks have abundant live residuals of both coniferous and deciduous woody species. With no damage to roots from harvesting activity beyond the skid trails, mycorrhizal roots likely remain intact after harvest. While microclimatic conditions may influence sporocarp production following understorey protection harvest, the root-fungus structure is likely well preserved.

Acknowledgements

Fungal collections, in the first sampling session of 2000, were made by Cris Gray, Dave McKinnon, Len Peleshok and Samantha Song; their attention to detail and persistence is gratefully acknowledged. Lisa Wilkinson provided comments to earlier versions of this chapter. Pat Soldan compiled and formatted the text, figures and tables.

Literature Cited

Allen, E., Morrison, D., and Wallis, G. 1996. Common tree diseases of British Columbia. Canadian Forest Service, Victoria, BC.

Allen, R.B., Buchanan, P.K., Clinton, P.W., and Cone, A.J. 2000. Composition and diversity of fungi on decaying logs in a New Zealand temperate beech (*Northofagus*) forest. Can. J. For. Res. 30:1025-1033.

Arora, D. 1986. Mushrooms Demystified. Ten Speed Press, Berkeley, CA.

Bradbury, S.M. 1996. Influence of clear-cutting on ectomycorrhizal fungi associated with lodgepole pine (*Pinus contorta*). Ph.D. Dissertation, University of Calgary, Calgary, AB.

Bradbury, S.M. 1997. The role of refuge plants in the maintenance of mycorrhizal inoculum in cut-blocks. Research Branch, Ministry of Forests, Victoria, BC.

Bradbury, S.M. 1998. Ectomycorrhizas of lodgepole pine (*Pinus contorta* Loud.) seedlings originating from seed in Southwestern Alberta cutblocks. Can. J. Bot. 76:213-217.

Bradbury, S.M., R.M. Danielson & S. Visser. 1998. Ectomycorrhizas of regenerating stands of lodgepole pine (*Pinus contorta* Loud.). Canadian Journal of Botany. 76: 218-227.

Crites, S. and Dale, M.R.T. 1998. Diversity and abundance of bryophytes, lichens and fungi in relation to woody substrate and successional stage in aspen mixedwood boreal forests. Can. J. Bot. 76:641-651.

Danielson, R.M. 1984. Ectomycorrhizal associations in jack pine stands in northeastern Alberta. Can. J. Bot. 62:932-939.

Dighton, J., Poskitt, J.M., and Howard, D.M. 1986. Changes in occurrence of

basidiomycete fruit bodies during forest stand development: with special reference to mycorrhizal species. Trans. Brit. Mycol. Soc. 87:163-171.

Edmonds, R.L. and Lebo, D.S. 1998. Diversity, production, and nutrient dynamics of fungal sporocarps on logs in an old-growth temperate rain forest, Olympic National Park, Washington. Can. J. For. Res. 28:665-673.

Environment Canada. 2004. Environment Canada. Canadian climate normals (online). Grovedale and Notikewin stations. Available at: http://www.climate.weather office.ec.gc.ca/ Welcome_e.html.

Freedman, B., Zelazny, V., Beaudette, D., Fleming, T., Flemming, S, Forbes, G., Gerrow, J.S., Johnson, G., and Woodley S. 1996. Biodiversity implications of changes in the quantity of dead organic matter in managed forests. Environ. Rev. 4:238-265.

Hintikka, V. 1988. On the macromycete flora in oligotrophic pine forests of different ages in south Finland. Acta Bot. Fenn. 136: 89-94.

Last, F.T., Dighton, J., and Mason, P.A. 1987. Successions of sheathing mycorrhizal fungi. Tr. Ecol. Evo. 2: 157-161.

Lee, P. 2002. Forest structure after wildfire and harvesting. In: Ecological basis for stand management. Alberta Research Council, Vegreville, AB.

Lumley, T.C., Timoney, K.P., and Currah, R.S. 1995. Effect of clearcut logging on the ectomycorrhizal fungus communities associated with white spruce forests in Wood Buffalo National Park. University of Alberta, Edmonton. AB.

Mason, P.A., Last, F.T., and Ingleby, K. 1982. Ecology of some fungi associated with an ageing stand of birches (*Betula pendula* and *B. pubescens*

O'Dell, T.E., Ammirati, J.F., and Schreiner, E.G. 1999. Species richness and abundance of ectomycorrhizal basidiomycete sporocarps on a moisture gradient in the *Tsuga heterophylla* zone. Can. J. Bot. 77:1699-1711.

SAS. 2000. JMP Statistics and Graphics Guide, Version 3.2.1, SAS Institute, Cary, NC.

Senn-Irlet, B. and Bieri, G. 1999. Sporocarp succession of soil-inhabiting macrofungi in an autochthonous subalpine Norway spruce forest of Switzerland. For. Ecol. Manage. 124:169-175.

Schalkwijk-Barendsen, H.M.E. 1991. Mushrooms of Western Canada. Lone Pine Publishing, Edmonton, AB.

ter Braak, C.J.F. and P. Smilauer.1998. CANOCO: a fortran program for canonical community ordination by (partial), (detrended), (canonical), correspondence analysis, principle components analysis, and redundancy analysis, version 4 for Windows. Microcomputer Power, Ithaca, NY.

Trappe, J.M. 1962. Fungus associates of ectotrophic mycorrhizae. Botan. Rev. 28:538-606.

Table 8.1. Sporocarp sampling schedule for the Grande Prairie and Manning study areas.

Grande Prairie and Manning Study Areas			Manning Study Area
2000	2001	2002	2003
mid June	late May	late May	
mid July	mid June	mid June	mid June
early August	early July	mid July	mid July
	late July	early August	

Table 8.2. Total fungal species richness (per treatment per year), average species richness (per stand per year), average Shannon diversity (per stand per year), and average fungal species relative abundance (average of relative abundance per sampling session) from the Grande Prairie (GP) and Manning (MN) study areas. All data were collected in 2000 from undisturbed forests (each treatment includes six stands: three stands before harvest and three reserves). Fungal taxa denoted with sp. could not be identified to species. Species were separated by carbohydrate acquisition strategy (*i.e.*, decomposer and mycorrhizal species); decomposers included both saprotrophic and parasitic species.

	Deciduous forest (GP)	Mixedwood forest (GP)	Mixedwood forest (MN)	Coniferous forest (MN)
Decomposer species				
Total species richness	50	41	36	45
Average species richness	$20.8^{a} \pm 2.9$	$17.0^{a} \pm 2.5$	$20.8^{a} \pm 0.9$	$20.3^{a} \pm 1.2$
Average Shannon diversity	$2.1^{a} \pm 0.2$	$1.8^{a} \pm 0.1$	$1.6^{a} \pm 0.2$	$1.5^{a} \pm 0.3$
Mycorrhizal species				
Total species richness	15	22	24	15
Average species richness	$8.2^{b} \pm 0.6$	$10.5^{ab} \pm 1.0$	$13.5^{a} \pm 1.5$	$7.8^{b} \pm 1.3$
Average Shannon diversity	$0.6^{ab} \pm 0.1$	$0.8^{a} \pm 0.1$	$0.5^{b} \pm 0.1$	$0.1^{c} \pm 0.04$
All species combined				
Combined species richness	65	63	60	60
Combined average species richness	$29.0^{a} \pm 3.1$	$27.5^{a} \pm 2.8$	$34.3^{a} \pm 1.6$	$28.1^{a} \pm 1.9$
Combined average Shannon diversity	$2.6^{a} \pm 0.1$	$2.5^{a} \pm 0.2$	$2.1^{ab} \pm 0.3$	$1.6^{b} \pm 0.3$
Decomposer Species Abundance				
Auricularia auricula	0.0021	0.0053	0.0000	0.0000
Cerrena unicolor	0.1048	0.0471	0.0000	0.0005
Chlorociboria aeruginascens	0.0003	0.0008	0.0000	0.0653
Chondrostereum purpureum	0.0707	0.0643	0.1664	0.0765
Clavariadelphus sachalinensis	0.0000	0.0000	0.0000	0.0013
Clavicorona pyxidata	0.0032	0.0000	0.0007	0.0001
Clitocybe geotropa	0.0000	0.0000	0.0000	0.0003
Clitocybe gibba	0.0318	0.0033	0.0017	0.0022
Clitocybe odora	0.0000	0.0000	0.0038	0.0001
Clitocybe robusta	0.0013	0.0000	0.0000	0.0011
Clitocybe sp.	0.0021	0.0000	0.0000	0.0001
Collybia acervata	0.0254	0.0633	0.0618	0.0049
Collybia confusa	0.0000	0.0000	0.0000	0.0080
Collybia dryophila	0.0345	0.1275	0.0329	0.0044

	Deciduous forest (GP)	Mixedwood forest (GP)	Mixedwood forest (MN)	Coniferous forest (MN)
Coprinus atramentarius	0.0004	0.0000	0.0000	0.0000
Coprinus elisii	0.0003	0.0000	0.0001	0.0000
Coprinus micaceus	0.0048	0.0000	0.0000	0.0000
Coprinus sp. (on moose dung)	0.0052	0.0006	0.0000	0.0000
Coprinus sp. (on forest floor)	0.0000	0.0000	0.0000	0.0007
Corticium sp.	0.0000	0.0006	0.0000	0.0000
Crepidotus applanatus	0.0000	0.0005	0.0001	0.0000
Crepidotus ellipsoideus	0.0112	0.0023	0.0055	0.0000
Crepidotus mollis	0.0364	0.0195	0.0066	0.0000
Cystoderma amiantinum	0.0004	0.0000	0.0018	0.0019
Dacrymyces palmatus	0.0000	0.0000	0.0000	0.0063
Discina perlata	0.0000	0.0000	0.0000	0.0006
Encoelia furfuracea	0.0061	0.0000	0.0000	0.0000
Exidia glandulosa	0.0004	0.0029	0.0000	0.0064
Fomes cajanderi	0.0000	0.0006	0.0045	0.0018
Fomes fomentarius	0.0059	0.0025	0.0000	0.0000
Fometopsis officinale	0.0000	0.0000	0.0000	0.0011
Fometopsis pinicola	0.0148	0.0072	0.0038	0.0058
Galerina autumnalis	0.0000	0.0040	0.0000	0.0000
Ganoderma applanatum	0.0092	0.0125	0.0000	0.0030
Geopyxis carbonaria	0.0011	0.0000	0.0000	0.0000
Gleophyllum sepiarium	0.0000	0.0000	0.0000	0.0112
Gymnopilus penetrans	0.0034	0.0100	0.0014	0.0009
Gyromitra esculenta	0.0044	0.0041	0.0000	0.0018
Helvella acetabulum	0.0012	0.0000	0.0000	0.0000
Helvella elastica	0.0089	0.0000	0.0000	0.0000
Hericium ramosum	0.0004	0.0079	0.0004	0.0031
Irpex lacteus	0.0154	0.0000	0.0000	0.0000
Lepiota alba	0.0019	0.0000	0.0000	0.0005
Lepista irina	0.0011	0.0000	0.0000	0.0000
Lycoperdon perlatum	0.0129	0.0125	0.0022	0.0010
Marasmius epiphyllus	0.0127	0.0006	0.0506	0.0826
Marasmius pallidocephalus	0.0000	0.1728	0.0670	0.0343
Marasmius sp.	0.0013	0.0000	0.0001	0.0000
Marasmius strictipes	0.0000	0.0000	0.0100	0.0001
Melanoleuca cognata	0.0000	0.0000	0.0043	0.0330
Morchella elata	0.0000	0.0020	0.0021	0.0002
Mycena leaiana	0.0107	0.0017	0.0000	0.0000
Mycena pectinata	0.0632	0.0122	0.0015	0.0003
Mycena psammicola	0.0000	0.0000	0.0000	0.0002
Mycena stannea	0.0000	0.0000	0.0008	0.0002
Omphalina epichysium	0.0007	0.0000	0.0000	0.0141
Penophora rufa	0.0346	0.0122	0.2646	0.0104
Peziza badia	0.0172	0.0006	0.0027	0.0000
Phaeocollybia similes	0.0000	0.0000	0.0225	0.2426
Phellinus chrysoloma	0.0111	0.0000	0.0000	0.0005
Phellinus tremulae	0.0420	0.0315	0.0101	0.0028
Pholiota alnicola	0.0000	0.0000	0.0000	0.0009

	Deciduous forest (GP)	Mixedwood forest (GP)	Mixedwood forest (MN)	Coniferous forest (MN)
Pholiota mutabilis	0.0000	0.0000	0.0000	0.0062
Pholiota squarrosa	0.0085	0.0029	0.0000	0.0000
Piptoporus betulinus	0.0017	0.0000	0.0000	0.0000
Pleurotus ostreatus	0.0256	0.0248	0.0017	0.0002
Pluteus cervinus	0.0000	0.0000	0.0004	0.0001
Pluteus pellitus	0.0028	0.0030	0.0007	0.0002
Polyporus abietinus	0.0000	0.0000	0.0000	0.0125
Polyporus elegans	0.0009	0.0019	0.0041	0.1384
Polyporus pargamenus	0.0697	0.0206	0.0461	0.0541
Polyporus varius	0.0023	0.0035	0.0041	0.0000
Psathyrella hydrophila	0.0087	0.0000	0.0000	0.1003
Psathyrella longipes	0.0000	0.0000	0.0000	0.0001
Psathyrella sp.	0.0045	0.0017	0.0002	0.0000
Scutellinia scutellata	0.0000	0.0087	0.0006	0.0000
Spathularia spathulata	0.0000	0.0000	0.0000	0.0001
Spongipellis delectans	0.0013	0.0000	0.0000	0.0000
Stereum sp.	0.0000	0.0000	0.0454	0.0018
Strobilurus lignitilis	0.0005	0.0000	0.0000	0.0010
Trametes versicolor	0.0000	0.0006	0.0000	0.0010
Tremella mesentarica	0.0287	0.0180	0.0433	0.0177
Tubaria furfuracea	0.0318	0.0359	0.0001	0.0043
Xeromphalina fraxinophila	0.0000	0.0000	0.0018	0.0003
Mycorrhizal species				
Amanita muscaria	0.0003	0.0040	0.0135	0.0006
Amanita vaginata	0.0000	0.0000	0.0063	0.0000
Boletus edulis	0.0000	0.0019	0.0017	0.0067
Cortinarius alboviolaceus	0.0019	0.0000	0.0041	0.0000
Cortinarius castaneus	0.0083	0.0157	0.0066	0.0019
Cortinarius cinnamomeobadius	0.0000	0.0017	0.0091	0.0009
Cortinarius mucosus	0.0215	0.0600	0.0180	0.0019
Cortinarius multiformis	0.0011	0.0011	0.0020	0.0009
Cortinarius sanguineus	0.0000	0.0000	0.0000	0.0020
Cortinarius scandens	0.0000	0.0006	0.0000	0.0000
Cortinarius trivialis	0.0000	0.0000	0.0003	0.0000
Hebeloma crustuliniforme	0.0037	0.0014	0.0000	0.0032
Hydnum repandum	0.0000	0.0005	0.0009	0.0004
Hygrocybe ceracea	0.0000	0.0000	0.0000	0.0005
Hygrocybe laeta	0.0000	0.0025	0.0020	0.0003
Hygrocybe sp.	0.0000	0.0000	0.0000	0.0001
Hygrophorus piceae	0.0000	0.0000	0.0000	0.0007
Inocybe fastigiata	0.0092	0.0000	0.0000	0.0000
Inocybe lacera	0.0000	0.0006	0.0000	0.0000
Inocybe languinosa	0.0067	0.0000	0.0000	0.0000
Inocybe ovatocystis	0.0000	0.0005	0.0000	0.0000
Laccaria laccata	0.0004	0.0005	0.0135	0.0003
Lactarius affinis	0.0000	0.0000	0.0018	0.0000
Lactarius deliciosus	0.0000	0.0010	0.0020	0.0000

	Deciduous forest (GP)	Mixedwood forest (GP)	Mixedwood forest (MN)	Coniferous forest (MN)
Leccinum boreale	0.0012	0.0010	0.0152	0.0006
Leccinum niveum	0.0000	0.0000	0.0002	0.0006
Leccinum ochraceum	0.0000	0.0000	0.0003	0.0000
Leccinum snellii	0.0000	0.0000	0.0004	0.0001
Russula aeruginea	0.0000	0.0000	0.0013	0.0000
Russula borealis	0.0092	0.0312	0.0059	0.0001
Russula chamaeoleontina	0.0109	0.0402	0.0066	0.0001
Russula fragilis	0.0030	0.0042	0.0054	0.0001
Russula laurocerasi	0.0968	0.0311	0.0000	0.0000
Russula nigricans	0.0107	0.0297	0.0016	0.0003
Russula paludosa	0.0104	0.0060	0.0000	0.0000
Russula peckii	0.0000	0.0000	0.0015	0.0000
Russula xerampelina	0.0016	0.0055	0.0000	0.0000
Thelephora terrestris	0.0000	0.0000	0.0004	0.0000
Tricholoma flavovirens	0.0000	0.0036	0.0004	0.0067
Tricholomopsis rutilans	0.0000	0.0012	0.0000	0.0000

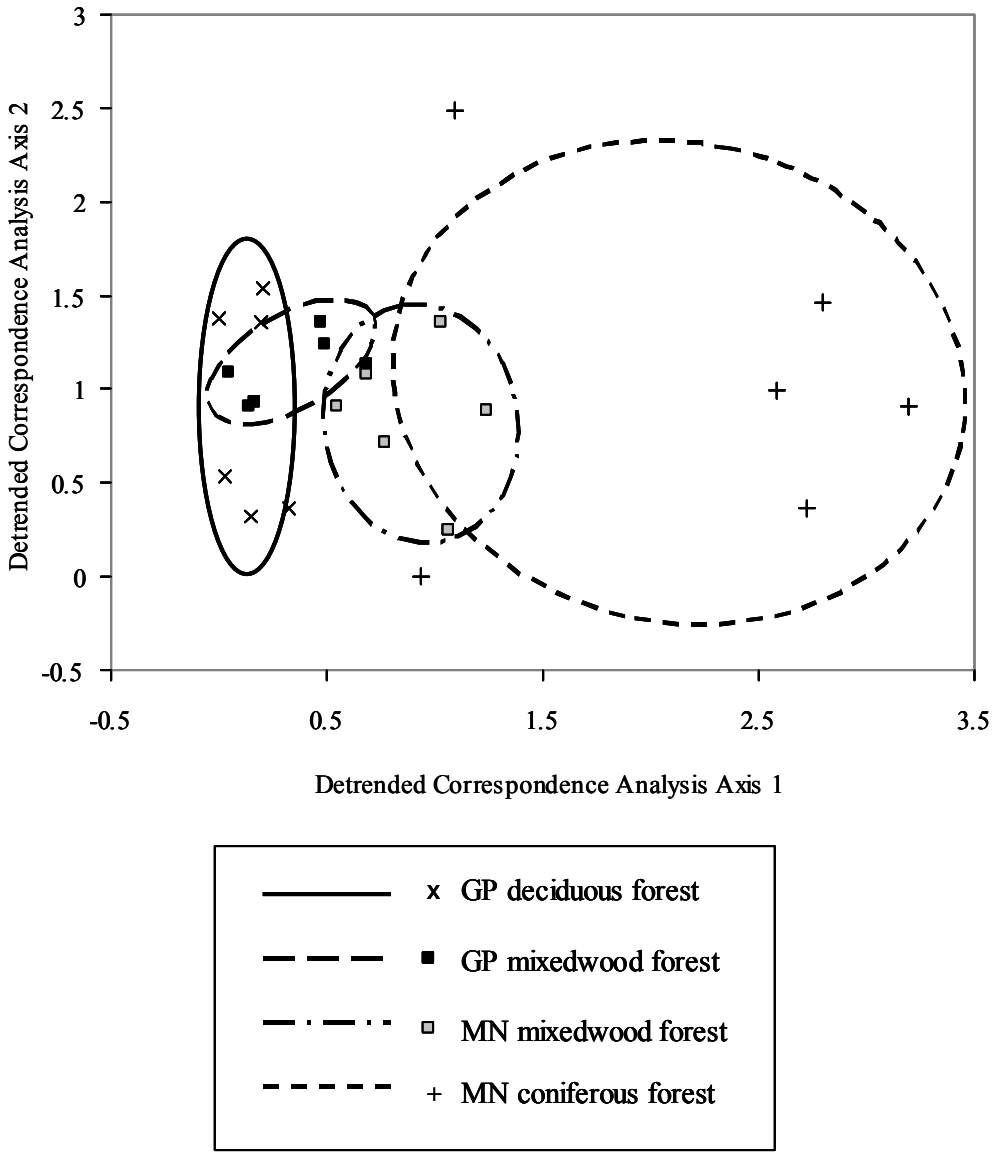


Figure 8.1. Detrended correspondence analysis of transformed (SqRt) relative abundance of fungal species from the Grande Prairie (GP) and Manning (MN) study areas. All data were collected in 2000 from undisturbed forests (each treatment includes six stands: three stands before harvest and three reserves).

Table 8.3. Total fungal species richness (per treatment), average species richness (per stand per year), average Shannon diversity (per stand per year), and average fungal species relative abundance (average of relative abundance per sampling session) from the Grande Prairie and Manning study areas. Means include data from 2001 and 2002 from the Grande Prairie study area, and 2002 and 2003 from the Manning study area. Fungal taxa denoted with sp. could not be identified to species. Species were separated into carbohydrate acquisition strategy (*i.e.*, decomposer and mycorrhizal species); decomposer species include both saprotrophic and parasitic species.

	Grande Prairie study area				**Manning study area**			
	Deciduous forest reserves	Deciduous clearcut stands	Mixedwood forest reserves	Mixedwood understorey protection cutblocks	Mixedwood forest reserves	Mixedwood understorey protection cutblocks	Coniferous forest reserves	Coniferous clearcut stands
Decomposer species								
Total species richness	30	15	29	20	15	21	30	11
Average species richness	$12.0^{a} \pm 1.9$	$4.0^{c} \pm 0.8$	$10.3^{a} \pm 1.7$	$6.8^{b} \pm 0.9$	$5.5^{bc} \pm 0.7$	$6.8^{a} \pm 1.2$	$8.8^{a} \pm 1.1$	$3.0^{c} \pm 1.1$
Average Shannon diversity	$1.7^{a} \pm 0.2$	$0.9^{b} \pm 0.3$	$1.6^{a} \pm 0.2$	$1.2^{ab} \pm 0.1$	$1.2^{a} \pm 0.1$	$1.3^{a} \pm 0.2$	$1.6^{a} \pm 0.1$	$0.6^{b} \pm 0.2$
Mycorrhizal species								
Total species richness	15	2	19	8	3	6	3	1
Average species richness	$3.8^{a} \pm 1.0$	$0.3^{c} \pm 0.3$	$5.2^{a} \pm 1.4$	$2.5^{b} \pm 0.2$	$1.0^{a} \pm 0.3$	$1.0^{a} \pm 0.3$	$0.7^{a} \pm 0.2$	$0.2^{b} \pm 0.2$
Average Shannon diversity	$0.5^{a} \pm 0.2$	$0.1^{b} \pm 0.1$	$0.4^{a} \pm 0.1$	$0.4^{a} \pm 0.1$	$0.19^{a} \pm 0.06$	$0.12^{ab} \pm 0.08$	$0.07^{b} \pm 0.03$	$0.02^{b} \pm 0.02$
All species combined								
Combined species richness	45	17	48	28	18	27	33	12
Combined average species richness	$15.8^{a} \pm 2.2$	$4.3^{c} \pm 1.0$	$15.5^{a} \pm 1.8$	$9.3^{b} \pm 1.1$	$6.5^{a} \pm 0.9$	$7.8^{a} \pm 1.2$	$9.5^{a} \pm 1.1$	$3.2^{b} \pm 1.1$
Combined average Shannon diversity	$2.2^{a} \pm 0.1$	$0.9^{c} \pm 0.3$	$2.0^{ab} \pm 0.2$	$1.6^{b} \pm 0.1$	$1.4^{a} \pm 0.1$	$1.5^{a} \pm 0.1$	$1.7^{a} \pm 0.1$	$0.6^{b} \pm 0.3$
Decomposer species								
Agaricus silvicola	0.0000	0.0000	0.0000	0.0000	0.0076	0.0104	0.0000	0.0000
Auricularia auricula	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0004	0.0000
Baeospora myriadophylla	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0269	0.0000
Cerrena unicolor	0.1246	0.0000	0.2846	0.0000	0.0000	0.0000	0.0000	0.0000
Chlorociboria aeruginascens	0.0050	0.0370	0.0043	0.0143	0.0000	0.0000	0.0000	0.0000
Clavicorona pyxidata	0.0077	0.0000	0.0236	0.0000	0.0222	0.0000	0.0000	0.0000
Clitocybe gibba	0.0000	0.0000	0.0000	0.0081	0.0000	0.0000	0.0094	0.0000
Clitocybe odora	0.0000	0.0000	0.0000	0.0000	0.0189	0.0000	0.0000	0.0000
Collybia acervata	0.0850	0.0278	0.0212	0.0557	0.0615	0.0034	0.0257	0.0095
Collybia confusa	0.0070	0.0000	0.0024	0.0000	0.0000	0.0000	0.0025	0.0000

	Grande Prairie study area				Manning study area			
	Deciduous forest reserves	Deciduous clearcut stands	Mixedwood forest reserves	Mixedwood understorey protection cutblocks	Mixedwood forest reserves	Mixedwood understorey protection cutblocks	Coniferous forest reserves	Coniferous clearcut stands
Collybia dryophila	0.0308	0.0650	0.0041	0.2683	0.1047	0.2568	0.0952	0.0000
Coprinus atramentarius	0.0056	0.0333	0.0000	0.0000	0.0000	0.0052	0.0000	0.0000
Coprinus elisii	0.0085	0.0041	0.0000	0.0014	0.0000	0.0096	0.0000	0.0000
Coprinus micaceus	0.0000	0.0000	0.0000	0.0000	0.0000	0.0942	0.0000	0.0088
Crepidotus applanatus	0.0026	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Crepidotus ellipsoideus	0.0074	0.0000	0.0024	0.0000	0.0000	0.0000	0.0013	0.0000
Crepidotus mollis	0.0197	0.0000	0.0268	0.0000	0.0221	0.0000	0.0000	0.0000
Fomes cajanderi	0.0000	0.0000	0.0029	0.0000	0.0000	0.0000	0.0000	0.0000
Fomes fomentarius	0.0042	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Fometopsis pinicola	0.0206	0.0000	0.0384	0.0015	0.1860	0.0258	0.1507	0.0000
Galerina autumnalis	0.0000	0.0000	0.0000	0.0000	0.0000	0.0029	0.0000	0.0000
Ganoderma applanatum	0.0000	0.0000	0.0000	0.1114	0.0000	0.0000	0.0476	0.0000
Gleophyllum sepiarium	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0202	0.0000
Gymnopilus liquitiae	0.0052	0.0000	0.0051	0.0000	0.0000	0.0000	0.0000	0.0000
Gymnopilus penetrans	0.0204	0.0163	0.0014	0.0015	0.0000	0.0000	0.0133	0.0000
Gyromitra esculenta	0.0000	0.0500	0.0000	0.0115	0.0000	0.0000	0.0000	0.0095
Irpex lacteus	0.0000	0.0000	0.0005	0.0000	0.0000	0.0000	0.0000	0.0000
Lentinellus vulpinus	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0513	0.0000
Marasmius epiphyllus	0.0000	0.0000	0.0000	0.0056	0.0000	0.0000	0.0000	0.0000
Marasmius oreades	0.0009	0.0000	0.0081	0.0000	0.0000	0.0000	0.0000	0.0000
Marasmius pallidocephalus	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0770	0.0000
Melanoleuca cognata	0.0000	0.0661	0.0000	0.0128	0.0000	0.0000	0.0081	0.0000
Morchella elata	0.0011	0.0000	0.0014	0.0136	0.0065	0.0012	0.0078	0.0000
Mycena galericiculata	0.0051	0.0707	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Mycena leaiana	0.0017	0.0000	0.0065	0.0000	0.0000	0.0000	0.0430	0.0000
Mycena pectinata	0.0084	0.0000	0.0010	0.0000	0.0221	0.0012	0.0004	0.0000
Mycena psammicola	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0047	0.0000
Mycena stannea	0.0113	0.0000	0.0097	0.0000	0.0000	0.0000	0.0000	0.0000
Nolanea juncina	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0840
Omphalina epichysium	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0252	0.0000
Otidea onoctida	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0095
Peziza badia	0.0093	0.1075	0.0080	0.0323	0.0000	0.0914	0.0004	0.7745

	Grande Prairie study area				Manning study area			
	Deciduous forest reserves	Deciduous clearcut stands	Mixedwood forest reserves	Mixedwood understorey protection cutblocks	Mixedwood forest reserves	Mixedwood understorey protection cutblocks	Coniferous forest reserves	Coniferous clearcut stands
Phellinus chrysoloma	0.0360	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0095
Phellinus tremulae	0.0803	0.0000	0.1493	0.0203	0.1365	0.0710	0.1519	0.0000
Pholiota alnicola	0.0000	0.0139	0.0207	0.0000	0.0000	0.0000	0.0133	0.0000
Pholiota mutabilis	0.0000	0.0000	0.0000	0.0000	0.0000	0.0451	0.0025	0.0000
Pholiota squarrosa	0.0239	0.0139	0.0139	0.0000	0.0000	0.0000	0.0000	0.0000
Phyllotopsis nidularis	0.0000	0.0000	0.0000	0.0000	0.0000	0.0217	0.0000	0.0000
Pleurotus ostreatus	0.0114	0.0000	0.0005	0.0357	0.0300	0.0062	0.0200	0.0048
Pluteus cervinus	0.0000	0.0111	0.0000	0.0000	0.0633	0.0137	0.0080	0.0036
Pluteus pellitus	0.0000	0.0000	0.0000	0.0000	0.0000	0.0015	0.0000	0.0000
Polyporus pargamenus	0.0000	0.0000	0.0072	0.1457	0.0000	0.0000	0.1008	0.0000
Polyporus varius	0.0038	0.0000	0.0126	0.0175	0.0000	0.0000	0.0000	0.0000
Psathyrella hydrophila	0.0242	0.0000	0.1334	0.0000	0.1465	0.0990	0.0000	0.0000
Psathyrella longipes	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0165	0.0000
Scutellinia scutellata	0.1451	0.4491	0.0326	0.0000	0.0000	0.0539	0.0000	0.0714
Simocybe serrulatus	0.0000	0.0000	0.0000	0.0027	0.0000	0.0000	0.0000	0.0000
Spongipellis delectans	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0076	0.0000
Tremella mesentarica	0.0000	0.0000	0.0181	0.0028	0.0227	0.1026	0.0338	0.0000
Tubaria furfuracea	0.0493	0.0139	0.0435	0.1061	0.0185	0.0312	0.0135	0.0095
Mycorrhizal species								
Amanita muscaria	0.0000	0.0000	0.0022	0.0000	0.0000	0.0000	0.0000	0.0000
Boletus edulis	0.0000	0.0000	0.0022	0.0000	0.0000	0.0217	0.0000	0.0000
Boletus piperatus	0.0009	0.0000	0.0043	0.0000	0.0261	0.0052	0.0000	0.0000
Cortinarius alboviolaceus	0.0009	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Cortinarius castaneus	0.0000	0.0000	0.0014	0.0000	0.0000	0.0000	0.0094	0.0000
Cortinarius multiformis	0.0000	0.0000	0.0000	0.0000	0.0973	0.0012	0.0090	0.0052
Hydnum repandum	0.0000	0.0000	0.0027	0.0000	0.0000	0.0000	0.0000	0.0000
Hygrocybe ceracea	0.0000	0.0000	0.0000	0.0000	0.0074	0.0000	0.0000	0.0000
Hygrocybe laeta	0.0013	0.0000	0.0014	0.0000	0.0000	0.0000	0.0000	0.0000
Hygrophorus piceae	0.0000	0.0000	0.0024	0.0000	0.0000	0.0000	0.0000	0.0000
Inocybe fastigiata	0.0164	0.0081	0.0145	0.0128	0.0000	0.0217	0.0000	0.0000
Inocybe lacera	0.0000	0.0000	0.0024	0.0000	0.0000	0.0000	0.0000	0.0000

	Grande Prairie study area				Manning study area			
	Deciduous forest reserves	Deciduous clearcut stands	Mixedwood forest reserves	Mixedwood understorey protection cutblocks	Mixedwood forest reserves	Mixedwood understorey protection cutblocks	Coniferous forest reserves	Coniferous clearcut stands
Laccaria laccata	0.0009	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Lactarius affinis	0.0013	0.0000	0.0048	0.0000	0.0000	0.0000	0.0000	0.0000
Lactarius deliciosus	0.0000	0.0000	0.0022	0.0206	0.0000	0.0000	0.0000	0.0000
Lactarius subdulcis	0.0045	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Leccinum boreale	0.0000	0.0000	0.0091	0.0231	0.0000	0.0015	0.0000	0.0000
Russula aeruginea	0.0142	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Russula borealis	0.0000	0.0000	0.0051	0.0071	0.0000	0.0000	0.0000	0.0000
Russula chamaeoleontina	0.0080	0.0000	0.0087	0.0000	0.0000	0.0000	0.0025	0.0000
Russula fragilis	0.0065	0.0000	0.0075	0.0088	0.0000	0.0000	0.0000	0.0000
Russula laurocerasi	0.1220	0.0000	0.0105	0.0326	0.0000	0.0000	0.0000	0.0000
Russula nigricans	0.0064	0.0000	0.0054	0.0000	0.0000	0.0000	0.0000	0.0000
Russula paludosa	0.0426	0.0000	0.0140	0.0113	0.0000	0.0000	0.0000	0.0000
Russula xerampelina	0.0071	0.0000	0.0153	0.0000	0.0000	0.0000	0.0000	0.0000
Tricholoma flavovirens	0.0013	0.0000	0.0000	0.0149	0.0000	0.0000	0.0000	0.0000
Tricholoma populinum	0.0000	0.0122	0.0000	0.0000	0.0000	0.0006	0.0000	0.0000

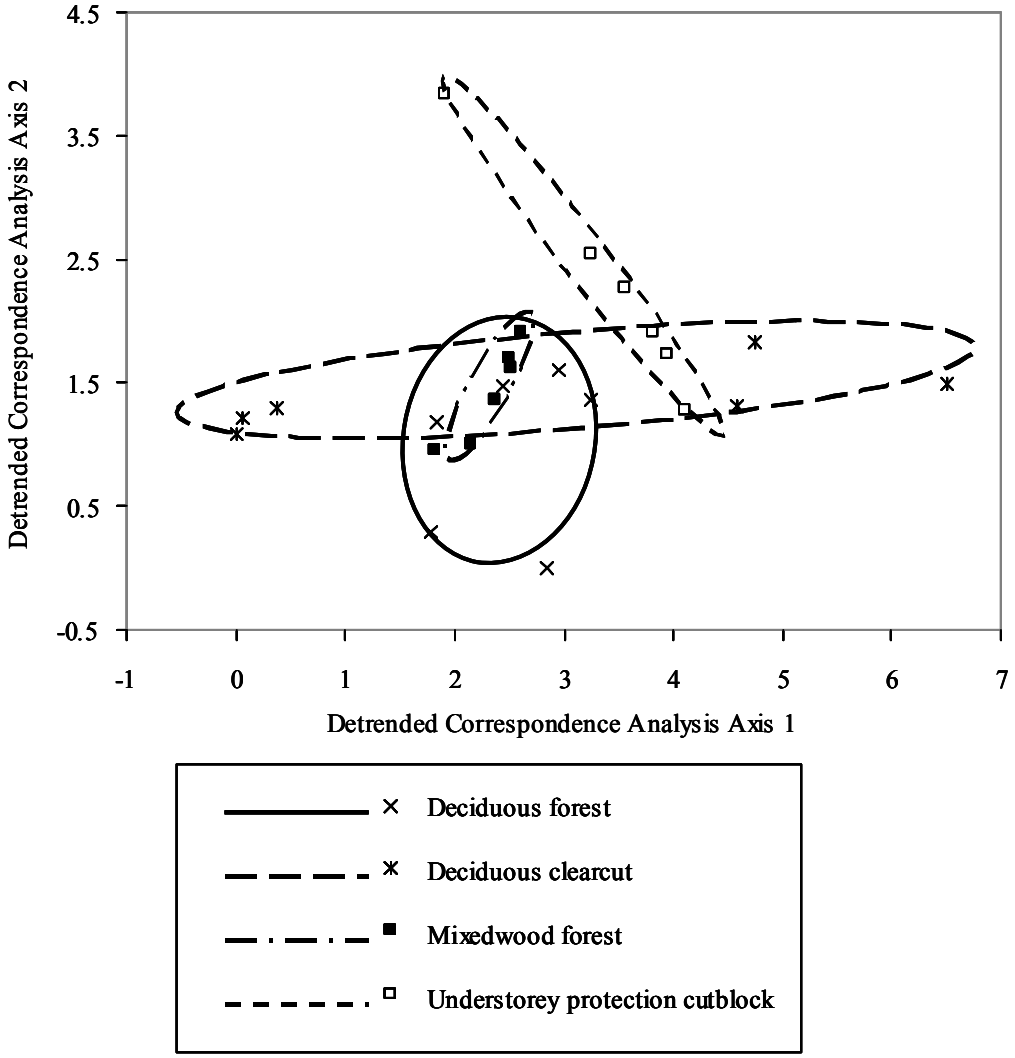


Figure 8.2. Detrended correspondence analysis of transformed (SqRt) relative abundance of fungal species from the Grande Prairie study areas. Treatments include deciduous forests and nearby deciduous clearcuts, and mixedwood forests and nearby mixedwood understorey protection cutblocks. Data were pooled from surveys conducted in 2001 and 2002.

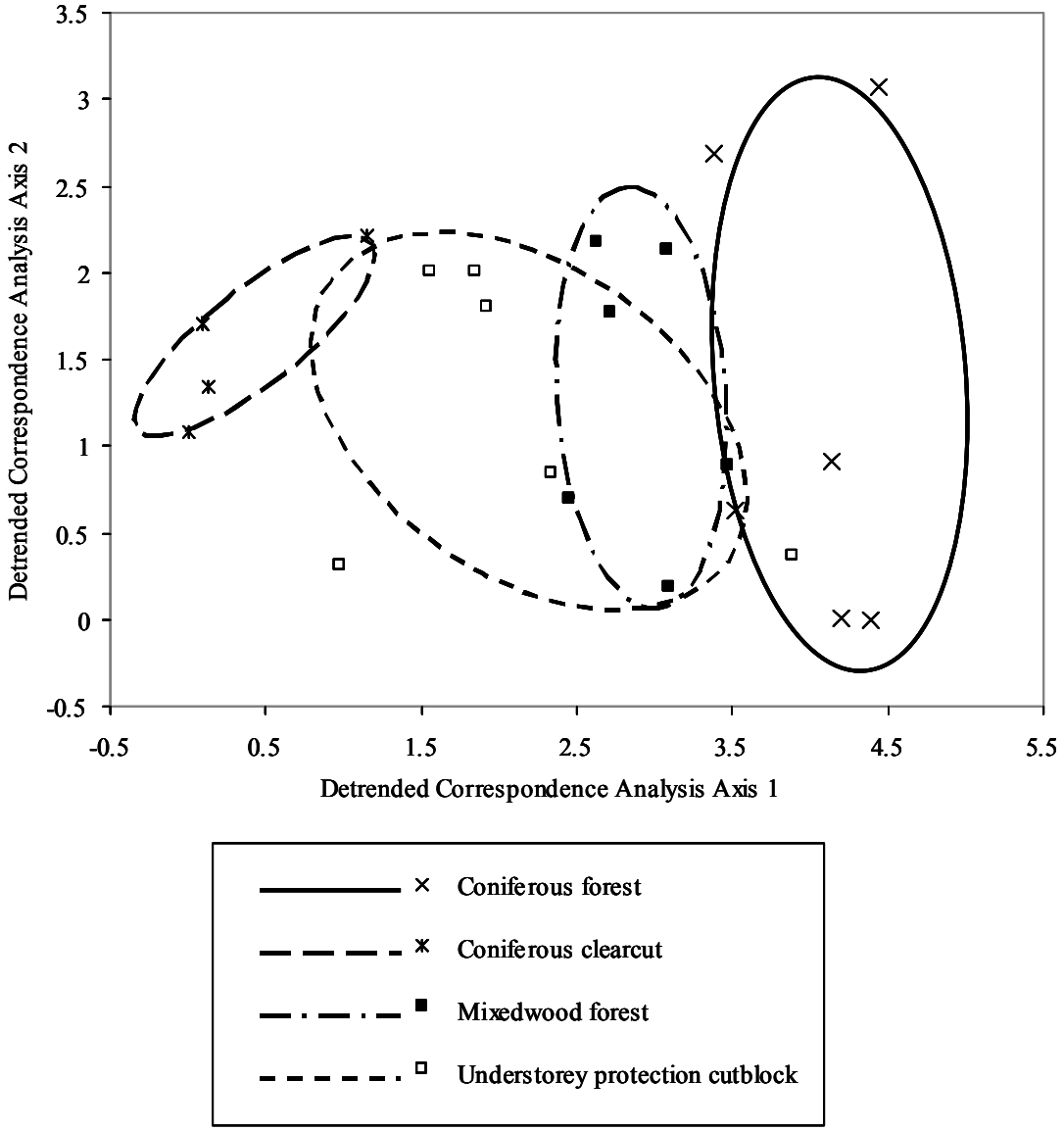


Figure 8.3. Detrended correspondence analysis of transformed (SqRt) relative abundance of fungal species from the Manning study areas. Treatments include coniferous forests and nearby coniferous clearcuts, and mixedwood forests and nearby mixedwood understorey protection cutblocks. Data were pooled from surveys conducted in 2002 and 2003.

Table 8.4. Orthogonal distances (mean ± standard error) in ordination space (detrended correspondence analysis) between undisturbed forest stands and post-harvest stand types. Fungal data was collected at the Grande Prairie study area in 2001 and 2002, and at the Manning study area in 2002 and 2003. Means in a row followed by the same letter are not significantly different at $p < 0.05$; study areas were analyzed separately.

	Grande Prairie study area		**Manning study area**	
	Deciduous forest reserves *versus* deciduous clearcuts	Mixedwood forest reserves *versus* understorey protection cutblock	Mixedwood forest reserves *versus* understorey protection cutblock	Coniferous forest reserves *versus* coniferous clearcuts
Distance[1]	$2.19^{a} \pm 0.17$	$1.77^{b} \pm 0.58$	$1.20^{b} \pm 0.12$	$4.00^{a} \pm 0.17$

[1] Distance values were calculated between each reserve stand and each harvested stand, resulting in n = 9 for each treatment.

CHAPTER 9: THE EFFECTS OF MIXEDWOOD UNDERSTOREY PROTECTION HARVESTING ON RED SQUIRRELS AND FLYING SQUIRRELS

Jason T. Fisher

Introduction

The mixedwood boreal forest of Alberta is characterised by a diverse forest structure and understorey vegetation community. Clearcutting these forests for timber and pulp has the effect of re-starting forest succession, and eliminating the in-stand old forest structure required by many species. In particular, recovery of the mammalian species assemblage to pre-harvest states can take well over a century in boreal mixedwood systems (Fisher and Wilkinson 2002), a timespan that is often less than rotation age in this landscape. Arboreal rodents constitute one species group that is heavily affected by the removal of trees from a stand. As forest-dependent species, the diversity of arboreal rodents is often used as an indicator of forest structural complexity and ecosystem function (Carey *et al.* 1999). In Alberta's northern boreal mixedwood forest this group includes the North American red squirrel, *Tamiasciurus hudsonicus*, and the northern flying squirrel, *Glaucomys sabrinus*. Both of these species are known to require mature or old growth forest structure as habitat; loss of this forest structure will affect individual survival and reproduction, and ultimately population size and persistence.

Flying squirrel ecology

Northern flying squirrels are mycophagists, feeding primarily on epigeous and hypogeous fungi (Hall 1991; Maser *et al.* 1985; Carey *et al.* 1999; Currah *et al.* 2000). Flying squirrels supplement their summer diets with lichen, male flowers, and animal tissue (Maser *et al.* 1985). Lichen has been identified as a key winter dietary component of flying squirrels (McKeever 1960; Hayward and Rosentreter 1994) though this may not necessarily be true in Alberta (Currah *et al.* 2000). Although they are not known to cache mushrooms for over-wintering (Maser *et al.* 1986), mushrooms have been found to be an important component of flying squirrels' winter diet in Alberta (Currah *et al.* 2000). This suggests that either caching does occur, or that thievery from red squirrel middens is common (Mowry and Zasada 1984). As mycophagists, flying squirrels are important dispersers of fungal spores (Maser *et al.* 1978). Maintaining flying squirrel populations facilitates the maintenance of fungal abundance and diversity, including mycorrhizal fungi required for tree re-growth; thus flying squirrels can influence forest regeneration post-disturbance (Rosentreter *et al.* 1997).

Flying squirrels are not territorial; colonial nesting in winter is common. Parturition occurs in early June, with lactation occurring July through September (Carey *et al.* 1997). Throughout their lifespan, flying squirrels are known to preferentially inhabit old-growth stands where food (Maser *et al.* 1985 1986, Waters and Zabel 1995) and nest sites (Mowrey and Zasada 1984; Rosenberg and Anthony 1992; Witt 1992; Carey 1995; Cotton and Parker 2000) are abundant. In Alberta's aspen-dominated boreal mixedwoods, flying squirrels were more abundant in old stands than in mature or young stands; flying squirrels were positively associated with mature white spruce (McDonald 1995) and intermediate decay stages of downed woody material which support fungi and lichen (Roy *et al.* 1995). Flying squirrels den in nests built in the cavities of large, old live trees (Cotton and Parker 2000), as well as dead trees, fallen trees, and stumps (Carey *et al.* 1997).

Due to their dependence on forest biota (lichen and fungi) and structure (tree cavities) associated with old-growth stands, forest clearcutting detrimentally impacts flying squirrel abundance; flying squirrels are largely absent from young clearcuts (see Fisher and Wilkinson 2002 for review). In his review, Kirkland (1990) found that abundances of flying squirrels were generally much reduced in clearcuts. Mowrey and Zasada (1984) found that that flying squirrels generally avoided large untreed areas.

Thus, in Alberta's boreal mixedwood forest, forest harvesting regimes that remove most or all in-stand structure is expected to decrease the abundance of flying squirrels. Similar responses to clearcutting have also been found for red squirrels.

Red squirrel ecology

The red squirrel is a conifer specialist. The seeds contained in the cones of conifer trees such as *Abies*, *Picea*, and *Pinus* spp. are red squirrels' primary food source (Smith 1968; Kemp and Keith 1970; Rusch and Reeder 1978; Riege 1991). Although red squirrels also feed on mushrooms, berries, and nuts (Gurnell 1983; Yahner 1987), they require conifer cones for overwinter survival (Rusch and Reeder 1978). Squirrels collect cones in the late summer and early fall, and cache them in middens (Hurly and Robertson 1990; Dempsey and Keppie 1993). Red squirrel middens are located on territories that are relatively permanent (Rusch and Reeder 1978) and heavily defended (Stuart-Smith and Boutin 1994). Males are permitted onto a female's territory only during a one-day oestrous, which is typically once a year (Lair 1985). Breeding occurs in early March to mid June, and litters are born between April and July (Larsen 1993; Becker *et al.* 1998). Young typically must find their own territories, although some evidence of bequeathal or sharing exists (Price and Boutin 1993). Squirrels without a permanent territory containing mature conifer trees, and thus a reliable source of over-wintering food, have a low probability of survival (Rusch and Reeder 1978).

As conifer specialists, the removal of mature cone-bearing trees from harvested stands has a deleterious effect on red squirrel abundance. Thompson *et al.* (1989) found that red squirrel tracks were significantly less abundant in young clearcuts than in old clearcuts and uncut stands. In Alberta mixedwoods, red squirrels forayed into cutblocks, but did not include them as part of defended core territories (Fisher 1999). In his review, Kirkland (1990) found that in general, abundances of squirrel species were much reduced in clearcuts. As with flying squirrels, harvesting practices that remove the majority of in-stand forest structure are expected to have significant negative impacts on red squirrel populations. The implementation of a harvesting regime that retains a significant portion of in-stand structure may help mitigate these impacts.

Objectives and hypotheses

As mixedwood understorey protection (MUP) harvesting alters stand structure by removing deciduous trees, releasing understorey conifer into the overstorey, and creating forest gaps, there is potential for MUP harvesting to impact red and flying squirrel populations in harvested stands. However, as MUP harvest retains significant numbers of mature or decadent trees and snags - which in turn allows for the maintenance of lichen, fungi, mature seed trees, and nesting tree cavities – this practice may support populations of flying squirrels (Carey 1995) and red squirrels that would otherwise be absent from clearcuts.

The goal of this component of the Mixedwood Understorey Protection Study was to examine the demography of red and flying squirrels in mixedwood understorey protection stands and unharvested reserves with differing dominant tree species. I hypothesised that mixedwood understorey protection harvesting, because it retains some older-stand structure, would in turn retain flying squirrel and red squirrel populations after harvest. I also hypothesised that MUP stands would have fewer squirrels than their mixedwood reserve counterparts, which would in turn have fewer squirrels than conifer reserves.

Methods

Study area and experimental design

A description of the study areas and experimental design is presented in Chapter 2.

Squirrel trapping

Red squirrels and flying squirrels were live trapped using Tomahawk Model 102 and 201 Live Traps (Tomahawk Livetrap Co.

Tomahawk, Wisconsin). Squirrels were trapped in conifer reserves (CR), deciduous reserves (DR), Manning mixedwood reserves (MMR), Manning mixedwood cuts (MMC), Grande Prairie mixedwood reserves (GMR), and Grande Prairie mixedwood cuts (GMC) (Figures 2.3 and 2.4). Ten trap stations were established in each stand. On the rectangular grids (Grande Prairie), trap stations were placed 50 m apart on each gridline, with the two gridlines 100m apart. On the linear transects (Manning), trap stations were placed 50 m apart along the length of the transect. In both study areas, trap stations overlapped with the fungal transects. At each station two traps were set: one at the base of the tree or at squirrel sign within 10 m of the tree, and one nailed to the bole of the tree approximately 1.5 m above the ground. Traps were baited with peanut butter and sunflower seeds. Cotton was provided for bedding, and clear plastic was used to cover the traps to minimise exposure. Traps were set between 1800 hrs and 2200 hrs, and checked the next morning between 0600 hrs and 1100 hrs to coincide with peaks in flying squirrel foraging activity (Witt 1992). Traps were set for 6 to 7 consecutive nights. Trapping occurred 9 June - 24 July 2001, 6 June - 23 July 2002, and, 5 June - 25 June 2003.

Captured animals were tagged with Monel #1 metal eartags and weighed with a Pesola ™ spring scale. As external features are a reliable method for assessment of gender and reproductive condition of some small mammals (McCravy and Rose 1992), these parameters, as well as the age-class of flying squirrels, were assessed based on the criteria delineated in Villa *et al.* (1999).

Squirrel call surveying

Red squirrels emit a territorial call or "rattle" that indicates their presence in an area, and advertises ownership of a territory (Lair 1990). Red squirrel calls were enumerated with the point count protocols used for boreal songbirds outlined in Chapter 7. The length of time sampled exceeded territorial call rates for red squirrels (S. Boutin, unpubl. data), suggesting we did not miss individuals that were present. The number of individual calls recorded were divided by total recording time to standardise between sampling sessions and stands; the result was a relative index of red squirrel abundance that was compared to the trapping results.

Statistics

Flying squirrel captures were low, and the corresponding abundance dataset did not satisfy assumptions of normality (Shapiro-Wilkinson's test, SPSS Inc.). Thus, I tested for differences across years and between stands using a non-parametric related-samples Friedman test (Zar 1996) in SPSS. As our primary hypothesis focussed on differences between stands within each year, I then tested for differences between stand types using standard Kruskal-Wallis tests (Zar 1996). Where significant differences were found in the Kruskal-Wallis analyses, I then used 2-sample Mann-Whitney U tests as post-hoc tests for differences between specific stand types.

Red squirrel abundance data were tested for normality using Shapiro-Wilkinson's statistic in SPSS. Where data were significantly different from normal, data were natural log (ln) transformed, or ln+1 transformed where zeros occurred in the dataset (Zar 1996), and tested again for normality. I used non-parametric tests Kruskal-Wallis tests where transformed data failed to meet the assumptions for normality, and used parametric one-way and repeated measures ANOVAs where transformed data did meet assumptions of normality.

Red squirrel abundance in Manning was compared between years (2001-2003) and between stands using a repeated measures mixed model (SAS Inc.) with YEAR as the within-subjects (fixed) factor. STAND TYPE and STAND TYPE * YEAR were included as between-subjects factors. Tukey-Kramer post-hoc tests were used to evaluate differences between stand types. This repeated measures factorial ANOVA design controls for effect of YEAR and is a statistically rigorous approach, in that it compensates for experiment-wise error rates associated with performing multiple tests across years. Red squirrel data were obtained in

Grande Prairie in 2002 only, and not across several years; as I was interested in testing for differences between stand types in Grande Prairie and Manning, within 2002 I conducted a one-way ANOVA (Zar 1996) for differences between stands using SPSS (SPSS Inc).

Masses of red squirrel adults were normally distributed and were analysed using one-way ANOVAs to test for differences between stand types. Red squirrel adults were discriminated from juveniles using a threshold mass of 180 grams (M. Wheatley, S. Boutin, unpubl. data). The percentage of reproductive females, a potential index of habitat quality (van Horne 1983), was analysed for differences between stands using Kruskal-Wallis tests.

Results

Flying squirrels across years

There were no differences in flying squirrel abundance between years, within stands (Friedman test; $X^2 = 0.400$; $d.f. = 2$; $p = 0.819$). With no annual variation in flying squirrel abundance noted, I tested for differences between stand types, within years.

Flying squirrels 2001

Ten flying squirrels were captured in 2001. Three (3) were reproductive females; 4 non-reproductive females; 1 reproductive male; and 2 non-reproductive males (sex ratio 2.3 F: 1 M; % reproductive females = 43%). Nine animals were identified as age class II or III; one was tentatively identified as an older age class I or younger age class II.

There were no significant differences in flying squirrel abundance between stand types (K-W; $X^2 = 4.213$; $d.f. = 5$; $p = 0.519$). However, it is notable that capture rates in MR stands were 1.26 and 0.74 captures /100 trap nights, with 0.68 captures /100 trap nights in pre-harvest MC stands, whereas no flying squirrels were captured in the year 1 harvested MC stands.

Flying squirrels 2002

In 2002, a total of 16 flying squirrels were captured (Table 9.2). One of these was a recapture from the previous year, in a DR stand. Of eight males, four were scrotal; the other four were non-reproductive. Of the eight females, seven were reproductive (sex ratio 1F: 1M; % reproductive females = 88%). All were age class II or III; no age class I animals were captured.

There were no significant differences in flying squirrel abundance between stand types (K-W; $X^2 = 6.586$; $d.f. = 5$; $p = 0.253$). No squirrels were caught in the MC stands in Manning, the first year post-harvest, just as no flying squirrels were captured in 1st-year post harvest stands in Grande Prairie in 2001. In contrast, flying squirrel abundance in year 2 post-harvest MC stands in Grande Prairie (Table 9.2) was very similar to flying squirrel abundance in MR stands in both 2001 and 2002.

Flying squirrels 2003

In 2003, only Manning sites were trapped, and only four flying squirrels were captured (Table 9.3). One flying squirrel was recaptured from the previous year in an MR stand. Two males and two females were captured (sex ratio 1F: 1M). Both males were scrotal and age class II. One female was a nulliparous age class II, the other was post-lactating age class III (% reproductive females = 50%). No age class I animals were captured.

No significant differences in flying squirrel abundance between stand types was noted (K-W; $X^2 = 3.810$; $d.f. = 2$; $p = 0.149$). No squirrels were caught in the MC (year 2) stands in 2003, as was the case in year 1 post-harvest stands in Manning in 2002. Unlike Manning, flying squirrel abundance in year 2 post-harvest MC stands in Grande Prairie (Table 9.2) was similar to flying squirrel abundance in MR stands in 2002.

Table 9.1. Flying squirrel capture rates in 2001.

Stand	*Flying squirrels captured*	*Trap Nights*	*Flying squirrels per 100 trap nights*
GP-DR	1	331	0.30
GP-MC (post Y1)	0	333	0.00
GP-MR	4	318	1.26
MN-CR	1	210	0.48
MN-MC(pre)	2	293	0.68
MN-MR	2	272	0.74

Table 9.2. Flying squirrel capture rates in 2002.

Stand	*Flying squirrels captured*	*Trap Nights*	*Flying squirrels per 100 trap nights*
GP-DR	4	308	1.30
GP-MC (post Y2)	4	303	1.32
GP-MR	4	310	1.29
MN-CR	1	200	0.50
MN-MC(post Y1)	0	332	0.00
MN-MR	3	328	0.91

Table 9.3. Flying squirrel capture rates in 2003.

Stand	*Flying squirrels captured*	*Trap Nights*	*Flying squirrels per 100 trap nights*
MN-CR	0	220	0.00
MN-MC(post Y2)	0	365	0.00
MN-MR	4	339	1.18

Red squirrels 2001

A total of 46 individual red squirrels were captured 113 times in 2001 (Table 9.4). Forty-five red squirrels were captured in Manning while only one was captured in Grande Prairie. As it was suspected that the low abundance of red squirrels in Grande Prairie was due to environmental variability (*i.e.*, a cone crop failure), and not to differences in stand quality or treatment effect, Grande Prairie stands were dropped from analysis. Only Manning stands were included in the statistical analysis for 2001.

In 2001 adult red squirrel masses (Table 9.5), with DR stands removed due to a single capture in these stands, differed between stand types (one-way ANOVA; $F = 3.502$; $d.f. = 2, 35$; $p = 0.041$). Post-hoc comparisons using Tukey's HSD detected marginal differences between CR stands and MC stands ($p = 0.092$), and between CR and MR stands ($p = 0.080$), and no differences between pre-harvest MC stands and MR stands ($p = 0.971$). There were no significant differences in % reproductive individuals between stand types in Manning (K-W; $X^2 = 3.915$; $d.f. = 2$; $p = 0.141$).

Table 9.4. Red squirrel capture rates in 2001.

Stand	*Red squirrels captured*	*Trap Nights*	*Red squirrels per 100 trap nights*
GP-DR	1	331	0.30
GP-MC (post Y1)	0	333	0.00
GP-MR	0	318	0.00
MN-CR	17	210	8.10
MN-MC(pre)	17	293	5.80
MN-MR	11	272	4.04

Table 9.5. Red squirrel mass, sex, and reproductive condition in 2001.

Stand	*Mean mass (g)*	*Sex ratio (M:F)*	*% reproductive (total)*
MN-CR	220.5	1.1 : 1	64.7 (17)
MN-MC(pre)	202.5	1.4 : 1	76.5 (17)
MN-MR	207.6	0.5 : 1	60.0 (11)

Red squirrels 2002

In 2002, 84 red squirrel individuals were captured 132 times. Forty-three were captured in Grande Prairie, and 41 were captured in Manning (Table 9.6). Red squirrel abundance differed among stand types (one-way ANOVA; $F = 4.944$; *d.f.* = 5,11; p = 0.013). Squirrel abundance was greater in CR stands than in DR stands (Tukey's HSD; $p = 0.022$) and Manning (Year 1) MC stands ($p = 0.030$). Squirrel abundance in CR stands did not significantly differ from abundance in other stand types ($p > 0.05$). Although Manning Year 1 post-harvest MC stands appear to have the lowest abundance – 0.97 squirrels /100 trap nights, similar to DR stands – there were no significant differences in red squirrel abundance between Year 1 post-harvest MC stands, and MR stands in Manning (Tukey's HSD; $p = 0.520$) or Grande Prairie ($p = 0.092$). As well, there were no statistically significant differences between Manning Year 1 MC stands and Grande Prairie Year 2 MC stands (Tukey's HSD; $p = 0.522$) despite the seemingly apparent differences in captures per trap night (Table 9.6). Red squirrel abundance in Year 2 MC stands did not significantly differ from MR stands, or any other stand type except CR ($p > 0.05$).

Adult red squirrel masses (Table 9.7), with DR stands removed due to low sample size, were significantly different between stands types (ANOVA; $F = 5.864$; *d.f.* = 4,48; $p = 0.001$). Red squirrel masses in CR stands were significantly greater than both GP-MC and MN-MC post harvest stands (Tukey's HSD; $p = 0.003$ and 0.050, respectively), but were not different from GP-MR stands ($p = 0.131$), and MN-MR stands ($p = 0.080$). There were no differences in adult masses between MR and MC stands. There were significant differences in % reproductive individuals between stand types (K-W; $X^2 = 11.613$; *d.f.* = 5; $p = 0.040$). Subsequent tests between stand types showed that Manning MC stands had more reproductive individuals than did Grande Prairie MC stands (MWU; $U < 0.000$; $n = 3,2$; $p = 0.046$). CR stands had a marginally significantly greater percentage of reproductive individuals than did Grande Prairie MC stands ($U < 0.000$; $n = 2,3$; $p = 0.053$).

Red squirrels 2003

In Manning in 2003, 64 red squirrels were captured 128 times (Table 9.8). There were no significant differences in adult red squirrel masses (Table 9.9) between stand types (one-way ANOVA; $F = 0.460$; $d.f. = 2,53$; p = 0.634). Of the red squirrels captured, the majority were reproductive animals. All animals captured in MC stands in 2003 were reproductive, as in 2002. Sex ratios in CR stands were skewed to females, unlike the nearly 1:1 ratios seen in 2001 and 2002**.** Conversely, sex ratios in MR stands were skewed towards males, unlike ratios seen in other years. There were no significant differences in % reproductive animals between stand types (K-W; $X^2 = 4.808$; $d.f. = 2$; $p = 0.090$).

Red squirrels across years

Both STAND TYPE and STAND TYPE * YEAR were significant terms in the red squirrel abundance repeated measures ANOVA model (STAND TYPE $F = 9.69$; $d.f. = 2, 4.58$; $p = 0.0226$; STAND TYPE * YEAR $F = 4.73$; $d.f. = 4, 8.96$; $p = 0.0251$). YEAR was not significant in the model ($F = 0.49$; $d.f. = 2, 8.96$; $p = 0.6275$). Tukey-Kramer pairwise comparisons revealed that CR stands had significantly more red squirrels per trap night than MC stands ($p = 0.0196$), and marginally more red squirrels than MR stands ($p = 0.0738$). MC stands did not differ from MR stands (p = 0.3475). In 2002, CR stands had significantly more red squirrels per trap night than did Year 1 post-harvest MC stands ($p = 0.0279$). In 2003, CR stands had significantly more red squirrels per trap night than did Year 2 post-harvest MC stands ($p = 0.0080$). Other stand types were not significantly different from one another.

Red squirrel call data

Squirrel calls were rarely recorded in DC and DR stands pre- or post-harvest (Table 9.10). There were significant differences in squirrels calls between stands in 2000 (one-way ANOVA; $F = 22.572$; $d.f. = 5,12$; $p < 0.000$). CR and pre-harvest CC stands were similar to each other (Tukey's HSD; $p = 0.937$) and different from every other stand type ($p < 0.005$). Squirrel calls in other stand types did not differ from one another ($p > 0.05$). In 2001, no differences were found between any stand types in Manning (one-way ANOVA; $F = 3.392$; $d.f. = 3,8$; $p = 0.074$). Grande Prairie stands were dropped from the analysis for reasons previously outlined. In 2002, analysis of all stands in Grande Prairie and Manning showed significant differences between stand types (one-way ANOVA; $F = 10.245$; $d.f. = 5,18$; $p < 0.000$). CR stands had a greater number of squirrel calls than any other stand type (Tukey's HSD; $p < 0.002$;) including post-harvest CC stands. Other stand types did not differ from one another (Tukey's HSD, p > 0.05).

Table 9.6. Red squirrel capture rates in 2002.

Stand	***Red squirrels captured***	***Trap Nights***	***Red squirrels per 100 trap nights***
GP-DR	3	308	0.97
GP-MC (post Y2)	13	303	4.29
GP-MR	27	310	8.71
MN-CR	27	200	13.50
MN-MC (post Y1)	3	332	0.90
MN-MR	11	328	3.35

Table 9.7. Red squirrel mass, sex, and reproductive condition in 2002.

Stand	*Mean mass (g)*	*Sex ratio M:F*	*% reproductive (total)*
GP-DR	153.0	1 : 2	0.0 (3)
GP-MC (post Y2)	161.1	0.62 : 1	0.0 (13)
GP-MR	168.4	1.6 :1	56.2 (25)
MN-CR	218.7	1.1 : 1	81.5 (27)
MN-MC (post Y1)	194.67	1 : 2	100.0 (3)
MN-MR	198.54	0.83 : 1	90.0 (10)

Table 9.8. Red squirrel capture rates in 2003.

Stand	*Red squirrels captured*	*Trap Nights*	*Red squirrels per 100 trap nights*
MN-CR	47	220	21.36
MN-MC (post Y1)	3	365	0.82
MN-MR	14	339	4.13

Table 9.9. Red squirrel mass, sex, and reproductive condition in 2003.

Stand	*Mean mass (g)*	*Sex ratio M:F*	*% reproductive (total)*
MN-CR	218.7	0.49 : 1	76.6 (47)
MN-MC (post Y2)	194.67	2 : 1	100 (3)
MN-MR	198.54	6 : 1	85.7 (14)

Table 9.10. Number of red squirrel calls by stand type and year.

	Number of squirrel calls		
Stand Type	*2000*	*2001*	*2002*
CC	114	51	8
CR	130	59	82
DC	1	0	0
DR	1	0	0
MC (MN/GP)	6	4 / 0	10 / 7
MR	27	11	50

Discussion

Flying squirrels

Very few flying squirrels were captured throughout the three years of this study, suggesting they exist in this region of the mixedwood boreal forest in very low densities. Although statistical analyses did not reveal any differences in flying squirrel abundance between stand types, samples sizes were very low, necessitating the use of non-parametric tests that can fail to detect existing relationships (Zar 1996). Trends in the flying squirrel capture rates do tend to suggest that flying squirrel populations decreased the summer immediately following MUP harvesting. In Grande Prairie, flying squirrel populations appeared to increase again the second year post-harvest, although they did not in Manning. In Grande Prairie flying squirrels occupied Year 2 post-harvest MUP cuts, and abundance in these stands did not differ from unharvested mixedwood stands. Furthermore, flying squirrels captured in Year 2 MUP stands were mature, reproductive individuals, not immature subadults that would potentially indicate suboptimal habitat (van Horne 1983). As flying squirrels recolonised MUP cuts the second year post-harvest in Grande Prairie, it appears that in some cases understorey protection harvest stands may retain some of the forest structural elements required by flying squirrels. It is not known why this was not the case in Manning, but may be due to regional variability in mixedwood forest structure, and concomitant heterogeneity in vascular plant communities (Chapter 6).

Flying squirrels are known to rely on forest structure that includes decadent trees for nest sites, and the appropriate growing conditions for fungi and lichen food sources (Hall 1991; Mowrey and Zasada 1984; Maser *et al.* 1985, 1986, Rosenberg and Anthony 1992; Carey 1995; Walters and Zabel 1995). Such structure is typically found in old-growth forests. North *et al.* (1997) found that small mammal consumption of hypogeous fungi biomass in young managed stands was less than in older stands, suggesting fungal resources were limited in younger stands. Witt (1992) found that that flying squirrel densities were six times greater in old uncut (old growth) stands than in managed stands, due to greater availability and variety of den sites in old growth stands. Witt (1992) also attributed greater flying squirrel abundance in old stands to a multi-layered canopy, which provided a more favourable microclimate for the growth of hypogeous sporocarps. Similarly, Carey *et al.* (1999) found that flying squirrels were more abundant in late seral stage forests than in managed stands. In California, Waters and Zabel (1995) found that densities of northern flying squirrels were greater in old stands than in 5-year-old logged shelterwood stands. One would expect that flying squirrel populations would be likewise reduced in harvested stands in the Alberta's boreal mixedwood.

In contrast, my findings suggest that the forest structure remaining in mixedwood understorey protection cuts may, in some cases, be facilitating flying squirrel occupation of these stands. This is consistent with Carey *et al.* (1995), who found that flying squirrels in old forests were twice as abundant as in young managed forests without 'old-growth legacies', but that flying squirrel abundance in old stands may have equalled young stands that retained these old-growth structures. Forest structure retained in MUP stands are likely to confer added benefits for flying squirrels as the stand ages. Rosenberg and Anthony (1992) suggest flying squirrel abundance in mature second-growth stands where old-growth remnants persist, may approximate abundance in old growth stands.

In summary, MUP stands in this study contained more fungal, lichen, and decadent tree resources than did clearcuts, thus allowing the persistence of flying squirrels within some of these stands in the second year after harvest. However, the length of time post-harvest that flying squirrels will be able to persist in these stands is unknown. Ransome and Sullivan (1997) found significantly lower abundances of flying squirrels in managed 20-30 year-old *Pinus* stands than in old-growth stands, suggesting that population sizes do not reach pre-harvest states within this time-span. In contrast, Martin and

Anthony (1999) found that flying squirrel densities and home range sizes did not differ between old growth (>400 year old stands) and second growth (40 year old) managed stands. It can be hypothesized that as skid trails regenerate in MUP stands, and residual trees age and decay, these stands may increase in habitat quality and flying squirrel populations may persist or even increase. However, verification of this hypothesis can only occur through additional flying squirrel abundance data collected throughout successional time. In addition, the degree to which flying squirrel populations are maintained in MUP stands is likely mediated by the extent of harvest in the surrounding landscape, as regional patterns in landscape structure have been shown to influence the persistence of flying squirrel populations elsewhere (Reunanen *et al.* 2000). The influence of surrounding landscape structure has also been shown to be important for red squirrels in Alberta's mixedwood boreal forest (Fisher *et al.* in press).

Red squirrels

Conifer stands had higher abundances of red squirrels than any other stand type studied. Red squirrels occupying conifer stands had the greatest masses, and the highest percentage of reproductive individuals than did red squirrels in any other stand type studied, indicating that conifer stands represented the highest quality habitat for red squirrels. Mixedwood stands represented the next highest quality habitat; deciduous stands provided the least suitable intact habitat for red squirrels. This ranking is quite consistent with the literature, which maintains that conifer trees (in particular, white spruce) provide the highest quality forage for red squirrels, and support the largest and most dense populations (C. Smith 1968; Kemp and Keith 1970; Rusch and Reeder 1978; though see Wheatley *et al.* 2002). In Alberta's southern boreal forest, red squirrels were most abundant in mature mixed spruce stands, followed by jack pine, and then aspen stands (Rusch and Reeder 1978). Deciduous stands had lower squirrel densities and higher overwinter mortality (Rusch and Reeder 1978). The majority of red squirrels found in aspen stands were juveniles (Kemp and Keith 1978, Rusch and Reeder 1978), indicating that such stands without mature cone-bearing conifers may be functioning as population sinks (*sensu* Pulliam 1988), and represent suboptimal habitat relative to conifer stands.

Red squirrel call data demonstrated that squirrel abundance in conifer stands dropped significantly post-harvest. Squirrels were much reduced in conifer clearcuts, and were not recorded at all in deciduous clearcuts. This is consistent with Fisher (1999), who noted that although red squirrels did travel through and forage in clearcuts, these stands did not comprise part of defended territories or core home ranges. Marinelli (1999) also found that red squirrel abundance after clearcutting was much reduced. Thompson *et al.* (1989) found that red squirrel tracks were less abundant in young clearcuts than in old clearcuts and uncut stands. Although red squirrels may make use of clearcuts for supplemental ephemeral forage, clearcuts do not supply conifer seed; without conifer seeds the probability of overwinter survival is low (Rusch and Reeder 1978).

In contrast, there were very few differences in red squirrel abundance between MUP harvest stands and mixedwood reserves. Our red squirrel capture data indicate that mixedwood understorey protection harvest does not result in a significant reduction of red squirrel abundance, suggesting that MUP stands support red squirrel populations in numbers closely approximating unharvested stands.

However, relative abundances or densities of animals can often provide a misleading indicator of habitat quality (van Horne 1983), as poor habitats may be occupied by dispersing juveniles or non-reproductive individuals in poor condition, with low masses, and high probabilities of mortality (Wheatley *et al.* 2002). Differences in masses between habitats have been observed in Eurasian red squirrels (Wauters and Dhondt 1989) and North American red squirrels (Rusch and Reeder 1978). Larger masses generally correlate with increased reproductive and recruitment rates in red squirrels (Rusch and Reeder 1978; Wauters *et al.* 1990). This study's comparison of adult

red squirrel masses between treatments revealed that conifer stands had larger squirrels than did mixedwood reserves, pre-harvest MUP stands, and harvested MUP stands, again suggesting that conifer stands represented the highest quality habitat. Similarly, Rusch and Reeder (1978) recorded larger red squirrels in old white spruce stands than in other habitat types in the mixedwood boreal forest. However, I found no differences in squirrel mass between mixedwood reserves and MUP stands. This may suggest a gradient in red squirrel size (and hence habitat quality) from conifer stands > mixedwood reserves > MUP stands, with only the ends of the spectrum being detected by this analysis. Conifer stands also had a higher percentage of reproductive animals than did harvested MUP stands.

Results indicate that in the first year after harvest, MUP stands were occupied by smaller, non-reproductive, and ostensibly less fit individuals, suggesting these stands represented suboptimal habitat for red squirrels. In 2003, however, there were no differences in red squirrel masses or percent reproductive individuals between conifer stands, mixedwood reserves or MUP stands. This suggests that either resident squirrels remained in-stand and attained a greater mass and better reproductive condition one year after colonisation of the MUP stands, or that other squirrels in better condition annexed territories from smaller, less competitive squirrels.

The lack of differences between control mixedwood reserves and year 2 harvested MUP stands suggest that MUP harvesting facilitates the maintenance of red squirrel populations in mixedwood stands. Red squirrel persistence is likely due to the presence of overstorey trees for cover and nest sites, and most importantly, to the presence of mature cone-bearing spruce left as residuals within MUP stands. However, as with flying squirrels, the length of time post-harvest that red squirrels will be able to persist in these stands is unknown. It can be hypothesized that as understorey white spruce is released into the canopy, matures and produces cones, that MUP stands may increase in habitat quality and red squirrel populations may continue to persist. However, verification of this hypothesis requires additional red squirrel abundance surveys conducted throughout successional time. As mentioned, the degree to which red squirrel populations are maintained in MUP stands is likely mediated by the extent of harvest in the surrounding landscape, as surrounding landscape structure has also been shown to influence red squirrel distribution in Alberta's mixedwood boreal forest (Fisher *et al.* in press). Further analysis of landscape-level implementation is required before we fully understand the context presented by apparent benefits of in-stand structural retention.

Conclusions and Management Implications

These results suggest that the retention of old growth forest structural attributes in MUP harvesting allows for the maintenance of red squirrels and flying squirrels in some MUP stands the second year after harvest. As MUP stands sampled in this study retained some overstorey, snags, decadent and live mature cone-bearing trees, this structure likely provided nests, suitable growth conditions for lichen and fungi, and conifer seed. Thus, it appears that the habitat loss incurred through MUP harvesting was mitigated in comparison with clearcutting. As understorey release promotes the maturation of conifer and recruitment into the overstorey, and allows in-stand residuals to senesce and decay, the benefits of MUP harvesting are likely to compound over time, resulting in an accelerated convergence of the squirrel community to pre-disturbance states. I recommend that further analysis be conducted over successional time to test these hypotheses.

The degree to which populations of red and flying squirrels are maintained is likely mediated by harvest intensity, site productivity, age, and stand type. Thus, the results for squirrels obtained in this study apply only to mixedwood stands within the age range studied herein, and harvested under the operational parameters employed in this study. I therefore recommend that MUP harvesting proceed under the parameters used in this study. Variations in

operational implementation, and in other stand types, should receive further evaluation.

It is also important to note that the maintenance of red and flying squirrel populations will occur only within the successional period occurring between MUP harvesting and second-phase harvesting of the stand. Squirrel population persistence will be related to the amount of in-stand residual retention. If second-phase harvest employs clearcutting, diversity of both squirrel species will decline dramatically. Therefore, the landscape pattern of deployment of MUP harvesting will also affect the overall persistence of red and flying squirrels within a region, suggesting planning processes occur that spatially stagger initial MUP harvesting with second-phase cutting of a stand.

Caveats aside, I can conclude that in second year after cutting, understorey protection harvesting of mixedwoods stands does appear to maintain stand-level populations of reproductive adults in abundances that 1) are greater than those occurring in clearcuts stands, and 2) in some cases do not differ significantly from unharvested mixedwood stands.

Acknowledgements

The author and research team would like to thank Michelle Hiltz for statistical advice, and Matthew Wheatley for review of this manuscript, and helpful discussions, and insightful commentary.

References

Becker, C.D., S. Boutin, and K.W. Larsen. 1998. Constraints on first reproduction in North American red squirrels. Oikos **81**: 81-92.

Carey, A.B. 1995. Sciurids in Pacific Northwest managed and old-growth forests. Ecological Applications **5**(3): 648-661.

Carey, Andrew P. and Murray L. Johnson. 1995. Small mammals in managed, naturally young, and old-growth forests. Ecological Applications **5**: 336-352.

Carey, A.B., T.M. Wilson, C.C. Maguire, and B.L. Biswell. 1997. Dens of northern flying squirrels in the Pacific Northwest. Journal of Wildlife Management **61**(3): 684-699.

Carey, A.B., J. Kershner, B. Biswell, and L. Domínguez de Toledo. 1999. Ecological scale and forest development: squirrels, dietary fungi, and vascular plants in managed and unmanaged forests. Wildlife Monographs **142**: 1-71.

Cotton, C.L., and K.L. Parker. 2000. Winter habitat and nest trees used by northern flying squirrels in subboreal forests. Journal of Mammalogy **81**(4): 1071-1086.

Currah, R.S., E.A. Smreciu, T. Lehesvirta, M. Niemi, and K.W. Larsen. 2000. Fungi in the winter diets of northern flying squirrels and red squirrels in the boreal mixedwood forest of northeastern Alberta. Canadian Journal of Botany **78**: 1514-1520.

Dempsey, J.A., and D.M. Keppie. 1993. Foraging patterns of eastern red squirrels. Journal of Mammalogy **74**(4): 1007-1013.

Fisher, J.T. 1999. The influence of landscape structure on the distribution of the North American red squirrel *Tamiasciurus hudsonicus* in a heterogeneous boreal forest mosaic. Master of Science Thesis, University of Alberta, Edmonton, Alberta. 101 pp.

Fisher, J.T. and L. Wilkinson. 2002. The mammalian response to forest harvesting and fire. *In* S. Song, (Ed.) *The Ecological Basis for Stand Management*. Alberta Research Council, Vegreville, Alberta.

Fisher, J.T., S. Boutin, and S.J. Hannon. Accepted to *Landscape Ecology*. The Protean nature of landscape effects on red squirrels in a heterogeneous boreal forest landscape.

Gurnell, J. 1983. Squirrel numbers and the abundance of tree seeds. Mammal Review **13**(2/3/4): 133-148.

Hall, D.S. 1991. Diet of the northern flying squirrel at Sagehen Creek, California. Journal of Mammalogy **72**(3): 615-617.

Hayward, G.D., and R. Rosentreter. 1994. Lichens as nesting material for northern flying squirrels in the northern Rocky Mountains. Journal of Mammalogy **75**(3): 663-673.

Hurly, T.A., and R.J. Robertson. 1990. Variation in the food hoarding behaviour of red squirrels. Behavioural Ecology and Sociobiology **26**: 91-97.

Kemp, G.A., and L.B. Keith. 1970. Dynamics and regulation of red squirrel (*Tamiasciurus hudsonicus*) populations. Ecology **51**(5): 763-779.

Kirkland, G. L. Jr. 1990. Patterns of initial small mammal community change after clearcutting of temperate North American forests. Oikos **59**: 313-320.

Lair, H. 1985. Mating seasons and fertility of red squirrels in southern Quebec. Canadian Journal of Zoology **63**: 2323-2327.

Lair, H. 1990. The calls of the red squirrel: A contextual analysis of function. Behaviour **115** (3-4): 254-282.

Larsen, K.W. 1993. Female reproductive success in the North American red squirrel, *Tamiasciurus hudsonicus*. Ph.D. Thesis, University of Alberta, Edmonton.

Marinelli, L. 1999. Mammal diversity in wildfire and harvest stands of aspen-dominated mid-boreal forest. Pages 267-285 in P. Lee, editor. *Fire and harvest residual (FAHR) project: The impact of wildfire and harvest residuals on forest structure and biodiversity in aspen-dominated boreal forests of Alberta, a final report*. Alberta Research Council Forest Resources Business Unit, Vegreville, AB.

Martin K.J., and R.G. Anthony. 1999. Movements of northern flying squirrels in different-aged forest stands of western Oregon. Journal of Wildlife Management **63**(1): 291-297.

Maser, C., J.M. Trappe, and R.A. Nussbaum. 1978. Fungal-small mammal interrelationships with emphasis on Oregon coniferous forests. Ecology **59**(4): 799-809.

Maser, Z., C. Maser, and J.M. Trappe. 1985. Food habits of the northern flying squirrel (*Glaucomys sabrinus*) in Oregon. Canadian Journal of Zoology **63**: 1084-1088.

Maser, C., Z. Maser, J.W. Witt, and G. Hunt. 1986. The northern flying squirrel: a mycophagist in southwestern Oregon. Canadian Journal of Zoology **64**: 2086-2089.

McCravy, K.W., and R.K. Rose. 1992. An analysis of external features as predictors of reproductive status in small mammals. Journal of Mammalogy **73**(1): 151-159.

McDonald, L. 1995. Relationships between northern flying squirrels and stand age and structure in aspen mixedwood forests in Alberta. In *Relationships between stand age, stand structure, and biodiversity in Aspen Mixedwood Forests in Alberta*. pp 227-240. Alberta Environment Centre, Vegreville, AB.

McKeever, S. 1960. Food of the northern flying squirrel in Northeastern California. Journal of Mammalogy **41**(20): 270-271.

Mowrey, R.A., and J.C. Zasada. 1984. Den tree use and movements of northern lying squirrels in interior Alaska and implications for forest management. In *Fish and Wildlife Relationships in Old-growth Forests*. W.R. Meehan, T. R. Merrell Jr., and T. A. Hanley eds. 351-356.

North, M., J. Trappe, and J. Franklin. 1997. Standing crop and animal consumption of fungal sporocarps in Pacific Northwest forests. Ecology **78**(5): 1543-1554.

Price, K., and S. Boutin. 1993. Territorial bequeathal by red squirrel mothers. Behavioural Ecology **4**: 144-150.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. American Naturalist **132(5)**: 652-661.

Ransome, D.H., and T.P. Sullivan. 1997. Food limitation and habitat preference of *Glaucomys sabrinus* and *Tamiasciurus hudsonicus*. Journal of Mammalogy **78**(2): 538-549.

Reunanen, P., M. Mönkkönen, and A. Nikula. 2000. Managing boreal forest landscapes for flying squirrels. Conservation Biology **14**(1): 218-226.

Riege, D.A. 1991. Habitat specialization and social factors in distribution of red and grey squirrels. Journal of Mammalogy **72**(1): 152-162.

Rosenberg, D.K., and R.G. Anthony. 1992. Characteristics of northern flying squirrel populations in young second- and old-growth forests in western Oregon. Canadian Journal of Zoology. 70:161-166.

Rosentreter, R., G.D. Hayward, and M. Wicklow-Howard.1997. Northern flying squirrel seasonal food habits in the Interior conifer forests of central Idaho, USA. Northwest Science 71(2): 97-101.

Roy, L., J.D. Stelfox, and J.W. Nolan. 1995. Relationships between mammal biodiversity and stand age and structure in aspen mixedwood forests in Alberta. In *Relationships between stand age, stand structure, and biodiversity in Aspen Mixedwood Forests in Alberta*. pp 159-189. Alberta Environment Centre, Vegreville, AB.

Rusch, D., and W. Reeder. 1978. Population ecology of Alberta red squirrels. Ecology **59**(2): 400-420.

Smith, C.C. 1968. The adaptive nature of social organization in the Genus of three (*sic*) squirrels *Tamiasciurus*. Ecological Monographs **38**(1): 31-63.

Stuart-Smith, K., and S. Boutin. 1994. Costs of escalated territorial defence in red squirrels. Canadian Journal of Zoology **72**: 1162-1167.

Thompson, I. D., I. J. Davidson, S. O'Donnell, and F. Brazeau. 1989. Use of track transects to measure the relative occurrence of some boreal mammals in uncut forest and regeneration stands. Canadian Journal of Zoology **67**: 1816-1823.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management. **47**(4):893-901.

Villa, L.J., A.B. Carey, T.M. Wilson, and K.E. Glos. 1999. Maturation and reproduction of northern flying squirrels in Pacific northwest forests. United States Department of Agriculture Forest Service, Pacific Northwest Research Station, General Technical Report PNW-GTR-444.

Waters, J.R., and C.J. Zabel. 1995. Northern flying squirrel densities in fir forests of northeastern California. Journal of Wildlife Management **5**9:858-866.

Wauters, L.A. & A.A. Dhondt. 1989. Body weight, longevity and reproductive success in Red Squirrels (*Sciurus vulgaris*). Journal of Animal Ecology **58**:637-651.

Wauters, L., A.A. Dhondt and R. De Vos. 1990. Factors affecting male mating success in red squirrels (*Sciurus vulgaris*). Ethology, Ecology and Evolution **2**:195-204.

Wheatley, M.T., K.W. Larsen, and S. Boutin. 2002. Does Density Reflect Habitat Quality for Red Squirrels During a Spruce Cone Failure? Journal of Mammalogy **83**(3): 716-727.

Witt, J.W. 1992. Home range and density estimates for the northern flying squirrel, *Glaucomys sabrinus*, in western Oregon. Journal of Mammalogy **73**: 921-929.

Yahner, R.H. 1987. Feeding site use by red squirrels, *Tamiasciurus hudsonicus*, in a marginal habitat in Pennsylvania. Canadian Field Naturalist **101**(4): 586-589.

Zar, J.H. 1996. *Biostatistical Analysis*. Third Edition. Prentice Hall, New Jersey.

CHAPTER 10: THE EFFECTS OF MIXEDWOOD UNDERSTOREY PROTECTION HARVESTING ON FOREST-DWELLING BATS

Jason T. Fisher and Lisa Wilkinson

Introduction

Bats (Order Chiroptera) are small flying mammals; forest-dwelling bats are considered to rely heavily on old-growth forests for habitat. Bat species occurring in Alberta include the little brown bat (*Myotis lucifugus*), big brown bat (*Eptesicus fuscus*), silver-haired bat *(Lasionycteris noctivagans*), hoary bat (*Lasiurus cinereus*), long-legged bat (*Myotis volans*), western small-footed bat (*Myotis ciliolabrum*), northern long-eared bat (*Myotis septentrionalis*), long-eared bat (*Myotis evotis*), and red bat (*Lasiurus borealis*).

All bat species occurring in Alberta are insectivorous. Bats emit ultrasonic echolocation pulses for insect prey location, as well as for orientation and communication between individuals (Barclay *et al.* 1979). Echolocation 'passes' – typical pulse frequencies emitted for navigation and communication – are distinct from 'feeding buzzes' – high pulse repetition rates emitted by bats when attempting to catch insects (Griffin *et al.* 1960). Whereas echolocation passes indicate only general bat activity, feeding buzzes allow the identification of actively foraging bats.

Bat species exist sympatrically (in part) by temporally (Reith 1980) and spatially (Barclay 1991) partitioning insect prey resources, and employing different foraging strategies (Barclay 1985). For example, *M. lucifugus* is known to forage over water for chironomid prey, while *M. evotis* is known to forage along forest paths for moths (Barclay 1991). *M. evotis* is considered more flexible in its feeding patterns, and thus more adaptable to different areas, than is *M. lucifugus* (Barclay 1991). Even within species, there is evidence that spatial partitioning occurs between sexes (Wilkinson and Barclay 1997).

Resource partitioning between species is partially a function of bat morphology. Larger bats such as *Lasiurus cinereus*, *Lasionycteris noctivagans*, and *E. fuscus*, have wing aspect ratios that render them less manoeuvrable than smaller bats. For these larger species, clutter - defined as high canopy and subcanopy tree and snag density - can provide obstructions to flight (see Patriquin and Barclay 2003 for discussion). In contrast, the wing aspect ratios of smaller *Myotis* species facilitate manoeuvrability (Fenton 1990). Consequentially, larger less manoeuvrable non-*Myotis* species tend to be associated with open areas, whereas smaller, more manoeuvrable *Myotis* species can occupy more cluttered environments (Crome and Richards 1988; Kalcounis and Brigham 1995).

Old-growth stands provide tree cavities in which to roost, and canopy gaps in which to forage (Kunz 1982; Wunder and Carey 1996). Bat roosts have typically been found in large-diameter tall trees, often in a state of decay, in old uncluttered stands (Campbell *et al.* 1996, Vonhof and Barclay 1996; Brigham *et al.* 1997; Callahan *et al.* 1997; Betts 1998; Crampton and Barclay 1998; Vonhof and Wilkinson 1999). Roost trees are typically infected with heartrot (*Phellinus tremulae*) or root rot (*Armillaria sinapina*) (Parsons *et al.* 2003), or have been holed by primary cavity excavators such as yellow-bellied sapsuckers (*Sphyrapicus varius)* (Kalcounis and Brigham 1998). The cavities thus formed provide escape cover and an ambient temperature suitable for bat thermoregulation (Kalcounis and Brigham 1998). In addition to providing roost sites, the structure of old-growth stands is also more conducive to bat movement; old stands have less clutter due to high canopy, low tree density, and abundant forest gaps, that create spatial heterogeneity favoured by bats (Crampton and Barclay 1998; Erickson and West 2003).

The juxtaposition of roosting habitat with adjacent foraging habitat is an important predictor of bat abundance. This juxtaposition

often occurs in old-growth stands, as the canopy breaks up and gaps are created adjacent to decadent roost trees. In Ontario, silver-haired bats and hoary bats were significantly more abundant in old-growth white pine mixedwood stands than in mature mixedwood or selective logged stands (Jung *et al.* 1999). An analysis of forest attributes showed that *Myotis* species responded to intact stands with an open understorey and closed canopy; other species responded to canopy caps and super-canopy trees (Jung *et al.* 1999). In California redwoods, old-growth forest is also suggested to be a vital component of bat habitat (Zielinski and Gellman 1999). In Pacific Northwest hemlock forests, bat activity was higher in old-growth stands than in mature (50 – 100 year-old) stands (Humes *et al.* 1999). Thomas (1988) also found that bat activity in the Pacific north west was greater in old-growth stands (>200 years) than in mature (100-165 years) or young (<75 years) stands. This difference was attributed to a comparative lack of roost trees in mature and young stands in comparison to old growth stands. In northern Alberta, too, bats showed higher foraging activity in old aspen-dominated mixed-wood stands, than in than in young or mature stands (Crampton and Barclay 1998). Roost trees of little brown bats and silver-haired bats were all located in old stands. Thomas (1988) urged that managing a landscape for even-aged rotation-stage stands without senescent old-growth would likely have dire ramifications for bat populations.

Despite bats' long-held association with old-growth forest, conflicting data exist regarding the actual importance of old-growth stands. In their review, Miller *et al.* (2003) found that 80% of the studies they examined claimed that timber harvest is detrimental to bats. However, many of these studies were restricted to old-growth environments and could not justifiably infer beyond those stand types. Of those studies that actually examined bat activity in cutblocks, 80% of these determined that bat activity in response to forest harvesting was either positive or neutral. In fact, harvested stands may provide uncluttered habitat suitable for bat foraging (Patriquin and Barclay 2003), although roosting sites may be limited or completely absent (Swystun *et al.* 2001). Hence, the use of existing research to predict the effects on bats of an alternative forest harvesting practice, such as mixedwood understorey protection (MUP) harvesting, is not entirely practicable.

There is evidence that in boreal Alberta, mixedwood stands may represent preferred bat habitat. In the boreal forest and aspen parkland, bats were more active in boreal aspen-white spruce mixedwood stands than in aspen or jack pine stands (Kalcounis *et al.* 1999). Bats preferred deciduous trees for roosts over other species (Kalcounis and Brigham 1998). Based on our current knowledge of bat ecology and habitat selection, the harvesting of old or mature aspen-mixedwood stands has the potential to significantly affect bat populations. Mixedwood understorey protection harvesting may mitigate this impact through the retention of live residual trees and snags.

In this component of the Mixedwood Understorey Protection project, bat activity was measured in experimental and control stands using *Anabat* sonic detectors, to determine if bat activity differed between harvest strategies, stand types, or before and after harvest.

Methods

Study Area and Experimental Design

Bats were surveyed in control and experimental stands as described in previous Chapters.

Species detection

In June and July 2000, 2001, and 2002, we sampled bat activity using *Anabat II* bat detectors (Titley Electronics Ltd., NSW, Australia) set to sensitivity 8 (of 10), connected to a night-time delay switch (Titley Electronics) and a sound-activated tape recorder. Electronics were powered with a 12-volt battery. This assembly was housed in a waterproof container with a hole punched in one side to allow the microphone to protrude. Detector units were strapped to trees at 1.0 to 1.5 m up the bole, to prevent attenuation of sound by surrounding

vegetation. Detectors were placed at a 45° angle, such that microphones were able to sample the airspace between the forest floor and canopy; in aspen mixedwood forests, bats are active both within and above the forest canopy (Kalcounis *et al.* 1999).

Two bat detectors were placed in each stand for three consecutive nights, and were situated a minimum of 250 m apart. Bat detectors were checked daily. If rain or mechanical failure prevented bat sampling, these results were discarded and an additional night was sampled to compensate. Upon completion of a sample period, detectors were moved to different locations within the stand for subsequent recording sessions. Detectors were active in each stand for a total of five to six nights. This protocol was repeated for each stand type: conifer reserve (CR), conifer cut (CC), deciduous reserve (DR), deciduous cut (DC), Manning mixedwood reserve (MMR), Manning mixedwood cut (MMC), Grande Prairie mixedwood reserve (GMR), and Grande Prairie mixedwood cut (GMC). There were three replicates of each stand type, for a total of 24 stands sampled.

Pre-harvest bat detection data were collected in both Grande Prairie and Manning in 2000. Year 1 post-harvest data were collected in Grande Prairie sites in 2001, and in Manning sites in 2002.

Species identification

A bat produces a series of individual echolocation calls, and we defined the complete series as a single bat pass. In addition, we distinguished feeding buzzes from echolocation passes based on pulse repetition rates. We analysed bat detector audio-tapes and recorded 1) the time a bat pass was recorded, 2) whether a feeding buzz or pass was recorded, and 3) whether the pass was produced by a *Myotis* species or a large non-*Myotis* bat species (*e.g.*, silver-haired, big brown, or hoary bat). Large-genera non-*Myotis* bat species produce lower frequency calls than smaller species; thus these two groups can be distinguished by differences in pitch (see Patriquin and Barclay 2003; Patriquin *et al.* 2003). Large bat species were not distinguishable from one another.

To differentiate between species, we transformed the recorded passes to a visual frequency-time display using a Zero Crossing Analysis Interface Module (Z-CAIM) and *Anabat6* software (Titley Electronics). We then used *Analook6* software (Titley Electronics) to determine which species of bat produced the recorded passes. All background noise and fragmented calls were removed using the 'mark-off points' function. Criteria established by Patriquin and Barclay (2003) were used for discriminating between background noise and calls. Individual points greater than 5 kHz above or below the clear signal of a call were removed. Likewise, if points were greater than 10 kHz above or below the signal, they were removed. If a signal was not clear it was not analysed. As well, all calls with a maximum frequency below 60kHz were not analysed, as they do not provide an accurate representation of the call variables.

Many call variables are measured automatically using *Analook6* software. However, we used maximum frequency (the highest frequency of a call), minimum frequency (the lowest frequency of a call), and call duration, for species identification as these variables are believed to be species specific (O'Farrell *et al.* 1999). From these parameters we calculated slope: the difference between the maximum and minimum frequency, divided by duration. This slope value differs from those provided in *Analook*, and we believe provides a better representation of the shape of the call. We compared these variables to a library of reference calls collected from individuals identified to species by Patriquin and Barclay (2003). The reference calls were collected in nearby Peace River, Alberta; thus geographic variation should not influence the reliability of the calls detected herein.

We followed methods outlined in Patriquin and Barclay (2003) to discriminate between species. They used a multivariate analysis of variance (SAS 8.1, Proc GLM) to determine which call variables discriminated between *Myotis* species, and determined that slope was the best variable to distinguish between little brown bats and

northern long-eared bats. *M. lucifugus* produced longer and less steep calls than *M. septentrionalis*. The slope of echolocation calls of little brown bats (n = 75) ranged between 3.5 and 15.9 kHz/ ms, while that of northern long-eared bats (n = 55) ranged between 8.5 and 27.4 kHz/ ms. These values overlap for the two species between 11.0 and 12.9, so all calls falling within this range were identified simply as *Myotis* species. *M. lucifugus* calls were defined as those with slopes between 3.5 and 10.9, while *M. septentrionalis* calls fell between 13.0 and 27.4. Nine and 21.8% of little brown and northern long-eared reference calls, respectively, fell in the unknown range. Only 7% of little brown and northern long-eared bat reference calls fell within the range of the other species.

Statistics

We summarised data into: 1) total number of bat passes, 2) total number of feeding buzzes, 3) number of *Myotis* spp. passes; 4) number of *Myotis* spp. feeding buzzes; 5) number of large species passes; 6) number of large species feeding buzzes; 7) number of *M. lucifugus* passes, 8) number of *M. lucifugus* feeding buzzes; 9) number of *M. septentrionalis* passes; and 10) number of *M. septentrionalis* feeding buzzes. Each of these sums were standardised by dividing by the number of trap nights in each stand, within a given year. This yielded, for example, *total mean passes per trap night*, an index of bat activity that is statistically comparable between stands, but not an absolute measure of abundance.

Kolmogrov-Smirnov tests for normality of data were conducted in SPSS (SPSS Inc.) for each year of data. Where data deviated from a normal distribution, a natural-log transformation was applied (Zar 1996). Where ln-transformed data were not significantly different from a normal distribution (Kolmogrov-Smirnov test, $p<0.05$), differences in ln-transformed detections per trap night, between different stand types, within each year, were tested using one-way ANOVAs in SPSS (SPSS Inc.). Where data could not be normalised, non-parametric Kruskal-Wallis tests were used to look for differences in bat detections between stand types. Where significant differences were noted, Mann-Whitney U tests were then used post-hoc to look for differences between specific stand types.

Differences within stands, between years pre- and post-harvest were tested using repeated measures analysis. Repeated measures general liner models (GLM; SPSS Inc.) were created for the Manning and Grande Prairie *total mean passes* data, using YEAR (pre and post harvest) as a within-subjects factor, and STAND type as a between-subject factor.

Results

Bat activity by stand type

2000: Pre-harvest in Grande Prairie and Manning

There were a total of 243 detector nights in 2000: 115 in Manning, and 128 in Grande Prairie. Passes of *Myotis* spp., *M. lucifugus*, and *M. septentrionalis* were recorded (Table 1). Feeding buzzes for total *Myotis* spp. were recorded but sample sizes were small (n = 13). Buzzes for separate *Myotis* species were not distinguishable. No passes or feeding buzzes for large genera were recorded. ANOVA analyses detected no differences in mean total bat passes (synonymous with total *Myotis* spp., since no large genera were recorded) between stand types ($F = 1.276$; $d.f. = 7,16$; $p = 0.322$). *M. lucifugus* and *M. septentrionalis* passes could not be normalised; Kruskal-Wallis tests showed no differences between stand types for these species (*M. lucifugus* $X^2 = 8.513$; $d.f. = 7$; $p = 0.290$; *M. septentrionalis* $X^2 = 6.082$; $d.f. = 7$; $p = 0.530$).

2001: Post-harvest Grande Prairie

There were a total of 112 detector nights in 2001 in Grande Prairie. Passes of *Myotis* spp., *M. lucifugus*, and *M. septentrionalis* were recorded (Table 2). Thirty-two passes of larger genera were recorded. Feeding buzzes for total *Myotis* spp. were recorded, but again feeding buzzes for different species were not distinguishable. No feeding buzzes for large genera were recorded.

Although large differences seem to exist in bat detections between stand types (Table 2), especially between DR and DC stands, ANOVA analyses detected no differences in mean total passes between stand types ($F = 0.131$; *d.f.* = 3,8; p = 0.939), including MC stands and MR stands. Examination of the DR data showed that 1 stand, DR3, recorded only 5 passes, whereas DR1 recorded 329 and 375 passes, respectively. When DR3 was removed from analysis as an outlier, a subsequent t-test (SPSS Inc.) for differences between total mean passes in DC and DR stands showed significantly more passes in DR stands than in DC stands ($t = -3.558$; *d.f.* = 3; p = 0.038).

No differences in *Myotis* spp. passes were detected between stand types (ANOVA; $F = 0.159$; *d.f.* = 3,8; $p = 0.921$). Large genera passes would not normalise with transformations, so a Kruskal-Wallis test was run in SPSS, and did detect differences between stand types ($X^2 = 9.180$; *d.f.* = 3; $p = 0.027$). Subsequent Mann-Whitney U's showed significantly greater large genera bat activity in DC stands compared with DR stands types ($U = 0.000$; $n = 3,3$; $p = 0.046$), and in MC stands compared to MR stands types ($U = 0.000$; $n = 3$; $p = 0.037$).

Ln-transformed *M. septentrionalis* passes did not differ between stand types ($F = 0.357$; *d.f.* = 3,8; $p = 0.785$); neither did *M. lucifugus* passes differ between stand types (Kruskal-Wallis; ($X^2 = 0.983$; *d.f.* = 3; $p = 0.805$).

2002: Post-harvest Manning

There were 93 detector nights in 2002 in Manning (Table 3). Passes of total *Myotis* spp. and *M. septentrionalis* were recorded, but no *M. lucifugus* were distinguishable. Six passes of larger genera were recorded. No feeding buzzes of any species or species group were recorded.

There were no significant differences in mean total bat passes between stand types (ANOVA; $F = 1.243$; *d.f.* = 3,8; p = 0.357). Total *Myotis* spp. pass data, separated from large genera passes, did not differ between stand types ($F = 1.153$; *d.f.* = 3,8; $p = 0.385$). Large genera passes would not normalise with transformations; a Kruskal-Wallis test did not detect differences between stand types ($X^2 = 3.177$; *d.f.* = 3; $p = 0.365$). *M. septentrionalis* passes would not normalise either, and did not differ between stand types (Kruskal-Wallis; $X^2 = 5.518$; *d.f.* = 3; $p = 0.138$).

Bat activity across years

In Manning, repeated measures tests on mean total bat passes showed no effect of YEAR ($F = 0.170$; *df* = 1,8; $p = 0.691$); nor was the YEAR*STAND interaction term significant ($F = 0.426$; *df* = 3, 8; $p = 0.740$). In Grande Prairie, repeated measures tests on total mean passes showed that YEAR was significant ($F = 7.132$; *df* = 1,8; $p = 0.028$); though the YEAR*STAND interaction term was not significant ($F = 0.665$; *df* = 3, 8; $p = 0.597$).

Table 10.1. Total bat activity rates in pre-harvest (2000) stands in Manning and Grande Prairie.

Stand	*Total passes detected*	*Total buzzes detected*	*Trap Nights*	*Mean total passes per trap night*
GP-DC(pre)	34	0	29	1.17
GP-DR	259	2	33	7.84
GP-MC(pre)	53	1	27	1.96
GP-MR	119	1	39	3.05
MN-CC(pre)	109	7	29	3.76
MN-CR	82	1	34	2.41
MN-MC(pre)	21	0	28	0.75
MN-MR	15	1	24	0.62

Table 10.2. Total bat activity rates in post-harvest (2001) stand types in Grande Prairie.

Stand	*Total passes detected*	*Total buzzes detected*	*Trap Nights*	*Mean total passes per trap night*
GP-DC(post)	220	2	32	6.88
GP-DR	709	9	22	32.22
GP-MC(post)	313	0	36	8.69
GP-MR	261	4	22	11.86

Table 10.3. Total bat activity rates in post-harvest (2002) stand types in Manning.

Stand	*Total passes detected*	*Total buzzes detected*	*Trap Nights*	*Mean total passes per trap night*
MN-CC(post)	49	0	21	2.33
MN-CR	56	0	23	2.43
MN-MC(post)	15	0	25	0.60
MN-MR	38	0	24	1.58

Discussion

Bat detection assumptions and design

Critiques of studies employing bat detectors have appeared in the recent literature (*e.g.* Gannon *et al.* 2003; Miller *et al.* 2003). These authors have prompted that assumptions of bat detection studies be explicitly stated, and used to couch interpretations of the results. Following Gannon *et al.* (2003), in this study, we assumed that 1) acoustic recordings were related to stand type in which they were recorded; 2) call 'captures' were discreet events; 3) call types were not equal, and were separated as feeding buzzes and echolocation passes; 4) call types were randomly distributed in 3-dimensional space; 5) bat detectors operating within the same stand were independent observations; 6) bat detectors operating at a point within a stand on different nights were independent observations; and 7) replication occurred at the stand level. The third assumption is of particular importance, in that call type distinguishes between different forms of bat activity. Bat passes, which we most

frequently detected, indicate only general bat activity (fly-bys, orientation, communication, prey surveys). Feeding buzzes, which indicate active foraging, were rarely detected. Hence, we could not readily assign a biological significance to relative levels of bat activity. It is unknown whether bats in this study were using experimental or control stands for roosting, foraging, transit, or combinations thereof.

The final assumption (8) pertains to species / guild identification. We were unable to consistently distinguish *Myotis* spp. from one another. Large bat genera were distinguishable from *Myotis* spp., but not from one another. Therefore, our analysis included the bat community as a whole, followed by analysis of species or species groups where possible. This may have prevented us from detecting trends, as different bat species may have different responses to forest harvesting (Patriquin and Barclay 2003).

Hayes (1997) suggested that due to considerable between-night variability in bat activity, seven nights are required to sample bat activity with enough confidence to accurately estimate the mean. High temporal variability will result in high variance in the dataset within stand types, thus masking between-stand effects. This may explain why we failed to detect many differences between stand types. However, Hayes (1997) suggested that a sample smaller than seven nights could be compensated for by using a paired experimental design, which we employed in this study. In contrast, Mills *et al.* (1996) suggested that two or three nights are sufficient to sample ultrasonic bat vocalisations, if weather does not cause detector failure. In this study, we surveyed each point for three rain-free nights, and we are confident that within-point variability was captured in our sampling protocol.

Patriquin *et al.* (2003) found that ultrasounds with frequencies used by bats for echolocation were not equally detectable by *Anabat II* detectors across different habitat types. Detectability of 25 kHz sounds – produced by *Myotis* spp. – was higher in thinned conifer and mixedwood forests than in thinned deciduous forests. Detectability was also higher in thinned stands than in intact stands, within forest types. Detectability was lower in cutblocks than in uncut stands. However, detectability of 40 kHz sounds – produced by larger genera of non-*Myotis* species - did not differ between habitat types (Patriquin *et al.* 2003). These results suggest that our detection rate for 25 kHz sounds – produced by *Myotis* spp. – may have been under-sampled in cutblocks relative to other stands, and in intact harvest stands relative to MUP stands. This may have contributed to a Type I error had differences been found; as few differences were found, we may assume that our results were not influenced by differential detectability.

Bat communities

Crampton and Barclay (1998) found that the bat community in aspen mixedwood stands in northern Alberta was dominated by *M. lucifugus,* with *M. septentrionalis* and *L. noctivagans* also abundant. *E. fuscus* and *L. cinereus* were also present.

We found that, of the *Myotis* calls that could be identified to species for any given year, *M. lucifugus* outnumbered *M. septentrionalis*. Working in the same area, Patriquin and Barclay (2003) found more *M. lucifugus* than *M. septentrionalis*, suggesting that the pooled *Myotis* group was more influenced by the habitat associations of *M. lucifugus*. As distinguishable differences between numbers of the two species were marginal in this study, it is difficult to ascertain which species, if any, was driving the habitat associations of the pooled *Myotis* bat activity.

Bats in aspen mixedwoods

Kalcounis *et al.* (1999) recorded significantly more bat activity in mature aspen / white spruce mixedwood forest than in pure aspen or jack pine forests of the same age class. They suggested that the high bat activity in these stands was due to the aforementioned juxtaposition of both roost trees and foraging opportunities. Increased diversity of other animal species in mixedwood stands may also

result in greater bat usage of these stands. For example, as big brown bats are secondary cavity nesters, their ecology is likely tightly linked to cavity excavators such as yellow-bellied sapsuckers. Sapsuckers prefer old aspen mixedwoods stands with large old trees and snags (Schieck and Nietfeld 1995). Therefore, maintaining the elements of forest structure – older mixedwood features - for primary cavity excavators is likely important to maintaining bat abundance and diversity in mixedwood stands.

Little brown bats and silver-haired bats also selected old growth characteristics in northern Alberta aspen mixedwoods. Bat activity in aspen mixedwoods was higher in old growth (120+ years) than in young (20-30 years) or mature (50-65 years) stands (Crampton and Barclay 1998). All bats that were monitored roosted in old growth stands, in *P. tremuloides* that were taller than average, and that were either dead or infected with fungal heart rot. These trees were largely absent from young and mature stands in Crampton and Barclay's (1998) study.

In Alberta, bats preferred to roost in deciduous trees rather than conifers (Crampton and Barclay 1998). In contrast, Patriquin *et al.* (2003) found that conifer stands had higher activity of small bats than did deciduous or mixedwood stands. They found that larger bats were not influenced by stand type. In this study, no differences were found between pre-harvest deciduous, mixedwood, or coniferous stand types, for any species or species group of bats; thus bats do not appear to have more activity in mixedwood stands compared to deciduous or coniferous stand types, as we hypothesised.

Bat use of harvested stands and patches

Some differences in bat activity between harvested and unharvested were recorded. The repeated measures analysis within stands between years also indicated changes in bat activity; in Grande Prairie there were significantly more total bat passes post-harvest than pre-harvest.

Large genera bats were completely absent in 2000, before harvesting occurred, but appeared post-harvest in both Grande Prairie and Manning. In Grande Prairie, large genera bats were found more often in clearcut deciduous and MUP mixedwood stands than in their unharvested control counterparts. These results concur with those of Patriquin and Barclay (2003), who found that *L. noctivagans*, a larger and less manoeuvrable species, preferred cutblocks and avoided forest interiors; bat activity was influenced by harvesting treatment, with more activity in clearcuts. Our results, and those of Patriquin and Barclay (2003), suggest that clearcut harvesting may facilitate foraging activity for larger bats.

In contrast, we recorded a larger number of total mean passes (numerically dominated by *Myotis* species) in deciduous reserves than in deciduous cuts, suggesting that clearcutting deciduous stands deleteriously impacted habitat quality for small *Myotis* bats. Also in Alberta, Hogberg *et al.* (2002) found that *M. lucifugus* and *M. septentrionalis* were least active in the middle of cutblocks.

We found few other differences in small (*Myotis* spp.) bat activity between experimental and control stands. There were no differences between the harvested and unharvested conifer or mixedwood Manning stands. Similarly, Patriquin and Barclay (2003) found that although differences between harvested and unharvested stands did occur for some species in some habitats, overall small bat activity was not influenced by treatments, and did not differ between control and clearcut stands. Tibbels and Kurta (2003) recorded no significant differences in bat activity between thinned and un-thinned red pine stands despite differences in stand structural complexity.

Elsewhere, the creation of transitional forest-clearcut habitat (termed "edge"), has been shown to have positive effects on bat activity. *Myotis* bats may preferentially use forest edges for escape cover, orientation landmarks, and to utilise increased abundances of insects occurring there (see Patriquin and Barclay 2003 for discussion). Foraging bats are known to move more along forest edges than in the forest interior (Black 1974; Crampton and Barclay

1998), which may be due to facilitation of aerial navigation through removal of stand clutter (see Hogberg *et al.* 2002 for review). For example, Grindal and Brigham (1998) found that bat activity in western hemlock (*Tsuga heterophylla*) and western redcedar (*Thuga plicata*) cutblocks increased 1-year post-harvest relative to pre-harvest activity. Similarly, bat activity increased in sites along a forestry access road one year post-construction, relative to pre-construction (Grindal and Brigham 1998). Note that caution should be taken when interpreting these results, as no controls were employed, and sample sizes were small. In northern hardwoods / conifer forests of Maine, bat activity was greater in old (120+ years) stands and in young (<10 years) stands than in intermediate age classes (Krusic *et al.* 1996). In the Pacific north west, bat activity was higher in thinned (selectively logged to reduce density of overstorey trees) mature stands than in unthinned mature stands, and was not significantly different from bat activity in old-growth stands (Humes *et al.* 1999). In Newfoundland, Grindal (1998) found that all bat roosts located were found in forests 80+ years old or cutblocks < 20 years old, and most were within 15 m of the forest / cutblock edge. This proximity to edge was attributed to the trade-off of adjacency to available habitat in forests, and ease of access created by the cutblock. In British Columbia, western long-eared bats have been noted roosting in stumps within 9-year old conifer clearcuts (Vonhof and Barclay 1997), though is likely a species-specific characteristic.

We found that the effects of the creation of forest – cutblock edge are not consistent across species due to differences in manoeuvrability, effected by morphological differences in wing aspect ratio between large and small species. This finding is supported by other research. In Alberta, *M. lucifugus* and *M. septentrionalis* activity along forest edges did not differ from residual edges; both species were least active in the middle of cutblocks (Hogberg *et al.* 2002). However, activity of the larger *L. noctivagans* did not differ between edges or cutblock centre. In Queensland, Australia, selective logging produced canopy gaps that exhibited higher overall bat activity than did closed-canopy forests. On a species level however, gaps created by selective logging were used or avoided by different species, depending on wing morphology (Crome and Richards 1988).

We found no differences in small or large bat activity between unharvested mixedwood stands and MUP harvested stands in this study. This is not unexpected. A lack of change in bat activity following forest harvesting or fragmentation has been found by a number of authors (see Zielinski and Gellman 1999 for review). Swystun *et al.* (2001) found that there was no significant difference in bat activity between clear-cut edges and residual patch edges. They did, however, note a change in activity with distance of residual from the clearcut edge: patches *ca.* 150 m from the edge had high bat activity, while those < 100m or >250m from the edge had low activity (Swystun *et al.* 2001). This was attributed to wind dynamics and insect abundance at the different patch distances.

Erickson and West (2003) suggested that, based on observed relationships to forest structure, bats should be able to use stands of any seral stage, provided the appropriate roosting structure - trees and snags - were present. Patriquin and Barclay's (2003) findings indicate that selective logging (thinning) provide nominal immediate advantages to foraging bats, but suggest that thinning is more beneficial to bats in the long-term than are clear-cuts, due to accelerated convergence to pre-disturbance states - a finding supported by Fisher and Wilkinson's (2002) review. This is likely also the case for MUP harvesting. In contrast, clearcutting improves foraging habitat quality for large bats, but reduces habitat quality for small bats, thereby detrimentally impacting bat community diversity. The apparent maintenance of bat community diversity suggests that MUP harvesting is a preferred alternative to clearcutting.

Implications for Species-at-Risk

The northern long-eared bat (*Myotis septentrionalis*) has been listed as *May be at Risk* in Alberta (Alberta Sustainable Resource Development 2001). This species occurs in the research area and was recorded in this study. We did not detect any differences in *M. septentrionalis* activity between stand types, although our power to detect differences was low. Our results suggest that MUP stands may provide foraging habitat for *M. septentrionalis,* and likely represent more suitable habitat than do clearcut stands. Further research is required to determine if MUP stands provide adequate retention of roost sites to allow for support of minimum viable populations.

Conclusions and Management Implications

We found that bats were active in mixedwood understorey protection harvest stands. Our results suggest that forest structural attributes created by canopy break-up in old-growth stands, which serve to facilitate bat activity in natural conditions, may be emulated by MUP harvesting. As MUP stands sampled in this study left standing live mature decadent trees and snags, and introduced open areas for foraging, the habitat loss incurred through harvest may be somewhat offset by the forest structural benefits that ensue. However, it is unknown whether bats in this study were using experimental and control stands for solely foraging, or for roosting and foraging; the latter combination is required for the persistence of bat populations at the stand level.

As understorey release promotes the maturation of conifer and recruitment into the overstorey, and allows in-stand residuals to senesce and decay, the benefits of MUP harvesting are likely to compound over time, resulting in an accelerated convergence of the bat community to pre-disturbance states. We recommend that further analysis be conducted over successional time to test these hypotheses.

The degree to which natural gaps are emulated is likely mediated by harvest intensity, site productivity, age, and stand type - the results for bats we obtained apply only to mixedwood stands within the age range studied herein, and harvested under the operational parameters outlined. Variations in operational implementation, and in other stand types, should receive further evaluation.

In addition, the effects on bats recorded here apply only to the successional period between MUP harvesting and second-phase harvesting of the stand, when the understorey becomes merchantable age. If second-phase harvest employs clearcutting, diversity of all bat species will decline dramatically. Clearcutting may provide foraging areas for some species but alone will not support bat populations. Large-scale retention of old senescing or decadent live trees and snags are required for bat roosts, which are limiting factors of population persistence. Bat population persistence will therefore be related to the amount of residual retention. Hence, the landscape pattern of deployment of MUP harvesting will also affect the overall persistence of bats within a region, suggesting planning processes occur that spatially stagger initial MUP harvesting with second-phase cutting of a stand.

These caveats aside, understorey protection harvesting of mixedwoods stands do appear to foster greater levels of bat activity and diversity than would be expected in clearcuts - levels activity that do not appear to differ significantly from unharvested mixedwood stands.

Acknowledgements

The authors and research team would like to thank Krista Patriquin for her analysis of the *Anabat* recordings.

References

Alberta Sustainable Resource Development. 2001. The general status of Alberta wild species 2000. Alberta Sustainable Resource Development, Fish and Wildlife Service. 46 pp.

Barclay, R.M.R., M.B. Fenton, and D.W. Thomas. 1979. Social behaviour of the little brown bat, *Myotis lucifugus*. II. Vocal communications. Behavioural Ecology and Sociobiology **6**: 137-146.

Barclay, R.M.R. 1985. Long- versus short-range foraging strategies of hoary (*Lasiurus cinereus*) and silver-haired (*Lasionycteris noctivagans*) bats and the consequences for prey selection. Canadian Journal of Zoology **63**: 2507-2515.

Barclay, R.M.R. 1991. Population structure of temperate zone insectivorous bats in relation to foraging behaviour and energy demand. Journal of Animal Ecology **60**: 165-178.

Betts, B.J. 1998. Roosts used by maternal colonies of silver-haired bats in northeastern Oregon. Journal of Mammalogy **79**: 643-650.

Black, H.L. 1974. A north temperate bat community: structure and prey populations. Journal of Mammalogy **55**: 138-157.

Brigham, R.M., M.J. Vonhof, R.M.R. Barclay, and J.C. Gwilliam. 1997. Roosting behaviour and roost-site preferences of forest-dwelling California bats (*Myotis californicus*). Journal of Mammalogy 78(4): 1231-1239.

Callahan, E.V., R.D. Drobney, and Richard L. Clawson. 1997. Selection of summer roosting sites by Indiana bats (*Myotis sodalis*) in Missouri. Journal of Mammalogy **78**: 818-825.

Campbell, L.A., J.G. Hallett, and M.A. O'Connell. 1996. Conservation of bats in managed forests: use of roosts by *Lasionycteris noctivagans*. Journal of Mammalogy **77**: 976-984.

Crampton, L.H., and R.M.R. Barclay. 1998. Selection of roosting and foraging habitat by bats in different-aged aspen mixedwood stands. Conservation Biology **12**: 1347-1358.

Crome, F.H.J., and G.C. Richards. 1988. Bats and gaps: microchiropteran community structure in a Queensland rainforest. Ecology **69**(6): 1960-1969.

Erickson, J.L., and S.D. West. 2003. Association of bats with local structure and landscape features of forested stands in western Oregon and Washington. Biological Conservation **109**: 95-102.

Fenton, M.B. 1990. The foraging behaviour and ecology of animal-eating bats. Canadian Journal of Zoology **68**: 411-422.

Fisher, J.T. and L. Wilkinson. 2002. The mammalian response to forest harvesting and fire. *In* S. Song, (Ed.) *The Ecological Basis for Stand Management.* Alberta Research Council, Vegreville, Alberta.

Gannon, W.L., R.E. Sherwin, and S. Haymond. 2003. On the importance of articulating assumptions when conducting acoustic studies of habitat use by bats. Wildlife Society Bulletin **31**(1): 45-61.

Griffin, D.R., F.A. Webster, and C.R. Michael. 1960. The echolocation of flying insects by bats. Animal Behaviour **8**: 141-154.

Grindal, S.D. 1998. Habitat use by bats, *Myotis* spp., in western Newfoundland. Canadian Field-Naturalist **113**(2): 258-263.

Grindal, S.D., and R.M. Brigham. 1998. Short-term effects of small-scale habitat disturbance on activity by insectivorous bats. Journal of Wildlife Management **62**(3): 996-1003.

Hayes, J.P. 1997. Temporal variation in activity of bats and the design of echolocation-monitoring studies. Journal of Mammalogy **78**(2): 514-532.

Hogberg, L.K., K.J. Patriquin, and R.M.R. Barclay. 2002. Use by bats of patches of residual trees in logged areas of the boreal forest. American Midland Naturalist **148**: 282-288.

Humes, M.L., J.P. Hayes, and M.W. Collopy. 1999. Bat activity in thinned, unthinned, and old-growth forests in western Oregon. Journal of Wildlife Management **63**(2): 553-561.

Jung, T., I.D. Thompson, R.D. Titman, and A.P. Applejohn. 1999. Habitat selection by forest bats in relation to mixed-wood stand types and structure in central Ontario. Journal of Wildlife Management **63**(4): 1306-1319.

Kalcounis, M.C., K.A. Hobson, R.M. Brigham, and K.R. Hecker. 1999. Bat activity in the boreal forest: Importance of stand type and vertical strata. Journal of Mammalogy **80**: 673-682.

Kalcounis, M.C., and M.R. Brigham. 1998. Secondary use of aspen cavities by tree-roosting big brown bats. Journal of Wildlife Management **62**: 603-611.

Krusic, R.A., M. Yamasaki, C.D. Neefus, and P.J. Pekins. 1996. Bat habitat use in White Mountain National Forest. Journal of Wildlife Management **60**(3): 625-631.

Kunz, T.H. 1982. Roosting ecology of bats. Pages 1-55 in T.H. Kunz, editor. Ecology of bats. Plenum Press, New York.

Miller, D.A., E.B. Arnett, and M.J. Lacki. 2003. Habitat management for forest-roosting bats of North America: a critical review of habitat studies. Wildlife Society Bulletin **31**(1): 30-44.

Mills, D.J., T.W. Norton, H.E. Parnaby, R.B. Cunningham, and H.A. Nix. 1996. Designing surveys for microchiropteran bats in complex forest landscapes – a pilot study from south-east Australia. Forest Ecology and Management **85**: 149-161.

O'Farrell, M.J., B.W. Miller, and W.L. Gannon. 1999. Qualitative identification of free-flying bats using the Anabat detector. Journal of Mammalogy **80**: 11-23.

Patriquin, K.J., and R.M.R. Barclay. 2003. Foraging by bats in cleared, thinned, and unharvested boreal forest. Journal of Applied Ecology **40**: 646-657.

Patriquin, K.J., L.K. Hogberg, B.J. Chruszcz, and R.M.R. Barclay. 2003. The influence of habitat structure on the ability to detect ultrasound using bat detectors. Wildlife Society Bulletin **31**(2): 475-481.

Parsons, S., K.J. Lewis, and J.M. Psyllakis. 2003. Relationships between roosting habitat of bats and decay of aspen in the sub-boreal forests of British Columbia. Forest Ecology and Management **177**: 559-570.

Reith, C.C. 1980. Shift in times of activity by *Lasionycteris noctivagans*. Journal of Mammalogy **61**(1): 104-108.

Schieck, J., and M. Nietfeld. 1995. Bird species richness and abundance in relation to stand age and structure in aspen mixedwood forests in Alberta. Pages 115-157 *In* J.B. Stelfox, Editor. Relationships between stand age, stand structure, and biodiversity in aspen mixed wood forests in Alberta. Alberta Environmental Centre, Vegreville, Alberta, Canada.

Swystun, M.B., J.M. Psyllakis, and R.M. Brigham. 2001. The influence of residual tree patch isolation on habitat use by bats in central British Columbia. Acta Chiropterologica **3**(2): 197-201.

Thomas, D.W. 1988. The distribution of bats in different ages of Douglas-fir forests. Journal of Wildlife Management **52**:619-626.

Tibbels, A.E., and A. Kurta. 2003. Bat activity is low in thinned and unthinned stands of red pine. Canadian Journal of Forest Research **33**: 2436-2422.

Vonhof, M.J., and R.M.R. Barclay. 1996. Roost-site selection and roosting ecology of forest-dwelling bats in southern British Columbia. Canadian Journal of Zoology **74**: 1997-1805.

Vonhof, M.J., and R.M.R. Barclay. 1997. Use of tree stumps as roosts by the western long-eared bat. Journal of Wildlife Management **61**(3): 674-684.

Vonhof, M.J., and L. Wilkinson. 1999. Roosting habitat requirements of northern long-eared bats (*Myotis septentrionalis*) in the boreal forests of northeastern British Columbia: Year 2. Prepared for British Columbia Ministry of Environment, Victoria, B.C.

Wilkinson, L., and R.M.R. Barclay. 1997. Differences in the foraging behaviour of male and female big brown bats (*Eptesicus fuscus*) during the reproductive period. Ecoscience **4**(3): 279-285.

Wunder, L., and A.B. Carey. 1996. Use of the forest canopy by bats. Northwest Science **70**: 79-85.

Zielinski, W.J., and S.T. Gellman. 1999. Bat use of remnant old-growth redwood stands. Conservation Biology **13**(1): 160-167.

Zar, J.H. *Biostatistical Analysis.* 3rd Edition. Prentice Hall, New Jersey.