INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps.

Photographs included in the original manuscript have been reproduced xerographically in this copy. Higher quality 6" x 9" black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.

Bell & Howell Information and Learning
300 North Zeeb Road, Ann Arbor, MI 48106-1346 USA
800-521-0600

UMI®

University of Alberta

Variability in forest structure and composition along edge-to-interior gradients from lakeshore and clearcut edges and in riparian buffers in the aspen-dominated mixedwood boreal forest

by

Karen Amanda Harper ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment

of the requirements for the degree of Doctor of Philosophy

in

Forest Biology and Management

Department of Renewable Resources

Edmonton, Alberta

Fall 1999

National Library
of Canada

Acquisitions and
Bibliographic Services

395 Wellington Street
Ottawa ON K1A 0N4
Canada

Bibliothèque nationale
du Canada

Acquisitions et
services bibliographiques

395, rue Wellington
Ottawa ON K1A 0N4
Canada

Your file Votre référence

Our file Notre référence

0-612-46847-X

University of Alberta

Library Release Form

Name of Author: Karen Amanda Harper

Title of Thesis: Variability in forest structure and composition along edge-to-interior gradients from lakeshore and clearcut edges and in riparian buffers in the aspen-dominated mixedwood boreal forest

Degree: Doctor of Philosophy

Year this Degree Granted: 1999

Karen Harper

9826 - 76th Avenue
Edmonton, AB, T6E 1K5

30 September, 1999

University of Alberta

Faculty of Graduate Studies and Research

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled Variability in forest structure and composition along edge-to-interior gradients from lakeshore and clearcut edges and in riparian buffers in the aspen-dominated mixedwood boreal forest, submitted by Karen A. Harper in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Forest Biology and Management.

Ellen Macdonald
Dr. S. Ellen Macdonald

M R T Dale
Dr. Mark R. T. Dale

Susan H
Dr. Susan Hannon

Victor Lieffers
Dr. Victor Lieffers

Dr. Uldis Silins

Dr. Christian Messier

Sept. 30, 1999

Vegetation presents a field of phenomena notably lacking in fixed points of reference, lines of division, invariable rules, and easy definitions.

Robert H. Whittaker, 1953

ABSTRACT

On the boreal forest landscape, inherent edges are already prominent features and edges created by timber harvesting are also becoming common. Both types of edges border unharvested buffer zones left around lakes following harvest. I investigated forest structure and composition along edge-to-interior gradients from lakeshore and clearcut edges, and within buffer strips of different width. I had three objectives: 1) To quantify trends in forest structure and composition and to determine distance of edge influence for different response variables for both lakeshore and clearcut forest edges; 2) To assess edge influence on forest structure and composition at edges of different aged cutblocks; 3) To model edge influence and to predict the width of interior forest in buffers of different widths. Trees, coarse woody material, saplings, shrubs and herbs were sampled at different distances from lakeshore edges and created edges adjacent to 1, 2, 5, and 16 yr old cutblocks, within buffer zones of three different widths (25, 100, 200m), and in interior forest. I developed a new method for quantifying distance of edge influence by comparing averages of response variables at different distances from the edge to critical values determined by randomization tests of data collected in interior forest. There was a structurally diverse 40m wide lakeshore forest edge community with greater amounts of coarse woody material, and more saplings and mid-canopy trees than in interior forest. Following harvest, clearcut edges experienced damage to live trees and snags, increasing the amount of coarse woody material. Prolific suckering of *Populus tremuloides* and *P. balsamifera* was accompanied by a decrease in total shrub cover, and changes in understory composition. Overall, distance of edge influence from clearcut edges extended

about 20m into the forest, and this did not differ substantially among edges at different aged cutblocks. Edge influence in narrow buffers is predicted to be greater for combined edge influence from lakeshore and clearcut edges, and less if the riparian forest is resistant to edge influence. The 200m buffers are the only ones predicted (of the three studied (25, 100, 200m)) to have substantial interior forest habitat over time.

In memory of my grandmother, Dr. G. I. Harper.

ACKNOWLEDGEMENTS

I thank Lisa Cuthbertson, Trevor Lantz, Kimberly Ozeroff, Lisa Matsuba, Jason Miller, Julie Mills and Julie Perkins for their invaluable field assistance; Fiona Schmiegelow for the use of her Calling Lake camp; and Mark Dale, Susan Hannon, Victor Lieffers, Gavin Kernaghan, Jeanine Rhemtulla and other colleagues in the Department of Renewable Resources for their helpful comments on earlier versions of parts of this dissertation. I am grateful to Marko Mah who performed the wavelet analysis for me, and to Russ Sampson for his help with computer programming and developing equations. Funding was provided through an interdisciplinary project, TROLS, by the Natural Sciences and Engineering Research Council (Canada), Alberta Economic Development and Tourism, Alberta Environmental Protection, Alberta-Pacific Forest Industries, Manning-Diversified Forest Products Research Trust, Syncrude (Canada) Ltd., Weyerhaeuser (Alberta) Ltd., Ainsworth Lumber and C&S Resources; as well as a Grant-In-Aid from the Northern Scientific Training Program of the Department of Indian Affairs and Northern Development through the Canadian Circumpolar Institute of the University of Alberta; and a grant from the Challenge Grants in Biodiversity Program funded by the Department of Biological Sciences, University of Alberta and the Alberta Conservation Association. I also gratefully acknowledge scholarship support from the University of Alberta and the Killam Trust.

I was privileged to work with a wonderful group of fellow graduate students who provided advice, constructive criticism, support and friendship (Carl, George, Jon, Barb, Pete, Jeanine, Kendall, Sue, Vern, Lisa, Treena, Suzanne and Anisul). I also benefitted tremendously from the help of my committee (Mark Dale, Susan Hannon, Vic Lieffers) and additional examiners (Christian Messier, Uldis Silins). Thanks also to my parents for their support, and to Gavin for his intellectual companionship, support and advice. Most of all, I thank Ellen Macdonald, my supervisor, for providing help, understanding, advice and support. She remained committed to me and my project, and provided valuable input at all stages.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF PLATES

LIST OF ABBREVIATIONS

CWM	Downed coarse woody material
DEI	Distance of edge influence
DEIc	Distance of edge influence for change
MEI	Magnitude of edge influence
SMW	Split moving window analysis
TROLS	Terrestrial Riparian Organisms Lakes and Streams, an acronym for the project, "The role of buffer strips in the maintenance of aquatic and terrestrial communities in the aspen-dominated mixedwood boreal forest"

CHAPTER 1. INTRODUCTION

Forest edges are abrupt transitions between forested and non-forested communities, or between two different forested communities. Forest edges can be readily discernible or imperceptible. The goal of an entire field of research, edge detection, is to determine the locations of boundaries on the landscape by delineating areas of the greatest change in vegetation (e.g. Brunt and Conley 1990, Fortin 1994). In this study, I investigated forest edges abutting non-forested communities, including inherent lakeshore forest edges and edges created by forest harvesting. Natural, inherent edges are the result of steep gradients in topography, soil type, microclimate and/or geomorphology, and tend to be stable and relatively permanent features of the landscape. Created edges are edges that have formed as a result of a natural or anthropogenic disturbance; these edges are short-lived and dynamic (Thomas et al. 1979).

Edges are important features of the landscape because they contribute to spatial heterogeneity and diversity within the forest landscape, but they have often been neglected in previous research which has focused on homogeneous areas (Holland and Risser 1991, Risser 1995). Influence from the adjacent non-forest environment alters forest structure and species composition at the edge. Research on edge influence is important for habitat conservation and management, and for understanding processes in forest communities by investigating the response of vegetation to edge-induced gradients. In this dissertation, I examine the phenomenon of edge influence from inherent and created edges in the boreal forest.

RESEARCH ON EDGES

Investigations of natural, inherent forest edges are very limited. Within forests, much of the heterogeneity has been visualized along edaphic gradients (e.g. moisture, temperature, nutrient availability), often related to elevation or latitude. Only a few studies have considered the variation in species composition along a spatial edge-to-interior gradient at natural inherent edges (but see Wood and Wood 1989, Hibbs and Giordano 1996, Pabst and Spies 1998). One of the fundamental principles of ecology is the relatively high level of diversity at edges and other ecotones (Wiens 1976, Harris 1988). However, there is a lack of empirical data on diversity at edges and few studies have examined changes in diversity and composition across ecotones (Risser 1995).

Previously, research on edge influence from created edges has focused on old, permanent, maintained edges next to agriculture or other fields in eastern deciduous forests of the United States (e.g. Ranney et al. 1981, Matlack 1993, 1994), and in tropical rainforests (e.g. Fox et al. 1997). At these well-developed forest edges, a different microclimate leads to changes in species composition and forest structure as compared to the interior forest (Wales 1972, Ranney et al. 1981). Greater light can create a proliferation of shade-intolerant species and relatively high species richness (Wales 1972, Ranney et al. 1981). Over time, a side canopy, comprised of higher stem densities of trees and saplings, shrubs and side branches of trees, can block out light and wind, and decrease the extent of edge influence (Brothers and Spingarn 1992, Matlack 1993). More recently, studies have investigated younger created edges and have observed structural changes such as wind damage, tree mortality and tree recruitment (e.g. DeWalle 1983, Williams-Linera 1990, Laurance et al. 1998a and b). One major study that focused on edge influence from 15 yr old clearcut edges in an old-growth Douglas-fir forest in Oregon also found altered forest structure with fewer trees, lower canopy cover, and more snags and downed logs (Chen et al. 1992). There is also evidence of changes in shrub cover or the abundance of individual species at edges only one or two years after edge (Matlack 1994) or gap creation (Moore and Vankat 1986).

Edges of different ages have been examined for a few tropical (Williams-Linera 1990, Laurance et al. 1998a) and eastern deciduous forests (Matlack 1993, 1994). Williams-Linera (1990) and Matlack (1994) found a decrease in edge influence with time; however, Laurance et al. (1998a) found that edge influence on tree mortality and damage rates was constant for 18 years following edge creation. Ranney et al. (1981) developed a conceptual model which outlines stages of succession at maintained edges based on the closure of the side canopy and competition at the edge, in which they predicted a continual increase in basal area at the edge, and a peak of stem density at 20 years. More studies are needed that explicitly address the persistence of edge influence over time in order to understand the dynamic nature of edges (Murcia 1995, Bierregaard et al. 1997), particularly in harvested forested landscapes with edges next to regenerating cutblocks.

Forest structure is one component of several contributing to edge influence on wildlife (McCollin 1998). Relative abundance and diversity of small mammals was greater within 10m of older clearcut edges in a temperate forest in New Brunswick (Sekgororoane and Dilworth 1995). In Michigan, dense understory vegetation provided cover for birds while nesting and feeding; the number of nests was greater within 15m of edges (Gates and Gysel 1978). However, despite overall increases in diversity, the abundance of interior forest wildlife species can decrease near edges. In a tropical forest study on fragmentation, fewer interior forest birds were found within 50m from edges (Lovejoy et al. 1986). Increased predation and nest parasitism of interior forest birds is also a concern near edges (Saunders et al. 1981, Paton 1994).

ANALYSIS OF EDGE INFLUENCE

Research on edges has often included a determination of the extent of edge influence. Distance of edge influence (DEI) or 'edge width', is difficult to quantify. Even in an ideal homogeneous ecosystem, changes in forest structure and composition along edge-to-interior gradients are almost always gradual with no obvious single discontinuity (Ranney et al. 1981). I define distance of edge influence as the distance from the forest edge where forest structure and composition is significantly different from the range of variability within the interior forest.

The extent of edge influence varies with ecosystem type, time since disturbance and response variable. Estimates of DEI reported from older temperate and tropical maintained forest edges include: 20m (Wales 1972), 15m (Ranney et al. 1981), 5-45m (Palik and Murphy 1990) and 4-16m (Fox et al. 1997). Results of DEI are considerably greater for recent tropical forest edges (85-335m, Laurance et al. 1998a) and recent clearcut edges in Douglas-fir forests (16-137m, Chen et al. 1992), particularly for structural damage.

Researchers have employed several different methods to study edge influence (Table 1-1), most of them based on examination of created edges. Some studies have documented the existence of edge influence, but were not designed to determine DEI (e.g. Wales 1972, Brothers 1993, Young and Mitchell 1994). Most methods that have been used to quantify DEI, including regression and non-parametric procedures, appear to violate assumptions of independence of samples, as a result of spatial autocorrelation along transects (e.g. Wales 1972, Ranney et al. 1981, Matlack 1993, 1994). Spatial autocorrelation occurs when samples are more or less similar than random due to their proximity, and therefore are not independent (Legendre and Legendre 1998). Further, methods employing regression analyses using linear response models could easily fail to detect nonlinear trends along the edge-to-interior transect (Ranney et al. 1981, Williams-Linera 1990, Matlack 1993). Replication has also been a problem; Murcia (1995) found that almost half of edge studies lacked appropriate replication. Gosz (1991) highlights the need for new techniques that can analyze the nonnormal, autocorrelated data that are common in research on landscape boundaries.

An essential component of the assessment of edge influence is an objective and relevant standard for comparison. Few methods for determining DEI have considered the usefulness of variation within interior forest for this purpose. Laurance and Yensen (1991) introduced a model that accounts for the variation in DEI at different edges, but failed to provide a criterion to quantify DEI. Chen et al. (1992) provided an objective, but arbitrary, criterion when they introduced DEI as the point along a regression curve at which a variable reached 2/3 the condition of the interior forest environment; Chen et al. (1996) later changed the criterion to 90%. By arbitrarily defining 'interior forest' as the average condition at 240m from the edge, Chen et al.'s method does not incorporate variability in interior forest. Laurance et al. (1998a) provided an appropriate measure of the variability in interior forest through a 95% confidence interval of forest interior plots. However, their determination of DEI as the intersection of a fitted curve with the confidence interval may lead to inaccurate estimates of DEI if the model of the curve is inappropriate or if the data cannot be well fit to any curve.

A new method is necessary for assessing DEI that can handle autocorrelated data using an objective and relevant standard for comparison. An assessment of variation in interior forest is particularly important for ecosystems like the boreal forest that contain within-stand heterogeneity. Quantifying DEI is important for determining the extent of edge influence from natural and created edges on the landscape, and determining the effective size of interior forest habitat in natural and managed landscapes (e.g. Laurance and Yensen 1991).

EDGES IN THE LANDSCAPE

Previously, research focused on homogeneous areas within the landscape (Gosz 1991, Holland and Risser 1991, Wiens 1992). However, a new approach to examining natural boundaries is emerging in the field of landscape ecology. Instead of assuming homogeneity, landscape ecology examines the effects of spatial pattern on ecological processes and considers spatial heterogeneity as a causal factor in ecological systems

(Pickett and Cadenasso 1995). Landscapes are viewed using a patch-corridor-matrix model, with boundaries as an important component (Forman 1997). Boundary dynamics theory examines the role of boundaries in landscape-level processes (Wiens et al. 1985, Forman and Moore 1992). Boundary permeability, a component of boundary dynamics, is partly a function of the structure of the edge (Wiens et al. 1985, Forman and Moore 1992). Determination of forest structure at natural boundaries is important for understanding the movement of organisms and other fluxes across the landscape (Wiens et al. 1985, Forman and Moore 1992).

On managed landscapes, clearcutting for timber harvest or conversion to agriculture often leads to forest fragmentation. Such fragmented landscapes used to be managed for relatively high amounts of edge with the goal of increasing diversity (Thomas et al. 1979). Landscape-level diversity indices were developed based on the amount of edge within a landscape (Patton 1975, Thomas et al. 1979). However, the recognition that an apparent increase in species diversity may in fact reflect a decrease in interior species (Noss 1983) changed the focus of research on fragmentation. Negative effects of edge influence became evident in research on fragmentation in tropical forests (Lovejoy et al. 1986, Laurance and Yensen 1991). Tropical researchers developed a new approach to the study of fragmentation that incorporates the role of edge influence, instead of exclusively relying on the traditional equilibrium theory of island biogeography which only considers size and isolation of forest 'islands' (Laurance and Yensen 1991). Laurance and Yensen (1991) developed a Core-Area Model which incorporates distance of edge influence in determining the proportion of interior forest within a fragment.

The study of natural forest boundaries or ecotones and the investigation of edge influence within fragmented landscapes have always been separate. However, in order to understand faunal response to habitat within a landscape fragmented by agriculture or forestry, it is important to know the extent of edge influence from both natural and created edges. This is particularly important in landscapes where natural forest edges are prominent, such as the boreal forest (see below).

Riparian buffers

Understanding edge influence on forest structure and composition from both natural and created edges is particularly important in riparian buffers. Buffer zones of unharvested forest are usually left around lakes and streams following clearcutting. Buffers are bordered by both a natural, inherent, lakeshore forest edge, and an artificial, created, clearcut forest edge. Vegetation patterns within riparian buffers are important for fauna that will encounter both lakeshore and clearcut edges within buffer strips.

Investigations of lakeshore or other riparian forest edges are very limited. Studies of riparian forests have been primarily descriptive, and have focused on floodplain communities near streams or rivers (Bell 1974, Ericsson and Schimpf 1986, Hedman and Van Lear 1995). A few studies have reported greater structural and plant species diversity in riparian forests near streams as compared to similar upland forests (Gregory et al. 1991). Riparian habitat is important for wildlife communities (Kelsey and West 1999). Bird abundance and richness in riparian forests may be higher than (Gates and Giffen 1991, LaRue et al. 1995, Wiebe and Martin 1998), the same as (Small and Hunter 1989, Murray and Stauffer 1995, Whitaker and Montevecchi 1997) or lower than (McGarigal and McComb 1992) in upland forests. One study on small mammals found that greater abundance and species richness in riparian forest compared to upland forest was partially due to forage availability (Doyle 1990).

THE TROLS OPPORTUNITY

My research was part of a study of various widths of buffer strips around lakes in northern Alberta. This NSERC-funded project, "The role of buffer strips in the maintenance of aquatic and terrestrial communities in the aspen-dominated mixedwood boreal forest" (hereafter referred to as TROLS which stands for Terrestrial Riparian Organisms Lakes and Streams), provided me with an excellent opportunity to investigate edge influence in the western boreal mixedwood forest of northern Alberta. The interdisciplinary nature of this large study allows for the investigation of relationships among different components of the ecosystem (e.g. microclimate, small mammals, birds, hydrology, aquatic ecosystems etc.). The goal of the overall project was to evaluate the effects of different widths of forested buffers on aquatic and terrestrial ecosystems in the boreal mixedwood forest. My role in the TROLS project was to investigate edge influence on forest structure and composition in different widths of buffer zones.

The ecosystem in which TROLS is conducted, the aspen-dominated mixedwood boreal forest, exhibits "multi-scaled heterogeneity" (Cumming et al. 1996). Topography, hydrology, natural disturbances (e.g. treefalls, insect outbreaks and fire) and the mixedwood nature of this forest ecosystem contribute to spatial and temporal variation in the physical environment at the stand and landscape scales. Methods of quantifying edge influence developed in other systems (which generally do not account for variation within the interior forest) may not be applicable to the heterogeneous boreal forest of northern Alberta. The boreal forest landscape can be considered a patchy environment with extensive natural edges (Plate 1-1), unlike continuous tropical forests in which edges are rare (Laurance and Bierregaard 1997). Over the past several decades, artificial edges have been added on the landscape, next to various roads, right-of-ways and clearings associated with oil and gas industries. More recently, forest harvesting has also contributed to habitat fragmentation.

Study sites description

Research was conducted in the Mid Boreal Mixedwood Ecoregion in central Alberta, Canada (Strong 1992, Figure 1-1). This aspen-dominated mixedwood forest covers most of central Alberta and ranges from northeastern British Columbia eastward into Saskatchewan and Manitoba (Rowe 1972, Strong 1992). All stands fall into the low-bush cranberry Aw ecosite phase (Beckingham and Archibald 1996) based on plant species composition, although site classification was not performed on site prior to sampling. A boreal climate regime is found in this ecoregion with a mean summer temperature of 13.5°C, a mean winter temperature of -13.2°C, and an annual precipitation of 397mm which occurs mostly in the summer (Strong 1992). Two climate stations near the study sites (Rock Lake and Round Hill fire towers) recorded mean summer temperatures of

16.5°C and 17.3°C, respectively, for 1990-1996. Gray Luvisol soils predominate on undulating morainal plains with some Eutric Brunisol soils on more xeric sites (Rowe 1972, Strong 1992).

My study encompassed three areas in central Alberta: South Calling Lake (55° N, 114° W, 640m elevation, south of the Athabasca River, near Calling Lake, Alberta), Calling Lake (55° N, 113° W, 670 elevation, north of the Athabasca River, near Calling Lake, Alberta), and Lac La Biche (55° N, 112° W, 610m elevation, north of Lac La Biche, Alberta). The farthest distance between transects within a study area was 17km. The TROLS experimental layout consisted of four different buffer widths (20m, 100m, 200m and 800m) each assigned to one lake within each of three study areas (South Calling Lake, Lac La Biche, and South Pelican Hills - which I did not use). Harvesting for the TROLS study occurred in winter, 1996/97.

All forest stands studied were dominated by *Populus tremuloides* and *P. balsamifera* (usually 90 to 100% of total canopy tree density), with some *Betula papyrifera* and *Picea glauca,* and very few *Abies balsamea*. Beneath the tree canopy, there was a prominent shrub layer (including *Amelanchier alnifolia, Corylus cornuta, Lonicera* spp., *Ribes* spp., *Rosa acicularis, Rubus idaeus, Symphoricarpos albus* and *Viburnum edule*) of up to 1.5m in height, and occasionally a layer of taller *Alnus* spp., *Prunus* spp. or *Salix* spp. (2-5m in height). The understory herb layer included: *Aralia nudicaulis, Aster* spp., *Calamagrostis canadensis, Cornus canadensis, Fragaria virginiana, Galium boreale, Lathyrus ochroleucus, Linnaea borealis, Maianthemum canadense, Mitella nuda, Petasites palmatus* and *Rubus pubescens*. Lichen and moss cover was generally less than 10%. Stand age ranged from 60 to 130 yr; canopy height ranged from 15 to 30m. Most transects were located entirely within the same stand, only a few crossed boundaries between stands of different age (according to stand composition descriptions in Silins 1994 based on Alberta Phase III Forest Inventory maps). Heterogeneity was apparent at all scales throughout the stands; thus, sampling interior forest was crucial in order to provide a basis for comparison for edge influence.

OBJECTIVES

I investigated spatial variability in forest structure and composition along edge-to-interior gradients from lakeshore and clearcut edges, and within buffer strips of different width, in the context of inherent heterogeneity in interior boreal forest. My objectives, which I addressed in the upcoming three chapters, were:

1. To characterize forest structure and composition in riparian forests.
   - A. To determine the lakeshore distance of edge influence (DEI): the distance from the lakeshore forest edge where edge influence becomes insignificant.
   - B. To assess the spatial pattern of heterogeneity in the riparian forest using selected species.
2. To characterize forest structure and composition at forest edges at various times following harvest.
   - A. To determine the clearcut DEI: the distance from the clearcut forest edge where edge influence becomes insignificant.

B. To assess differences in edge influence on forest structure and composition and DEI at edges of different aged cutblocks.

3. To model edge influence and to predict the amount of interior forest in buffer zones.
   A. To develop models to predict the magnitude and distance of edge influence in buffers of three different widths.
   B. To test the model predictions for 1 yr old buffers using empirical data.

An additional goal was to develop a new method for quantifying distance of edge influence by incorporating consideration of inherent variability in interior forest. In the concluding chapter (Chapter 5), I compare edge influence from lakeshore and clearcut edges, and synthesize findings related to the three main objectives into a landscape perspective of edge influence. I also provide recommendations for management within the context of TROLS, and for future research within the context of theory on edges.

LITERATURE CITED

Bell, D. T. 1974. Tree stratum composition and distribution in the streamside forest. The American Midland Naturalist **92**:35-46.

Bierregaard, R. O., Jr., W. F. Laurance, J. W. Sites Jr., A. J. Lynam, R. K. Didham, M. Andersen, C. Gascon, M. D. Tocher, A. P. Smith, V. M. Viana, T. E. Lovejoy, K. E. Sieving, E. A. Kramer, C. Restrepo, and C. Moritz. 1997. Key priorities for the study of fragmented tropical ecosystems. Pages 515-525 *in* W. F. Laurance and R. O. Bierregaard Jr., editors. Tropical forest remnants: Ecology, management and conservation of fragmented communities. The University of Chicago Press, Chicago.

Brothers, T. S. 1993. Fragmentation and edge effects in central Indiana old-growth forests. Natural Areas Journal **13**:268-275.

Brothers, T. S., and A. Spingarn. 1992. Forest fragmentation and alien plant invasion of central Indiana old-growth forests. Conservation Biology **6**:91-100.

Brunt, J. W., and W. Conley. 1990. Behaviour of a multivariate algorithm for ecological edge detection. Ecological Modelling **49**:179-203.

Chen, J., J. F. Franklin, and T. A. Spies. 1992. Vegetation responses to edge environments in old-growth Douglas-fir forests. Ecological Applications **2**:387-396.

Chen, J., J. F. Franklin, and J. S. Lowe. 1996. Comparison of abiotic and structurally defined patch patterns in a hypothetical forest landscape. Conservation Biology **10**:854-862.

Collins, B. S., and S. T. A. Pickett. 1988. Response of herb layer cover to experimental canopy gaps. The American Midland Naturalist **119**:282-290.

Cumming, S. G., P. J. Burton, and B. Klinkenberg. 1996. Boreal mixedwood forests may have no "representative" areas: some implications for reserve design. Ecography **19**:162-180.

DeWalle, D. R. 1983. Wind damage around clearcuts in the ridge and valley province of Pennsylvania. Journal of Forestry **81**:158-159, 172.

Doyle, A. T. 1990. Use of riparian and upland habitats by small mammals. Journal of Mammalogy **71**:14-23.

Ericsson, K. A., and D. J. Schimpf. 1986. Woody riparian vegetation of a Lake Superior tributary. Canadian Journal of Botany **64**:769-773.

Ferreira, L. V., and W. F. Laurance. 1997. Effects of forest fragmentation on mortality and damage of selected trees in central Amazonia. Conservation Biology **11**:797-801.

Forman, R. T. T. 1997. Land mosaics: The ecology of landscapes and regions. Cambridge University Press, Cambridge.

Forman, R. T. T., and P. N. Moore. 1992. Theoretical foundations for understanding boundaries in landscape mosaics. Pages 236-258 *in* A. J. Hansen, and F. di Castri. Landscape boundaries: consequences for biotic diversity and ecological flows. Springer-Verlag, New York.

Fortin, M.-J. 1994. Edge detection algorithms for two-dimensional ecological data. Ecology **75**:956-965.

Fox, B. J., J. E. Taylor, M. D. Fox, and C. Williams. 1997. Vegetation changes across edges of rainforest remnants. Biological Conservation **82**:1-13.

Fraver, S. 1994. Vegetation responses along edge-to-interior gradients in the mixed hardwood forests of the Roanoke River basin, North Carolina. Conservation Biology **8**:822-832.

Gates, J. E., and N. R. Giffen. 1991. Neotropical migrant birds and edge effects at a forest-stream ecotone. Wilson Bulletin **103**:204-217.

Gates, J. E., and L. W. Gysel. 1978. Avian nest dispersion and fledging success in field-forest ecotones. Ecology **59**(5):871-883.

Gosz, J. R. 1991. Fundamental ecological characteristics of landscape boundaries. Pages 8-30 *in* M. M. Holland, P. G. Risser and R. J. Naiman, editors. Ecotones: the role of landscape boundaries in the management and restoration of changing environments. Chapman and Hall, New York.

Gregory, S. V., F. J. Swanson, W. A. McKee, and K. W. Cummins. 1991. An ecosystem perspective of riparian zones. BioScience **41**:540-551.

Hansen, A. J., S. L. Garman, P. Lee, and E. Horvath. 1993. Do edge effects influence tree growth rates in Douglas-fir plantations? Northwest Science **67**:112-116.

Harris, L. D. 1988. Edge effects and conservation of biotic diversity. Conservation Biology **2**:330-332.

Hedman, C. W., and D. H. Van Lear. 1995. Vegetative structure and composition of Southern Appalachian riparian forests. Bulletin of the Torrey Botanical Club **122**:134-144.

Hibbs, D. E., and P. A. Giordano. 1996. Vegetation characteristics of alder-dominated riparian buffer strips in the Oregon Coast Range. Northwest Science **70**:21-222.

Holland, M. M., and P. G. Risser. 1991. The role of landscape boundaries in the management and restoration of changing environments: introduction. Pages 1-7 *in* M. M. Holland, P. G. Risser and R. J. Naiman, editors. Ecotones: the role of landscape boundaries in the management and restoration of changing environments. Chapman and Hall, New York.

Jose, S., A. R. Gillespie, S. J. George, and B. M. Kumar. 1996. Vegetation responses along edge-to-interior gradients in a high altitude tropical forest in peninsular India. Forest Ecology and Management **87**:51-62.

Kelsey, K. A., and S. D. West. 1999. Riparian wildlife. Pages 236-258 *in* R. J. Naiman and R. E. Bilby, editors. River Ecology and management. Lessons from the Pacific Coastal Ecoregion. Springer-Verlag.

LaRue, P., L. Belanger, and J. Huot. 1995. Riparian edge effects on boreal balsam fir bird communities. Canadian Journal of Forest Research **25**:555-566.

Laurance, W. F. 1991. Edge effects in tropical forest fragments: application of a model for the design of nature reserves. Biological Conservation **57**:205-219.

Laurance, W. F., and R. O. Bierregaard Jr., editors. 1997. Tropical forest remnants: ecology, management, and conservation of fragmented communities. The University of Chicago Press, Chicago.

Laurance, W. F., and E. Yensen. 1991. Predicting the impacts of edge effects in fragmented habitats. Biological Conservation **55**:77-92.

Laurance, W. F., L. V. Ferreira, J. M. Rankin-de Merona, and S. G. Laurance. 1998a. Rain forest fragmentation and the dynamics of Amazonian tree communities. Ecology **79**:2032-2040.

Laurance, W. F., L. V. Ferreira, J. M. Rankin-de Merona, S. G. Laurance, R. W. Hutchings, and T. E. Lovejoy. 1998b. Effects of forest fragmentation on recruitment patterns in Amazonian tree communities. Conservation Biology **12**:460-464.

Legendre, P. and L. Legendre. 1998. Numerical Ecology. Second English edition. Elsevier Science, Amsterdam, The Netherlands.

Lovejoy, T. E., R. O. Bierregaard, A. B. Rylands, J. R. Malcolm, C. E. Quintela, L. H. Harper, K. S. Brown, A. H. Powell, G. V. N. Powell, H. O. R. Schubart, and M. B. Hays. 1986. Edge and other effects of isolation on Amazon forest fragments. Pages 257-285 *in* M. E. Soule, editor. Conservation Biology. Sinauer Associates, Inc, Sunderland, Massachusetts.

Matlack, G. R. 1993. Microenvironment variation within and among forest edge sites in the eastern United States. Biological Conservation **66**:185-194.

Matlack, G. R. 1994. Vegetation dynamics of the forest edge - trends in space and successional time. Journal of Ecology **82**:113-123.

McCollin, D. 1998. Forest edges and habitat selection in birds: a functional approach. Ecography **21**:247-260.

McGarigal, K., and W. C. McComb. 1992. Streamside versus upslope breeding bird communities in the central Oregon Coast Range. Journal of Wildlife Management **56**:10-23.

Moore, M. R., and J. L. Vankat. 1986. Responses of the herb layer to the gap dynamics of a mature beech-maple forest. The American Midland Naturalist **115**:336-347.

Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. Trends in Ecology and Evolution **10**:58-62.

Murray, N. L., and D. F. Stauffer. 1995. Nongame bird use of habitat in central Appalachian riparian forests. Journal of Wildlife Management **59**:78-88.

Noss, R. F. 1983. A regional landscape approach to maintain diversity. BioScience **33**:700-706.

Pabst, R. J., and T. A. Spies. 1998. Distribution of herbs and shrubs in relation to landform and canopy cover in riparian forests of coastal Oregon. Canadian Journal of Botany **76**:298-315.

Palik, B. J., and P. G. Murphy. 1990. Disturbance versus edge effects in sugar-maple/beech forest fragments. Forest Ecology and Management **32**:187-202.

Paton, P. W. C. 1994. The effect of edge on avian nest success: how strong is the evidence. Conservation Biology **8**:17-26.

Patton, D. R. 1975. A diversity index for quantifying habitat "edge". Wildlife Society Bulletin **3**:171-173.

Pickett, S. T. A., and M. L. Cadenasso. 1995. Landscape ecology: spatial heterogeneity in ecological systems. Science **269**:331-334.

Ranney, J. W., M. C. Bruner, and J. B. Levenson. 1981. The importance of edge in the structure and dynamics of forest islands. Pages 67-95 *in* R. L. Burgess and D. M. Sharpe, editors. Forest Island Dynamics in Man-Dominated Landscapes. Springer-Verlag, New York.

Risser, P. G. 1995. The status of the science examining ecotones. BioScience **45**:318-325.

Rowe, J. S. 1972. Forest regions of Canada. Canadian Forestry Service Publication Number **1300**. Ottawa, Canada.

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

Sekgororoane, G. B., and T. G. Dilworth. 1995. Relative abundance, richness, and diversity of small mammals at induced forest edges. Canadian Journal of Zoology **73**:1432-1437.

Silins, U. 1994. The role of watercourse buffers in the maintenance of terrestrial and aquatic communities in the aspen dominated, boreal mixedwood forest: Lakes site selection survey. Technical report, Alberta Economic Development and Tourism, Forest Industrial Development Branch.

Small, M. F., and M. L. Hunter Jr. 1989. Response of passerines to abrupt forest-river and forest-powerline edges in Maine. Wilson Bulletin **101**:77-83.

Strong, W. L. 1992. Ecoregions and ecodistricts of Alberta. Volume 1. Alberta Forestry, Lands and Wildlife, Land information services division, Resource information branch. Edmonton, Alberta, Canada.

Thomas, J. W., C. Maser, and J. E. Rodiek. 1979. Edges. Pages 48-59 *in* J. W. Thomas, editor. Wildlife Habitats in Managed Forests: the Blue Mountains of Oregon and Washington. U.S. Department of Agriculture Forest Service.

Wales, B. A. 1972. Vegetation analysis of north and south edges in a mature oak-hickory forest. Ecological Monographs **42**:451-471.

Whitaker, D. M., and W. A. Montevecchi. 1997. Breeding bird assemblages associated with riparian, interior forest, and nonriparian edge habitats in a balsam fir ecosystem. Canadian Journal of Forest Research **27**:1159-1167.

Wiebe, K. L., and K. Martin. 1998. Seasonal use by birds of stream-side riparian habitat coniferous forest of northcentral British Columbia. Ecography **21**:124-134.

Wiens, J. A. 1976. Population responses to patchy environments. Annual Review of Ecology and Systematics **7**:81-120.

Wiens, J. A. 1992. Ecological flows across landscape boundaries: a conceptual overview. Pages 217-235 *in* A. J. Hansen and F. diCastri, editors. Landscape boundaries: consequences for biotic diversity and ecological flows. Springer-Verlag, New York.

Wiens, J. A., C. S. Crawford, and J. R. Gosz. 1985. Boundary dynamics: a conceptual framework for studying landscape ecosystems. Oikos **45**:421-427.

Williams-Linera, G. 1990. Vegetation structure and environmental conditions of forest edges in Panama. Journal of Ecology **78**:356-373.

Wood, C. E., and Wood, J. K. 1989. Riparian forests of the Leona and Sabinal Rivers. The Texas Journal of Science **41**:395-411.

Young, A., and N. Mitchell. 1994. Microclimate and vegetation edge effects in a fragmented podocarp-broadleaf forest in New Zealand. Biological Conservation **67**:63-72.

TABLE 1-1. Summary of previous studies that sampled vegetation at different distances from forest edges and their limitations for measuring distance of edge influence (DEI). Some studies were not specifically designed to measure DEI, but were included since they include data for different distances from edges. This list is not intended as a critique of previous methods, but is presented to illustrate the need for a new method which is more robust to assumptions of spatial independence and includes consideration of variation in interior forest. Edge detection methods were not included since their objective is to locate edges rather than determine DEI.

Reference	Analytical Method	Description	Limitations
Laurance 1991	Subjective	Distance of 'detectable' changes	4
Laurance and Yensen 1991#	Subjective	DEI: mean with 95% confidence interval; for each transect, DEI was the minimum distance inside the forest with interior forest conditions	4
Brothers and Spingarn 1992	Chi-Square	Chi-square with correction for continuity	1, 5
Chen et al. 1992	ANOVA	Single factor: distance from edge	1
Hansen et al. 1993	ANOVA	Single factor (distance from edge) with multiple range tests	2
Wales 1972	ANOVA	3-factors: aspect, distance from edge, and plot	1, 2
Fox et al. 1997	ANOVA	3 factors: remnant size, disturbance level, and distance from edge	1, 2, 5
Laurance et al. 1998a	ANOVA	3 factors: fragment area, proximity to edge, and edge aspect	1
Laurance et al. 1998b	ANOVA	3 factors: fragment area, fragment age and distance to edge, using 3-4 categories for each factor; followed by Tukey tests	1*
Ferreira and Laurance 1997	ANOVA	4 factors: distance to nearest edge, distance to eastern edge, fragment area, fragment age, using 3-4 categories for each factor; followed by Tukey tests	1*
Ranney et al. 1981	Regression	Multiple linear regression: distance intervals from edge as independent variables, edge width determined as the grouping of distance intervals with greatest R^2 and greatest number of slopes different from zero	2, 3, 5
Williams-Linera 1990	Regression	Piecewise linear regression: distance from edge as an independent variable	2, 3, 5

Matlack 1993, Fox et al. 1997	Regression	Continuous two-phase linear regression: edge width determined as the distance at which the trend changed sign, reached the mean value of a group showing no regression, or the farthest distance measured	2, 3, 5
Laurance 1991	Regression	Stepwise multiple regression: independent variables included log of edge distance, canopy cover and cyclone disturbance	1, 3
Jose et al. 1996	Regression	Linear, second order polynomial or power functions	1, 2, 5
Chen et al. 1992	Regression	Nonlinear regression model: distance of edge influence determined as the distance where the response variable reaches 2/3 the condition of the interior forest	3, 4
Laurance et al. 1998a	Curve-fitting	Nonlinear curve-fitting using maximum-likelihood procedure: distance of edge influence determined as the distance where the curve exceeded the upper 95% confidence limit for forest interior plots	3
Ranney et al. 1981	Other	Continuum index values with nonparametric sign test	1, 5
Palik and Murphy 1990	Other	Orthogonal contrasts and t-tests on position mean against mean of remainder of the transect	2
Fraver 1994	Other	Helmert procedure, p-values to detect significant change for contiguous plots	5
Fraver 1994	Other	Detrended correspondence analysis and cluster analysis, distance from edge where species composition stabilized was estimated	4, 5
Matlack 1994	Other	Kruskal-Wallis with 4 factors: sites, distances from edge, distances within sites, quadrats within sites	1, 5
Matlack 1994	Other	Log-likelihood procedure to test for non-uniformity with respect to edge distance	1, 5
Matlack 1994	Other	Modal values at 2-3 replicate sites to indicate edge effects	4, 5

1. Analysis was not designed to measure DEI.

1* Analysis designed to determine DEI by investigating differences in 4 categories of distance from edge.

2. Spatial autocorrelation violates assumptions of independence in statistical analysis (plots at different distances from the edge along the same transects were < 20m apart).

3. A particular response model was assumed (for regression).

4. The criterion and reference point for interior forest were subjective or arbitrary; there was no objective means of quantifying 'interior forest'.

5. There was no consideration of interior forest (> 100m from edge).

Although they sampled microclimate, this method could apply to vegetation

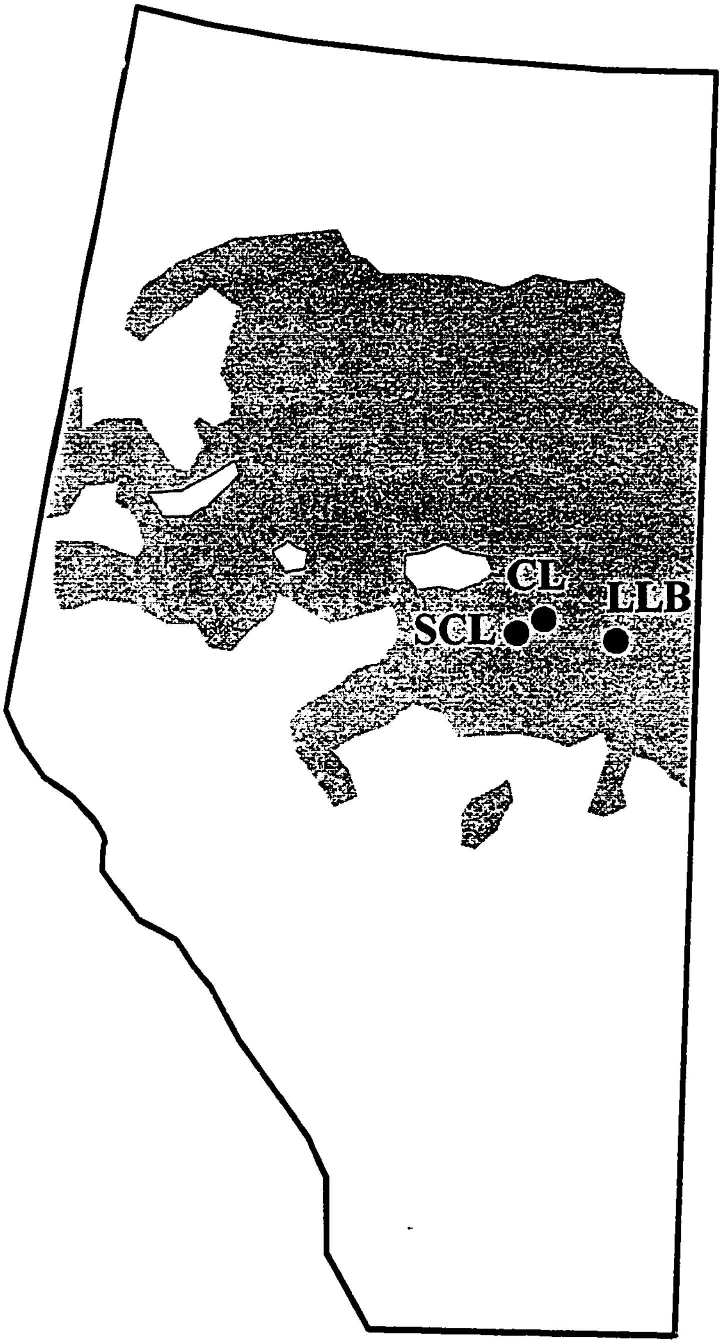


Figure 1-1. Map of Alberta showing the extent of the mid-boreal mixedwood forest (shaded, Strong 1992) and the three study areas: South Calling Lake (SCL), Calling Lake (CL) and Lac La Biche (LLB).

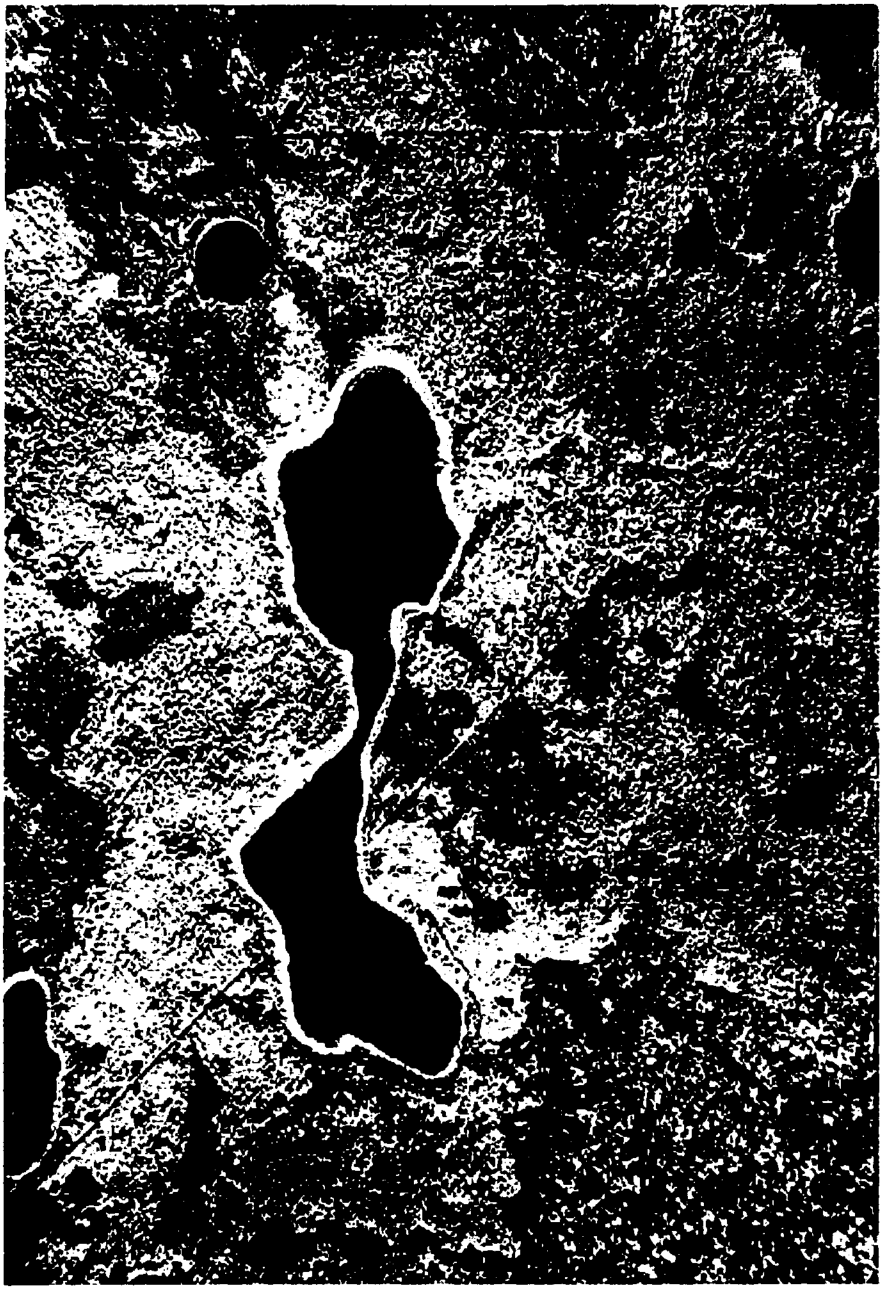


Plate 1-1. Aerial photograph of one of the study lakes in the Lac La Biche study area prior to harvest. Numerous natural forest edges surround lakes, wetlands, and separate different forest communities in this heterogeneous mixedwood landscape. (Aerial photograph obtained from Alberta Environment.)

CHAPTER 2. STRUCTURE AND COMPOSITION OF RIPARIAN FOREST [1]

Riparian ecotones at lakeshore edges are prominent features of the heterogeneity of the boreal forest landscape. To quantify distance of edge influence at lakeshore forest edges, I introduce a new method (the critical values approach) which incorporates inherent variability in interior forest. I applied this method to the variation in forest structure and composition along the lakeshore forest edge-to-interior gradient. My objectives were: 1) To quantify trends in forest structure and composition, and to determine distance of edge influence for different response variables; and 2) To investigate finer scale spatial patterns across the edge for a few selected species. Trees, coarse woody material, saplings, shrubs and herbs were sampled in plots at varying distances along 200m transects established perpendicular to lakeshore forest edges. A variable was considered to be significant if it lay outside critical values established from a randomization test of data from interior forest. I identified a distinct lakeshore forest edge community with a width of 40m. Edges were more structurally diverse with greater amounts of coarse woody material, saplings and mid-canopy trees than interior forest. Distance of edge influence for understory composition was generally greater than for forest structure. Spatial pattern of four selected species along the edge-to-interior gradient was assessed using split moving window analysis and wavelet analysis. Patterns of abundance along the gradient varied among the species, suggesting different species responses to edge influence.

INTRODUCTION

Natural forest edges and ecotones are common in forested landscapes and have a major influence on spatial heterogeneity. Research on natural forest edges can contribute to our understanding of landscape processes through: 1) documentation of 'edge influence', defined here as the change (e.g. in forest structure and composition) along the edge-to-interior gradient; and 2) characterization of the internal structure of edges. A knowledge of distance of edge influence is necessary for determining the width of riparian forest habitat that is different from interior forest. The internal structure of the edge affects boundary permeability, and therefore movement of organisms and other fluxes across the landscape (Wiens et al. 1985, Forman and Moore 1992). Knowledge of landscape patterns and processes is important to understanding the structure and functioning of heterogeneous landscapes (Wiens et al. 1985). In landscape ecology, spatial heterogeneity is considered valuable for explaining population structure and community composition (Pickett and Cadenasso 1995). There have been calls for more research on boundaries including: empirical data from ecotones (Holland 1988, Risser 1995) and documenting relationships between changes at edges and changes in more

---

[1] A version of this chapter has been accepted for publication (pending revisions). Harper, K.A. and S.E. Macdonald. Structure and composition of riparian boreal forest: new methods for analyzing edge influence. Ecology.

homogeneous areas (Gosz 1991).

Many studies have examined anthropogenically created forest edges (e.g. Ranney et al. 1981, Chen et al. 1992, Matlack 1994); created edges are edges that have formed as a result of a natural or anthropogenic disturbance. However, few studies have investigated natural, inherent edges. Natural edges and ecotones have become recognized as sensitive boundaries and areas of relatively high diversity (Holland 1988). Riparian plant communities along streams are known to have high structural and species diversity compared to upland forests due to the variety of microsites present, sharp gradients and frequent disturbance (Naiman et al. 1993, Gregory et al. 1991). In areas managed for timber production, lakeshore riparian forests are particularly important as forested buffer zones left around lakes. Land-water ecotones, including riparian forests, have been recognized for their importance in the regulation of hydrologic and biogeochemical processes (Naiman et al. 1993). Lakeshore forest edges differ from created edges in upland forests in that they form across complex gradients of topography, hydrology, soil, light and wind (Pabst and Spies 1998), and are dynamic, with intermittent disturbance from water table fluctuations (Naiman et al. 1993), ice-scour (Holt et al. 1995) and beaver activity (Johnston and Naiman 1987). However, only a few investigations of riparian forests have specifically considered variation along a spatial gradient (Wood and Wood 1989, Hibbs and Giordano 1996, Pabst and Spies 1998). Studying the changes in forest structure and composition along the edge-to-interior gradient from lakeshore forest edges could elucidate the spatial pattern of this complex gradient across the riparian ecotone and into interior forest.

The mixedwood boreal forest provides an appropriate context to investigate lakeshore forest ecotones within a heterogeneous landscape. Forest composition in the aspen-dominated boreal forest in northern Alberta exhibits 'multi-scaled heterogeneity' due to natural disturbance (insect outbreaks, fire), topography, hydrology, and the mixedwood nature of this forest ecosystem (Cumming et al. 1996). Amidst this background heterogeneity in 'interior' forest, edge influence from landscape features such as lakeshore forest edges may not be very dramatic.

I examined variation in forest structure and composition along an edge-to-interior gradient at lakeshore forest edges in the boreal mixedwood forest for two main objectives: 1. To quantify trends in forest structure and composition, and determine the distance of edge influence (DEI) for different response variables; and 2. To investigate finer scale spatial patterns for a few selected species. In the process, I explored new methods for assessing spatial pattern along the edge-to-interior gradient to examine the internal structure of the edge in more detail. Further, I developed a new 'critical values approach' for measuring DEI (the distance from the forest edge to where the forest becomes 'interior' forest) which incorporates inherent variability in interior forest and which does not assume random sampling.

ANALYSIS OF EDGE INFLUENCE

I introduce a new method, the 'critical values approach', which quantifies distance of edge influence (DEI) in the context of a community with inherent variability (see Chapter 1 for a review of methods to analyze edge influence). I define the limit of DEI as the point at which the variation due to edge influence is no longer significantly different from the inherent variation in interior forest (similar to the definition of edge width, Forman 1997). To determine statistical significance, I calculate critical values through randomization tests on data collected in interior forest. These critical values of the variation in interior forest provide an objective and relevant standard for comparison in the assessment of edge influence.

Randomization tests allow for more varied, nonconventional experimental designs and do not assume random sampling, but still maintain high statistical power (Crowley 1992, Manly 1997). They determine significance by repeated random permutations of the data among treatments. Since the data are randomly sampled, a random sampling design of the population is not required. The significance level is the proportion of permutations that have values of the test statistic that are at least as extreme as the statistic from the observed results (Crowley 1992, Manly 1997). Although randomization tests are generally used to calculate familiar test statistics to mimic parametric tests, special purpose statistics are also possible (Crowley 1992).

Although DEI can provide important information about edge influence, more detailed analysis at a finer scale is needed to determine the nature of change in vegetation along an edge-to-interior gradient, in order to understand the internal structure of the edge. Finer scale assessment of edge influence may be approached through edge detection techniques. These methods investigate changes in vegetation structure or composition along transects or grids of contiguous quadrats, with the purpose of finding locations of edges or discontinuities (defined as the areas of highest rate of change, Fortin 1994). Edge detection along one dimension is usually performed using split moving window analysis which measures dissimilarity between two halves of a window which is moved along the transect (Brunt and Conley 1990, Cornelius and Reynolds 1991). The approach by Fortin (1994) for two-dimensional data also measures change between adjacent sampling points on a grid; however, her objective was to detect significant boundaries in overall species composition rather than assess changes in abundance in individual species. I adapt the technique of split moving window analysis to analyze the spatial pattern of selected species along an edge-to-interior gradient.

Another edge detection technique, wavelet analysis, has only recently been introduced to plant ecology (Bradshaw and Spies 1992, Dale and Mah 1998). Wavelet analysis uses the same moving window concept but data within the window are compared to a wavelet function (Bradshaw and Spies 1992). Two wavelet functions have been used in plant ecology: the Mexican Hat to detect patches and gaps at different scales, and the Haar wavelet which is considered the most useful for detecting discontinuities in the data (Bradshaw and Spies 1992). Output for the Haar wavelet indicates locations of prominent discontinuities in the data. I explore the Haar wavelet for detecting abrupt changes in the abundances of selected species along an edge-to-interior gradient, a new application for wavelet analysis.

METHODS

Study area

The study area consisted of forest communities surrounding a total of seven lakes in two of the study sites: Lac La Biche and South Calling Lake (see Chapter 1). Study lakes ranged in size from 14 to 120 ha. Zones of non-forested vegetation between the lake and the sampled forest edges (as defined below) generally ranged from 0 to 40m. Slope ranged from 0 to 25% in the non-forested riparian zone and in the first 50m of the lakeshore forest edge.

Distance of edge influence

Sampling design.–Two types of transects were established to sample lakeshore forest edge-to-interior gradients and upland interior forest. A total of twelve transects were established perpendicular to lakeshore forest edges at six lakes, and extended from the forest edge to 200m into the forest. The forest edge was defined as the trees at the limit of the continuous canopy. Rather than compare edges with different aspects, I controlled for aspect by using only edges with predominantly south-facing aspects (120°-240°), which I expected to have the greatest distance of edge influence as others have found for created edges (e.g. Wales 1972, Palik and Murphy 1990, Fraver 1994). Ten 200m upland forest transects were located in interior forest stands of similar composition, but 300-800m away from any lake and 100m away from any major right-of-ways or other clearings. All transects were located to avoid uneven edges, conifer-dominated stands, and extensive wetlands. All transects were at least 100m apart, and there were no more than four lakeshore forest edge transects at a given lake, or more than two interior forest transects within $1 km^2$.

Plots (20m x 5m) were established along each lakeshore edge transect (length parallel to the forest edge) at the following distances from the edge (m): 0, 5, 10, 20, 40, 60, 100, 150, and 200. Plot locations were identical for the upland interior forest transects; distances were measured from one end of the transect. An additional plot along the lakeshore edge transects, established in the riparian zone at -10m (10m from the forest edge towards the lake), was used to sample shrubs, trees and downed coarse woody material (CWM). Within the plots, two shrub subplots (2m x 2m) and three herb subplots (0.5m x 0.5m) were established systematically along the major axis of the plot. Multiple subplots were used for better representation of the understory at a given distance from the edge along a given transect. Data were collected in summer, 1996.

Data collected.–Data were collected on structural characteristics and understory composition to provide an overview of the response of the overstory and understory to edge influence. Trees (≥5cm diameter at breast height) and snags (≥5cm diameter at breast height, ≥ 50cm tall) were tallied in the 20m x 5m plots. I recorded species and diameter at breast height for trees and snags, and classified canopy position (relative height) for trees as follows: mid-canopy (well below the canopy), sub-canopy (just below the canopy) and canopy. Diameter was noted for pieces of downed CWM (>8cm in diameter at the intersection point, decay classes 1-3 out of 7, Lee et al. 1995) intersecting the major axis of the plot. Data on canopy cover, and herb, shrub and sapling composition were collected for ten of the twelve lakeshore forest edge transects (due to time constraints) and all of the upland interior forest transects. Canopy cover was measured at the centre of each plot using a convex spherical densiometer. Percent cover of all shrub and sapling species, as well as the number and maximum height of saplings, were estimated within the shrub subplots; cover of all forbs and dwarf woody species, as well as lichen and moss cover, was estimated within the herb subplots. Cover was visually estimated to the nearest 1% up to 5%, and to the nearest 10% thereafter.

In order to investigate physiological responses to edge influence, proportion of plants that were flowering was estimated for *Galium boreale, Cornus canadensis* and *Maianthemum canadense*. These species were selected due to their relatively high frequency and signs of flowering or fruiting that persisted throughout the sampling period. Four leaflets each of *Petasites palmatus, Fragaria virginiana* and *Aralia nudicaulis* were collected systematically along the midline of each plot. Measurements of length of the longest leaflet of *A. nudicaulis*, length of the middle leaflet of *F. virginiana*, length of the petiole of *P. palmatus*, and width of the leaf for *P. palmatus* were made for each of the four leaves. Nomenclature follows Moss (1992).

Data analysis.–Additional response variables included shrub and herb species richness (the number of species within the subplots), and total shrub and herb cover (sum of the cover of all species in the subplots).

To quantify distance of edge influence (DEI), I used my new critical values approach. Randomization tests were performed to establish critical values for comparison with average values at difference distances from the edge. Two different reference data sets were used for this purpose. Data from plots at the three furthest distances from the lakeshore forest edge (100, 150 and 200m) along the lakeshore transects (the adjacent riparian forest reference data set) were used to compare edge influence to variability within the same stand. Data from sampling along the interior forest transects (the upland interior forest reference data set) were used to compare edge influence to variability within regional interior forest. For each response variable (e.g. tree density, cover of a particular species) within each reference data set, a randomization test was performed using Visual Basic in Excel (Microsoft Corporation) following these steps:

1A. For all response variables related to trees and CWM, one 'interior forest' value was randomly selected from each transect (total of 10 values): 1 of 3 possible values (at 100, 150, 200m) using the adjacent riparian forest reference data set, or 1 of 9 possible values using the upland interior forest reference data set.

1B. For response variables related to shrubs and saplings, two values were randomly selected from each transect (total of 20 values): 2 of 6 possible values from the six 'interior forest' subplots (two each at 100, 150 or 200m) using the adjacent riparian forest reference data set, or 2 of 18 possible values from the 18 'interior forest' subplots using the upland interior forest reference data set.

1C. For herbs, three values were randomly selected from each transect (total of 30 values): 3 of 9 possible values from the nine subplots (three each at 100, 150 or 200m) using the adjacent riparian forest reference data set, or 3 of 27 possible

values from the 27 subplots using the upland interior forest reference data set.
2. The average value of the data obtained in step 1 was calculated.
3. Steps 1 and 2 were repeated for a total of 5000 permutations.

Critical values were the 2.5 and the 97.5 percentiles of the 5000 permuted averages (2-tailed test, $\alpha=0.05$). Separate sets of critical values were established for the two reference data sets. Average values at different distances from the lakeshore forest edge were considered to be significant if they lay outside the critical values. For randomization tests, it is important to define the null hypotheses, which is usually H_0: The observed test statistic is no different than expected by chance (Crowley 1992). For the critical values approach, H_0 is: The average of observed values at a given distance from the edge is no different than would be expected by chance in the reference forest. Distance of edge influence was defined as the set of consecutive distances that were significantly different (H_0 was rejected) from the reference data set.

Subplots with missing values were excluded from the randomization tests. If there were more than two missing values, all the remaining values in the reference data set were pooled. Permuted averages were then calculated from random samples of 10 plots (twice and three times as many for the shrub and herb subplots respectively) from the pooled data.

Several response variables with strong edge-to-interior trends (CWM, density of canopy trees, density of mid-canopy trees, density of *Populus tremuloides* snags, density of *P. tremuloides* saplings, cover of *Amelanchier alnifolia*, cover of *Rubus idaeus*) were also subjected to curve-fitting for comparison with other methods of measuring DEI. Curves were fit to the entire data set for each of the variables (with distance from the lakeshore forest edge as the independent variable) using SPSS (SPSS Inc. 1996). Linear, quadratic, cubic and exponential curves (as in Chen et al. 1992) were tried for each variable; the curve with the highest R^2 was used. Distance of edge influence was determined as the intersection of the curve with the line: y = critical value (from the randomization test, similar to Laurance et al. 1998).

Spatial pattern analysis of selected species

Sampling design and data collected.–A total of seven transects of contiguous 10 cm x 10 cm quadrats were set up perpendicular to lakeshore forest edges at four lakes in June, 1997 for more intensive study on spatial pattern analysis. Transects extended from the water's edge up to 150m into the forest. I chose species based on observed strong trends along the lakeshore forest edge-to-interior gradient in the 1996 data (*Lathyrus ochroleucus, Linnaea borealis, Mitella nuda*). In addition, *Calamagrostis canadensis* was chosen as a relatively shade intolerant, disturbance-adapted species. Data included: presence/absence of *C. canadensis* and *L. ochroleucus* (6 of the 7 transects), and cover of *L. borealis* and *M. nuda* (cover to the nearest 5, 25, 50, 75 or 100%, all transects).

Data analysis.–Split moving window analysis (SMW) was employed to determine the magnitude of change (both increase and decrease) at two different scales along the edge-to-interior gradient. In SMW, a 'window' of size x is established at the start of the transect, and a measure of dissimilarity (D) is calculated between the two halves of the window (Turner et al. 1991). In my case, D was defined as the difference in average cover or frequency for each species. The window is then moved along the transect one quadrat at a time (Turner et al. 1991). Scale can be changed by varying x (Brunt and Conley 1990); therefore increasing scale involves assessing D within a larger series of contiguous quadrats (window). After trying several scales (window widths of 2, 4, 8, 12, 16, 20m), I selected two (4 and 20m) for further analysis. Although the choice was somewhat arbitrary, output of SMW at these two scales represented two different patterns along the edge-to-interior gradient: at 4m, the output was highly variable with many discontinuities, and at 20m, the output reflects broad changes with only a few discontinuities. I summarized the results by calculating averages of all positive and negative D values within 10m intervals, and plotting these as a function of distance from the forest edge. Analyses were performed in Excel using Visual Basic (Microsoft Corporation).

Wavelet analysis was also applied to the data from the contiguous quadrats using the Haar wavelet. Data within the window were compared to the Haar wavelet function; values for the wavelet transform (W) can be visualized as the degree to which the data matched the wavelet function (Bradshaw and Spies 1992). The output is a matrix of values of W for all positions at all scales (Bradshaw and Spies 1992). Position variance is the average of W^2 at all scales for a given distance (Dale and Mah 1998). Average values of position variance within 10m intervals were plotted against distance along the edge-to-interior gradient.

RESULTS

Distance of edge influence

Lakeshore forest edges were more structurally diverse than interior forest. The amount of downed coarse woody material (CWM) at 0-20m from the edge was significantly greater than the adjacent riparian forest, but not the upland interior forest since the critical values based on the two reference data sets differed dramatically (Figure 2-1). The results did not differ much when divided by decay class, but there were very few logs of decay class 1 further than 10m away from the edge (not shown). Diameter of CWM was significantly greater within 10m of the edge than in the upland interior forest (Table 2-1).

Canopy cover and total tree density did not exhibit any significant edge influence (Table 2-1) since the increase in the number of mid-canopy trees was balanced by the decrease in canopy trees (Figure 2-2). There was no edge-to-interior trend for sub-canopy tree density. Only four species of trees were found in the study area (*Populus tremuloides*, *P. balsamifera*, *Betula papyrifera*, and *Picea glauca*). However, at the lakeshore forest edge (0m), there was a relatively high number of shrubs with diameter at breast height over 5cm that were classified as trees (*Alnus* spp., *Prunus* spp., *Salix* spp., Table 2-1). Trends in density differed among the dominant tree species as *P. tremuloides* was significantly less dense 0-5m from the edge, and *P. balsamifera* was significantly more dense 10-20m from the edge, compared to the adjacent riparian forest (Table 2-2); other species had low densities. The distance of edge influence (DEI) for the density of mid-canopy trees of *P. tremuloides* extended to 150m using the upland interior forest as the reference data set (Table 2-1). Diameter of trees was relatively constant with averages from 16-18cm. Significantly greater numbers of snags of large diameter shrubs (only at -10, 0m, Table 2-1) and lower numbers of *P. tremuloides* snags (DEI=0-10m, Table 2-2) were found at or near the edge; there was no apparent trend for overall snag density (Table 2-1). Edge influence on *Populus* spp. saplings extended up to 20m, 60m and 0m for density, cover and height respectively (Figure 2-3). Distance of edge influence for the density and cover of saplings was greater for *P. tremuloides* than for *P. balsamifera* (Table 2-2). The riparian zone (-10m from the lakeshore forest edge) was characterized by a diverse structure with greater amounts of larger diameter CWM, mid-canopy trees, large diameter shrubs and taller saplings; but lower canopy cover, overall tree density, tree diameter, and snag density than interior forest (Table 2-1, Figures 2-1 to 2-3).

Total shrub cover at the lakeshore forest edge was generally not significantly different than in the adjacent riparian or upland interior forest; shrub richness also did not show any prominent trend (Table 2-1). Total herb cover was significantly lower at 0m, and significantly higher further away from the edge as compared to the upland interior forest (DEI=10-40m, Table 2-1). Greater herb species richness was found 20-40m from the lakeshore forest edge compared to both reference data sets.

Many individual herb and shrub species exhibited strong responses along the edge-to-interior gradient. Nine of the fifteen common (> 10% frequency) shrub species had significant DEI, generally up to 40m when compared with the adjacent riparian forest (Table 2-3). Six (*Amelanchier alnifolia, Lonicera dioica, Prunus* spp., *Salix* spp., *Symphoricarpos albus, Vaccinium myrtilloides*) were classified as 'edge-positive' species and three (*Alnus crispa, Ribes triste, Rubus idaeus*) as 'edge-negative' species (greater and lower cover near the edge respectively).

Of the 31 common herb species (>10% frequency), twelve (*Apocynum androsaemifolium, Aster conspicuus, Equisetum arvense, Fragaria virginiana, Galium boreale, Lathyrus ochroleucus, Maianthemum canadense, Orthilia secunda, Petasites palmatus, Pyrola asarifolia, Thalictrum venulosum, Vicia americana*) were classified as 'edge-positive' and five (*Aralia nudicaulis, Cornus canadensis, Linnaea borealis, Mitella nuda, Rubus pubescens*) as 'edge-negative' (Table 2-4). Distance of edge influence of the 'edge-negative' species was generally 0-5m or 0-10m; *Linnaea borealis* and *Mitella nuda* had cover at the edge that was significantly lower than in both the adjacent riparian forest and the upland interior forest. Some of the 'edge-positive' species had a peak in cover around 5-10m from the edge with a DEI that often started at either 5 or 10m. 'Edge-positive' species generally had greater DEI (up to 10m or more) than 'edge-negative' species (0-5 or 0-10m), resulting in overall greater herb cover 10-40m. The only trend in the response of flowering at the lakeshore forest edge was for *Galium boreale* which was only found flowering within 20m of the edge (Appendix 2-1). There were no significant differences in the selected leaf measurements along the edge-to-interior gradient except greater petiole length of *Petasites palmatus* (DEI=0-5m) and shorter leaflet length of *Aralia nudicaulis* (DEI=20-40m, Appendix 2-1).

Most response variables were significantly different from interior forest using either data set for within 20-40m from the lakeshore forest edge, with some differences persisting up to 60m or more from the edge (Figure 2-4). Within 20m of the edge, more response variables had significant DEI when put in the context of the adjacent riparian forest, than in the context of the upland interior forest (Figure 2-4A). For some variables, however, DEI extended to 60m or more using the upland reference data set. Few forest structure response variables had DEI that extended beyond 20m, whereas more understory species had greater DEI (Figure 2-4B,C).

By fitting a curve to the data along the edge-to-interior gradient, I was able to produce an estimate of DEI as the point along the fitted curve that corresponded to the critical value from the randomization test. However, fitting curves was only practical for a few response variables due to low R^2 and high significance levels. Using the critical values approach, DEI for these variables was quite variable, ranging from 2 to 92m (Table 2-5). Distance of edge influence using the upland interior forest was usually less than DEI using the adjacent riparian forest, except for the cover of *Amelanchier alnifolia*. The cover of *Rubus idaeus* presented an unusual situation (Figure 2-5). From 0-49m it was significantly less than in the adjacent riparian forest. Compared to the upland interior forest, however, the cover was not significantly different for the first 65m from the lakeshore forest edge, but was significantly greater than the upland interior forest 65-200m from the edge.

Spatial pattern analysis of selected species

All four selected species showed different patterns of abundance along the edge-to-interior gradient as shown by split moving window analysis (SMW). *Mitella nuda* showed a marked increase in cover 100-150m away from the edge (Figures 2-6, 2-7). Change in the abundance of *Linnaea borealis* was relatively constant along the gradient, except for an abrupt increase followed by a decrease near 50m. For both these species, increases in cover were followed by equivalent decreases. This was also the case for *Calamagrostis canadensis* which showed an increase, then decrease in cover just before the lakeshore forest edge. However, for *Lathyrus ochroleucus*, a large increase at the lakeshore forest edge was followed by more gradual decreases along the edge-to-interior gradient. Trends for the last two species were much more evident at the 20m scale (Figures 2-7, 2-8). Indeed, for *Calamagrostis canadensis* and *Lathyrus ochroleucus*, the amount of change at the 4m scale was relatively constant along the edge-to-interior gradient. Wavelet analysis showed very similar patterns to SMW using absolute difference between window halves (particularly using a window width of 20m), except for slightly larger peaks (Figure 2-6). However, for *Mitella nuda*, the peak near 130m was much larger using position variance.

DISCUSSION

Structure and composition of the lakeshore forest edge

Forest structure.–Overall, a 40m wide distinct lakeshore forest edge community was both structurally and compositionally different from interior forest, with some differences extending up to 60m from the edge. However, distance of edge influence (DEI) differed among variables, making it difficult to determine DEI for the entire community. Examinations of created edges have also shown that DEI can be highly variable for different factors within the same forest (e.g. 16m to 137m, Chen et al. 1992). Because my edges were all south-facing, I expect that DEI would be greater than for other aspects, as others have found for agricultural edges (Wales 1972, Brothers 1993, Fraver 1994). However, forests on the south side of the study lakes often have a band of conifers (pers. obs. and data from Chapter 4, not shown) which could dramatically affect edge influence for north aspects as a result of the different response of conifers to microclimate gradients and to a change in canopy composition along the edge-to-interior gradient.

Compared to interior forest, lakeshore forest edges were characterized by greater structural diversity including higher amounts of downed coarse woody material (CWM), saplings and mid-canopy trees; but fewer canopy trees and snags. A riparian forest in Oregon had similar structure with increased mid-canopy tree density and lower overstory cover, but also had increased shrub cover (McGarigal and McComb 1992). A riparian created edge (cutbank edge) also had greater sapling densities than interior forest (Kupfer and Malanson 1992). Fewer snags appear to be a common feature of North American riparian zones (McGarigal and McComb 1992, Murray and Stauffer 1995, Whitaker and Montevecchi, 1997), although created edges often have more snags (Chen et al. 1992, Young and Mitchell 1994). Fewer snags and greater amounts of CWM at the edge could be due to a combination of increased treefalls from exposure to wind, beaver activity or periodic flooding; and increased productivity leading to faster growth and earlier death. Chen et al. (1992) observed greater growth rates of dominant trees at clearcut edges. In a simulation study, Malanson and Kupfer (1993) found that greater productivity due to increased solar radiation resulted in an increase in woody debris at a riparian cutbank edge. Greater growth and subsequent treefalls can also be inferred by the higher average diameter of CWM.

Understory composition.–The zone of edge influence started at 5m into the forest for several individual species. Therefore, the cover of these species at the lakeshore forest edge (0m) was not significantly different from interior forest. In the boreal mixedwood forest, increased light from canopy openings is often compensated by shrub development, resulting in similar light levels at the ground surface under different types of overstory (Constabel and Lieffers 1996). Although shrub cover was not greater at the edge, greater sapling abundance could have counteracted the effects of increased light and related microclimatic factors at the edge. Beyond 0-5m from the edge, sapling cover and height was not as great, allowing understory herbs to respond to microclimatic effects at the edge. According to Murcia (1995), such interactions of edge influence may be more common than previously reported; other studies have found peaks in edge influence at intermediate distances (Palik and Murphy 1990, Williams-Linera 1990). More recently, Didham (1997) observed a bimodal pattern in the abundance of leaf litter invertebrates due to different response to edge influence by different taxa. The assumption of monotonic responses along the edge-to-interior gradient may, therefore, be unrealistic (Murcia 1995).

Others have predicted greater species richness and diversity at riparian ecotones along rivers (Naiman et al. 1993, Gregory et al. 1991, Pabst and Spies 1998). I found lower species richness 20-40m from the edge, but not at the edge. My results may lend support to van der Maarel's (1990) hypothesis that low species richness would be expected at ecotones using the strict definition as a tension zone subject to high disturbance. Lakeshore forest edges can experience frequent disturbance from flooding and ice scour.

At created edges, microclimate and light regimes lead to a proliferation of shade-intolerant species (Wales 1972, Ranney et al. 1981), often resulting in a decrease in interior species (Noss 1983). In my study, some 'understory obligates' (*Aralia nudicaulis, Linnaea borealis, Mitella nuda*, Lieffers 1995) decreased in cover at the lakeshore forest edge and thus were considered 'edge-negative'. *Calamagrostis canadensis*, an 'understory tolerator' (Lieffers 1995) was not considered an 'edge-positive' species as might be expected, although its abundance was much greater immediately outside the forest. Some of the 'edge-positive' species are commonly found in gaps and clearings (*Aster conspicuus, Fragaria virginiana*, pers. obs.).

Conceptual model.–Gregory et al. (1991) developed an ecosystem model for understanding the ecotonal nature of riparian zones by focussing on links between terrestrial and aquatic ecosystems. My study examines one component of this model: the influence of the edge environment on the riparian forest. I propose my own conceptual model to explain edge influence from lakeshore forest edges (Figure 2-9). This model is presented as a useful framework for possible mechanisms of the development of structure and composition at lakeshore forest edges; however, it is only based on data for forest structure and composition. Microclimate and soils data are being collected along lakeshore forest edge-to-interior gradients (also at clearcut edges and in buffer zones) by P. Presant (unpublished data). Exposure to wind, periodic disturbance from ice scour and water table fluctuations, and frequent beaver activity, could all contribute to increased tree mortality and treefalls at the lakeshore forest edge. This would result directly in fewer canopy trees, more CWM, and fewer snags. The subsequent opening of the canopy would allow greater penetration of light leading to increased sapling recruitment and changes in understory composition.

Factors contributing to changes in forest structure and composition at lakeshore forest edges may be related to edge influence (wind, light, relative humidity), topography (water table depth, soil moisture, nutrient availability) or a combination of both. Gradients of temperature and relative humidity occurred over a distance of 30-60m from streams in Douglas fir forests (Brosofske et al. 1997). A gradient in understory composition from streams to upland has also been related to topography and landform through mechanisms of hillslope processes, hydrologic disturbance, and tolerance to saturated soil (Pabst and Spies 1998). The topographic profile of the slope across the lakeshore forest ecotone into the riparian forest, and the elevation of the forest edge above the water table, would affect the magnitude and extent of edge influence within my study area. However, my objective was to quantify DEI from a representative sample of lakeshore forest edges for aspen-dominated mixedwood forest in the region rather than to differentiate among causal factors. My results are, thus, strictly applicable to the aspen-dominated mixedwood forest in Alberta at lakes with similar physiographic setting. As the first study on the structure and composition of lakeshore forest edges, however, conclusions should be of general interest to research on natural edges and ecotones.

From my results, I generated the hypothesis that edge influence extends further for primary responses than for secondary responses. Primary responses result directly from processes at the edge; for example, fewer canopy trees and greater coarse woody material (with DEIs of 0-5 and 0-20m) were direct results of tree mortality at the edge. Wider DEI was found for secondary responses such as sapling abundance, mid-canopy tree density and changes in the abundances of some understory species (DEI of up to 0-60m); these secondary responses were influenced indirectly by the edge environment (through microclimatic and structural changes). Distance of edge influence for understory composition generally extended even further into the forest than for forest structure. With the reduced number of canopy trees at the edge, the canopy is more open up to 5m from the edge; sapling recruitment and understory composition may then be responding to microenvironment changes due to the open canopy, and thus have greater DEI. Results from created edges corroborate my hypothesis. Williams-Linera (1990) found an increase in DEI from canopy openness and snags (primary responses) to density of woody plants (secondary response) for 12 year-old tropical edges. For 15 year-old edges in Douglas-fir forest, Chen et al. (1992) reported DEI for seedlings and saplings for 2 of 3 dominant species (secondary responses) that was greater than DEI for canopy cover, CWM and tree density (primary responses). Palik and Murphy (1990) and Malcolm (1994) also remarked that DEI for the canopy was less than that of the understory.

There is a dynamic component to lakeshore forest edges which differentiates them from created edges. At older, maintained edges (e.g. next to agricultural fields), sidewall vegetation (side branches from trees, shrubs and saplings) can block out light and wind, and decrease edge influence (Matlack 1993). However, at dynamic lakeshore edges, disturbance from water table fluctuations, ice scour or beaver activity can prevent such development. Due to the dynamic nature of lakeshore edges, greater numbers of treefalls and increased amount of CWM could persist for many years. However, the adjacent forest stand also develops with time where formation of gaps and self-thinning lead to an accumulation of CWM. Thus, at lakeshore edges of older riparian forests, edge influence on CWM may no longer be as dramatic or even detectable. It is unknown whether riparian forests ever reach that stage in aspen-dominated boreal forest.

Lakeshore forest edge as habitat.–More response variables exhibited significant edge influence when compared to the adjacent riparian forest, than compared to upland interior forest. Some response variables, however, had DEI of 60m and higher using the upland reference data set, suggesting some differences in forest structure and composition between riparian (50-200m from the lake) and upland forest. S. E. Macdonald (*unpublished manuscript*) also found some, but not many, differences between riparian and upland forests in the same study area.

Generally, the lakeshore forest edge community is more distinct within the context of a riparian forest stand, than it is within the larger context of the aspen-dominated forest on the landscape. This distinction is important for understanding the relevance of these edges for fauna. For example, the forest edge community might be more noticeably different to a bird establishing a territory within riparian forest, and would perhaps be avoided; whereas a raptor flying over the forested landscape might not see the forest edge as very different from other forest stands in the area.

The lakeshore forest edge can therefore be considered an important habitat feature within riparian forest stands in the aspen-dominated mixedwood boreal forest. Wildlife species that move across this ecotone will encounter a boundary with unique characteristics, which is in accord with the cellular membrane analogy (Forman and Moore 1992). At lakeshore forest edges, wildlife abundance may be different from interior forest. Within this ecoregion, Machtans et al. (1996) noted greater numbers of birds caught closer to lakeshores than further away. Some fauna in the boreal forest appear to avoid the lakeshore forest edge. For example, Lambert (1998) found no Ovenbird territories within 20m of the lakeshore forest edge, presumably a reflection of the high sapling abundance. It is possible that Ovenbirds may simply not use the riparian forest near the edge as habitat. Alternatively, Ovenbirds may not cross the lakeshore forest edge and therefore may be limited to interior forest habitat. The edge could therefore be acting as a barrier, as a result of its significantly different structure and composition than the adjacent forest, which would contradict van der Maarel's (1990) view that only landscape elements, but not ecotones, perform barrier functions.

Spatial pattern of selected species across the lakeshore forest edge

All four selected species exhibited different patterns along the edge-to-interior gradient. Thus, the edge-to-interior transition differs among species across the lakeshore forest ecotone. The edge has often been considered the peak of discontinuity or the location of the highest amount of change in multivariate species composition, along a gradient between two communities (Fortin 1994). If this criterion is extended to individual species, the 'edge' would be closer to the forest canopy edge for 'understory tolerators' (-10m for *Calamagrostis canadensis,* 10m for *Lathyrus ochroleucus*) than for 'understory obligates' (40m for *Linnaea borealis*, 120m for *Mitella nuda*, see Lieffers 1995 for classification). Thus, there appears to be a relationship between sensitivity to edge conditions (e.g. increased light) and the location of the highest change along the edge-to-interior gradient. Another study found different spatial boundaries in continuous forest for shrubs and trees (Fortin 1997). Even with only these four species, the lakeshore forest edge appears as a ecotone with changes in understory composition occurring along the edge-to-interior gradient from -30m to beyond 100m.

Different patterns of abundance of two species (*L. ochroleucus* and *C. canadensis*) at different scales, support the general perception that ecotones are scale dependent and that effects of ecological processes vary at different scales (Gosz 1991). Discontinuities are generally more distinct at a larger scale because increasing window width decreases the effects of "noise" (Brunt and Conley 1990, Cornelius and Reynolds 1991). At the smaller 4m scale with changes throughout the edge-to-interior gradient, the edge does not appear as distinct compared to the variation in abundance of these two species further away from the edge.

We can learn more about the internal structure of the edge by examining species responses along the edge-to-interior gradient. Species may respond to the edge in one of two ways: as a boundary of a patch, or as a continual gradient. The two understory species (*M. nuda* and *L. borealis*) appear to be responding to a gradient, with continual change from the lake to the forest. In contrast, the spatial patterns of the two other species suggest the lakeshore forest edge is acting as a boundary: *C. canadensis* had high abundance just before the edge followed by a dramatic decrease, and *L. ochroleucus* increased immediately at the edge. Following the cellular membrane analogy that describes boundaries as semi-permeable membranes (Forman and Moore 1992), the lakeshore forest edge could theoretically be considered semi-permeable to *C. canadensis*, only allowing some to go through the boundary into the forest.

Significance of new methods for studying edge influence

I have introduced new methods that consider edges as part of the landscape by measuring DEI within the context of a heterogeneous landscape, and by examining the internal structure of the edge. The critical values approach to quantifying DEI provides an objective criterion for determining DEI in the context of the range of variability within a reference forest, and does not assume random sampling. The critical values approach differs substantially from regression and other curve-fitting techniques which have used models that assume the maximum or minimum value is at the edge (e.g. Chen et al. 1992, Laurance et al. 1998). Curve-fitting may not be appropriate for all edge data. Due to the heterogeneous nature of the boreal forest, responses to edge influence generally do not follow a smooth curve. Only eight of my response variables could be fit to linear, quadratic, cubic or exponential curves. A comparison between these values and the DEI obtained using the method of Chen et al. (1992) showed no consistent trend (Table 2-4). In the critical values approach, DEI depends on the critical values from the interior forest data; greater variation (more heterogeneous forest) would result in a lower estimates for DEI.

Spatial pattern analysis of selected species along the lakeshore forest edge-to-interior gradient reveals new applications of split moving window analysis (SMW) and wavelet analysis to discontinuous data. Edge detection methods using overall species composition can reveal some information on the internal structure of the edge, such as different edge signatures for different patch structures (Brunt and Conley 1990). By examining one species at a time, however, I discovered different patterns of abundance across the edge, which would probably be identified as a diffuse edge using multivariate edge detection techniques (Brunt and Conley 1990). Also, by calculating positive and negative changes separately rather than considering only absolute change, I was able to gain more information about species response along the gradient. My experimental design also differs in that I combined information from several transects rather than examining only one (e.g. Webster 1973, Cornelius and Reynolds 1991).

Position variance from wavelet analysis using the Haar wavelet usually followed the same pattern as SMW at the larger scale, although the peaks were sometimes greater using wavelet analysis. Wavelet analysis was successful in identifying discontinuities in the data, but provided little additional information. On this basis, it seems more practical to use the simpler method of SMW which appears to give similar results and is easier to program using readily accessible software (Visual Basic in Excel). Wavelet analysis does, however, have other potential applications in plant ecology (Bradshaw and Spies 1992, Dale and Mah 1998).

I have contributed to boundary research by introducing new methods that examine edges in the context of a heterogeneous landscape, and by examining the internal structure of the edge. I found that plant species respond to the lakeshore forest edge as either a gradient or a boundary; and that even within the context of heterogeneous boreal forest, there is a distinct lakeshore forest edge community with a width of about 40m. Information on the structure and composition of these natural lakeshore forest edges provides a context for understanding the impact of edges created by harvesting in the boreal forest, and for predicting faunal behaviour in riparian forest and forested buffer zones left after harvesting.

LITERATURE CITED

Bradshaw, G. A., and T. A. Spies. 1992. Characterizing canopy gap structure in forests using wavelet analysis. Journal of Ecology **80**:205-215.

Brosofske, K., J. Chen, R. J. Naiman, and J. F. Franklin. 1997. Harvesting effects on microclimatic gradients from small streams to uplands in western Washington. Ecological Applications **7**:1188-1200.

Brothers, T. S. 1993. Fragmentation and edge effects in central Indiana old-growth forests. Natural Areas Journal **13**:268-275.

Brunt, J. W., and W. Conley. 1990. Behaviour of a multivariate algorithm for ecological edge detection. Ecological Modelling **49**:179-203.

Chen, J., J. F. Franklin, and T. A. Spies. 1992. Vegetation responses to edge environments in old-growth Douglas-fir forests. Ecological Applications **2**:387-396.

Chen, J., J. F. Franklin, and J. S. Lowe. 1996. Comparison of abiotic and structurally defined patch patterns in a hypothetical forest landscape. Conservation Biology **10**:854-862.

Constabel, A. J., and V. J. Lieffers. 1996. Seasonal patterns of light transmission through boreal mixedwood canopies. Canadian Journal of Forest Research **26**:1008-1014.

Cornelius, J. M., and J. F. Reynolds. 1991. On determining the statistical significance of discontinuities within ordered ecological data. Ecology **72**:2057-2070.

Crowley, P. H. 1992. Resampling methods for computation-intensive data analysis in ecology and evolution. Annual Review of Ecology and Systematics **23**:405-447.

Cumming, S. G., P. J. Burton, and B. Klinkenberg. 1996. Boreal mixedwood forests may have no "representative" areas: some implications for reserve design. Ecography **19**:162-180.

Dale, M. R. T., and M. Mah. 1998. The use of wavelets for spatial pattern analysis in ecology. Journal of Vegetation Science.**9**:805-814.

Didham, R. K. 1997. The influence of edge effects and forest fragmentation on leaf litter invertebrates in central Amazonia. Pages 55-69 *in* W. F. Laurance and R. O. Bierregaard Jr., editors. Tropical forest remnants: Ecology, management and conservation of fragmented communities. The University of Chicago Press, Chicago.

Forman, R. T. T. 1997. Land mosaics: The ecology of landscapes and regions. Cambridge University Press, Cambridge.

Forman, R. T. T., and P. N. Moore. 1992. Theoretical foundations for understanding boundaries in landscape mosaics. Pages 236-258 *in* A. J. Hansen, and F. di Castri. Landscape boundaries: consequences for biotic diversity and ecological flows. Springer-Verlag, New York.

Fortin, M.-J. 1994. Edge detection algorithms for two-dimensional ecological data. Ecology **75**:956-965.

Fortin, Marie-J. 1997. Effects of data types on vegetation boundary delineation. Canadian Journal of Forest Research **27**:1851-1858.

Fraver, S. 1994. Vegetation responses along edge-to-interior gradients in the mixed hardwood forests of the Roanoke River basin, North Carolina. Conservation Biology **8**:822-832.

Gosz, J. R. 1991. Fundamental ecological characteristics of landscape boundaries. Pages 8-30 *in* M. M. Holland, P. G. Risser and R. J. Naiman, editors. Ecotones: the role of landscape boundaries in the management and restoration of changing environments. Chapman and Hall, New York.

Gregory, S. V., F. J. Swanson, W. A. McKee, and K. W. Cummins. 1991. An ecosystem perspective of riparian zones. BioScience **41**:540-551.

Hibbs, D. E., and P. A. Giordano. 1996. Vegetation characteristics of alder-dominated riparian buffer strips in the Oregon Coast Range. Northwest Science **70**:21-222.

Holland, M. M. 1988. SCOPE/MAB technical consultations on landscape boundaries. Report of a SCOPE/MAB workshop on ecotones. Pages 47-106 *in* F. di Castri, A. J. Hansen, and M. M. Holland, editors. A new look at ecotones: emerging international projects on landscape boundaries. Biology International, Special Issue **17**.

Holt, T. D., I. Blum, and N. M. Hill. 1995. A watershed level analysis of the lakeshore plant community. Canadian Journal of Botany **73**:598-607.

Johnston, C. A., and R. J. Naiman. 1987. Boundary dynamics at the aquatic-terrestrial interface: The influence of beaver and geomorphology. Landscape Ecology **1**:47-57.

Kupfer, J. A., and G. P. Malanson. 1993. Observed and modelled directional change in riparian forest composition at a cutbank edge. Landscape Ecology **8**:185-199.

Lambert, J. D. 1998. Ovenbirds (*Seiurus aurocapillus*) in riparian buffer strips: short-term response to upland timber harvest in Alberta's boreal mixed-wood forest. M.Sc. thesis, University of Alberta, Edmonton, Canada.

Laurance, W. F., L. V. Ferreira, J. M. Rankin-de Merona, and S. G. Laurance. 1998. Rain forest fragmentation and the dynamics of Amazonian tree communities. Ecology **79**:2032-2040.

Lee, P. C., S. Crites, K. Sturgess, and J. B. Stelfox. 1995. Changes in understory composition for a chronosequence of aspen mixedwood stands in Alberta. Pages 63-80 *in* J. B. Stelfox, editor. Relationships between stand age, stand structure and biodiversity in aspen mixedwood forests in Alberta. Jointly published by Alberta Environment Centre, Vegreville, Alberta, and Canadian Forest Service, Edmonton, Alberta, Canada.

Lieffers, V. J. 1995. Ecology and dynamics of boreal understory species and their role in partial-cut silviculture. Pages 33-39 *in* C. R. Bamsey, editor. Innovative silviculture systems in boreal forests. Clear Lake Ltd., Edmonton, Canada.

Machtans, C. S., M.-A. Villard, and S. J. Hannon. 1996. Use of riparian buffer strips as movement corridors by forest birds. Conservation Biology **10**:1366-1379.

Malanson, G. P., and J. A. Kupfer. 1993. Simulated fate of leaf litter and large woody debris at a riparian cutbank. Canadian Journal of Forest Research **23**:582-590.

Malcolm, J. R. 1994. Edge effects in central Amazonian forest fragments. Ecology **75**:2438-2445.

Manly, B. F. J. 1997. Randomization, bootstrap and Monte Carlo methods in Biology. Chapman and Hall, London, United Kingdom..

Matlack, G. R. 1993. Microenvironment variation within and among forest edge sites in the eastern United States. Biological Conservation **66**:185-194.

Matlack, G. R. 1994. Vegetation dynamics of the forest edge - trends in space and successional time. Journal of Ecology **82**:113-123.

McGarigal, K., and W. C. McComb. 1992. Streamside versus upslope breeding bird communities in the central Oregon Coast Range. Journal of Wildlife Management **56**:10-23.

Moss, E. H. 1992. Flora of Alberta. Second Edition. Revised by J. G. Packer. University of Toronto Press, Toronto, Canada.

Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. Trends in Ecology and Evolution **10**:58-62.

Murray, N. L., and D. F. Stauffer. 1995. Nongame bird use of habitat in central Appalachian riparian forests. Journal of Wildlife Management **59**:78-88.

Naiman, R. J., H. Décamps, and M. Pollock. 1993. The role of riparian corridors in maintaining regional biodiversity. Ecological Applications **3**:209-212.

Noss, R. F. 1983. A regional landscape approach to maintain diversity. BioScience **33**:700-706.

Pabst, R. J., and T. A. Spies. 1998. Distribution of herbs and shrubs in relation to landform and canopy cover in riparian forests of coastal Oregon. Canadian Journal of Botany **76**:298-315.

Palik, B. J., and P. G. Murphy. 1990. Disturbance versus edge effects in sugar-maple/beech forest fragments. Forest Ecology and Management **32**:187-202.

Ranney, J. W., M. C. Bruner, and J. B. Levenson. 1981. The importance of edge in the structure and dynamics of forest islands. Pages 67-95 *in* R. L. Burgess and D. M. Sharpe, editors. Forest Island Dynamics in Man-Dominated Landscapes. Springer-Verlag, New York.

Risser, P. G. 1995. The status of the science examining ecotones. BioScience **45**:318-325.

SPSS Inc. 1996. SPSS for Windows 7.5.1. Standard Version.

Turner, S. J., R. V. O'Neill, W. Conley, M. R. Conley, and H. C. Humphries. 1991. Pattern and scale: statistics for landscape ecology. Pages 17-49 *in* M. G. Turner and R. H. Gardner, editors. Quantitative methods in landscape ecology: the analysis and interpretation of landscape heterogeneity. Springer-Verlag, New York.

van der Maarel, E. 1990. Ecotones and ecoclines are different. Journal of Vegetation Science **1**:135-138.

Wales, B. A. 1972. Vegetation analysis of north and south edges in a mature oak-hickory forest. Ecological Monographs **42**:451-471.

Webster, R. 1973. Automatic soil-boundary location from transect data. Mathematical Geology **5**:27-37.

Whitaker, D. M., and W. A. Montevecchi. 1997. Breeding bird assemblages associated with riparian, interior forest, and nonriparian edge habitats in a balsam fir ecosystem. Canadian Journal of Forest Research **27**:1159-1167.

Wiens, J. A., C. S. Crawford, and J. R. Gosz. 1985. Boundary dynamics: a conceptual framework for studying landscape ecosystems. Oikos **45**:421-427.

Williams-Linera, G. 1990. Vegetation structure and environmental conditions of forest edges in Panama. Journal of Ecology **78**:356-373.

Wood, C. E., and Wood, J. K. 1989. Riparian forests of the Leona and Sabinal Rivers. The Texas Journal of Science **41**:395-411.

Young, A., and N. Mitchell. 1994. Microclimate and vegetation edge effects in a fragmented podocarp-broadleaf forest in New Zealand. Biological Conservation **67**:63-72.

TABLE 2-1. Average values of response variables at different distances from the lakeshore forest edge, in the non-forested riparian zone (-10m) and in the upland interior forest. The superscripts 'a' and 'b' designate values that are significantly different from the adjacent riparian and upland interior reference data sets respectively. Values at two or more consecutive distances that are significantly different from either reference data set are shaded; values significantly different from both reference data sets are highlighted by a box. Twenty-four of the 129 significant results in this table were expected due to random chance.

	Distance from lakeshore forest edge (m)										
Response variable	**-10**	**0**	**5**	**10**	**20**	**40**	**60**	**100**	**150**	**200**	**interior**
Coarse woody material											
Diameter (cm)	15^{ab} ± 2	16^{ab} ± 1	13^{b} ± 1	13^{b} ± 1	12 ± 1	11 ± 1	11 ± 1	13^{b} ± 1	11 ± 1	9^{b} ± 0.3	11 ± 0.2
Canopy cover (%)	65^{ab} ± 7	81 ± 3	79 ± 4	77 ± 3	82^{b} ± 2	81 ± 2	81 ± 1	81 ± 2	81 ± 2	76 ± 6	77 ± 1
Tree density (# per ha)											
Total	380^{ab} ± 130	990 ± 140	990 ± 120	1260 ± 180	1180 ± 60	1420^{a} ± 190	1210 ± 180	1100 ± 160	1030 ± 140	1310 ± 180	1120 ± 60
Sub-canopy	40^{ab} ± 30	130 ± 30	140 ± 40	230 ± 60	240 ± 50	190 ± 40	130 ± 40	190 ± 50	170 ± 40	310 ± 100	190 ± 20
Populus tremuloides	120^{ab} ± 110	630^{a} ± 140	650^{a} ± 170	860 ± 190	770 ± 100	1170^{ab} ± 200	790 ± 180	860 ± 200	840 ± 150	900 ± 190	750 ± 60
P. tremuloides; canopy	30^{ab} ± 30	240^{ab} ± 60	300^{ab} ± 100	430^{a} ± 110	480 ± 70	780^{a} ± 120	640 ± 150	580 ± 150	590 ± 120	650 ± 120	570 ± 50
P. tremuloides; mid-canopy	70 ± 120	280^{ab} ± 70	240^{ab} ± 70	320^{ab} ± 90	120^{b} ± 30	230^{ab} ± 60	80^{b} ± 50	110^{b} ± 50	100^{b} ± 20	80 ± 40	40 ± 10
P. balsamifera	80 ± 30	170 ± 50	170 ± 80	250^{a}±150	270^{a} ± 90	140 ± 60	270^{a} ± 90	120 ± 70	130 ± 40	120 ± 60	190 ± 30
Large diameter shrubs (*Salix, Alnus, Prunus*)	110^{ab} ± 60	140^{ab} ± 90	60 ± 40	30 ± 20	30 ± 20	70^{a} ± 30	30 ± 10	40 ± 30	20 ± 20	20 ± 20	40 ± 10
Tree diameter (cm)	10^{ab} ± 1	16 ± 1	17 ± 1	16 ± 1	17 ± 1	16 ± 1	18 ± 1	18 ± 1	19 ± 1	16 ± 1	17 ± 0.4

Snag density (# per ha)											
Total	380^{ab}±180	440 ± 90	420^{ab}±90	510±100	680± 140	620± 100	640 ± 90	630± 130	530 ± 90	530 ± 100	640 ± 40
P. tremuloides	10^{ab} ± 10	140^{ab}±40	200^{ab}±70	150^{ab}±50	300 ± 80	460± 100	390 ± 70	470± 120	390 ± 90	310 ± 80	410 ± 40
P. balsamifera	40 ± 20	120 ± 40	80 ± 30	120 ± 40	150^{ab}±50	70 ± 30	130^{b}± 60	90 ± 60	40 ± 20	120 ± 60	60 ± 10
Large diameter shrubs (*Salix, Alnus, Prunus*)	110^{a} ± 70	130^{a} ± 50	50 ± 30	80 ± 40	60 ± 40	70 ± 40	50 ± 30	40 ± 20	40 ± 20	20 ± 10	70 ± 20
Sapling density (# per m^2)											
P. tremuloides	0,6^{ab}±0,2	0,8^{ab}±0,2	1,0^{ab}±0,2	0,7^{ab}±0,2	0,6^{ab}±0,2	0,5^{ab}±0,2	0,3 ± 0,1	0,2 ± 0,1	0,4^{a} ± 0,1	0,1 ± 0,05	0,2±0,03
P. balsamifera	0,4^{ab}±0,3	0,2^{a} ± 0,1	0,3^{ab}±0,2	0,1 ± 0,1	0,2^{ab}±0,1	0,1± 0,04	0,1± 0,05	0,04±0,02	0,05±0,03	0,2 ± 0,1	0,1±0,02
Sapling cover (%)											
P. tremuloides	6,3^{ab}±2,1	14^{ab}± 5,0	5,6^{ab}±2,0	3,5^{ab}±1,0	5,0^{ab}±1,7	1,8 ± 0,6	1,3 ± 0,5	0,8 ± 0,3	1,9 ± 0,7	0,9 ± 0,5	1,2 ± 0,1
P. balsamifera	4,0^{ab}±2,6	5,2^{ab}±2,3	1,3^{ab}±0,7	2,1^{ab}±1,0	0,9^{a} ± 0,4	0,5 ± 0,3	1,2^{ab}±0,6	0,4 ± 0,2	0,2 ± 0,1	0,4 ± 0,2	0,5 ± 0,3
Sapling max. height (m)											
P. tremuloides	2,3^{ab}±0,5	2,4^{a} ± 0,5	1,6^{a} ± 0,2	1,5 ± 0,2	1,7^{a} ± 0,2	1,6^{a} ± 0,3	1,1 ± 0,2	1,1 ± 0,1	1,2 ± 0,2	1,2 ± 0,2	1,2 ± 0,1
P. balsamifera^{c}	3,4^{b}± 1,3	4,2^{b}± 1,2	2,2 ± 0,7	2,0 ± 0,3	1,9 ± 0,4	1,8 ± 1,1	2,8^{b}± 0,4	1,5 ± 0,4	1,2 ± 0,4	1,9 ± 1,1	1,5 ± 0,2
Shrub richness (species per 0,75m^2)	4,6^{ab} ± 0,6	5,8 ± 0,4	5,8 ± 0,4	5,8 ± 0,5	5,9 ± 0,4	5,8 ± 0,5	6,4^{b} ± 0,4	6,2^{b} ± 0,4	5,8 ± 0,4	5,4 ± 0,5	5,4 ± 0,1
Shrub cover (%)	62 ± 10	63 ± 8	68 ± 8	64 ± 10	58 ± 10	66 ± 10	80^{ab} ± 11	61 ± 10	62 ± 9	56 ± 9	58 ± 3
Herb richness (species per 0,75m^2)		8,8 ± 0,8	9,7 ± 0,7	10,0± 0,5	11,3^{ab}±0,5	10,8^{ab}±0,6	9,5 ± 0,6	9,0 ± 0,6	10,1± 0,6	9,2 ± 0,5	9,2 ± 0,2
Herbaceous cover (%)		46^{ab} ± 7	66 ± 7	79^{b} ± 9	88^{ab} ± 6	78^{b} ± 8	67 ± 6	72 ± 7	75 ± 7	71 ± 7	66 ± 2

^{a} = Significantly different from the adjacent riparian forest.
^{b} = Significantly different from the upland interior forest.
^{c} = A randomization test could not be performed for the adjacent riparian forest data set.

TABLE 2-2. Distance of edge influence (DEI) for live tree and snag densities, and sapling characteristics, for *Populus tremuloides* and *P. balsamifera* (+/- = greater/less than in the reference data set), as compared to the adjacent riparian and the upland interior reference data sets. Numbers delimit DEI as a range of two or more consecutive distances with values significantly different from average values in interior forest. Numbers in brackets indicate single distances near the edge with average values that were significantly different from average values in the reference data set. Average values are tabulated in Table 2-1.

	Populus tremuloides				*Populus balsamifera*			
Reference data set	Adjacent riparian		Upland interior		Adjacent riparian		Upland interior	
	+/-	DEI (m)	+/-	DEI (m)	+/-	DEI (m)	+/-	DEI (m)
Tree density	- +	0-5 (40)	+	(40)	+	10-20(60)	ns	
Snag density	-	0-10	-	0-10	+	(20)	+	(20,60)
Sapling density	+	0-40(150)	+	0-40	+	0-5(20)	+	0-5(20)
Sapling cover	+	0-20	+	0-20	+	0-20(60)	+	0-10(60)
Sapling height	+	0-5,20-40	ns		N/A		+	(0,60)

ns = No significant DEI.

N/A = Not available, a randomization test could not be performed due to inadequate sample size.

TABLE 2-3. Cover of shrub species at lakeshore forest edges (+/- = greater/less than in the reference data set) and distance of edge influence (DEI) as compared to the adjacent riparian and the upland interior reference data sets. Numbers delimit DEI as a range of two or more consecutive distances with values significantly different from average values in interior forest. Numbers in brackets indicate single distances near the edge with average values that were significantly different from average values in interior forest. Species are subdivided into 'edge-positive' species (with greater cover at edges) and 'edge-negative' species (with lower cover at edges). Only species with significant DEI are included. Average values are tabulated in Appendix 2-1.

	Adjacent riparian		Upland interior	
	+/-	DEI (m)	+/-	DEI (m)
Edge-positive species				
Amelanchier alnifolia	+	0-40	+	0-60
Lonicera dioica	+	(10)	+	5-20,60-100(200)
Prunus spp. (*P. pensylvanica* and *P. virginiana*)	+	0-40	+	(5)20-40
Salix spp.	+	0-5(20,60)	+	0-5(60)
Symphoricarpos albus (could include *S. occidentalis*)	+	0-5,20-40	+	(5)20-40
Vaccinium myrtilloides	+	0-10	+	0-10,150-200
Edge-negative species				
Alnus crispa	-	20-40	-	20-60
Ribes triste	-	10-20	-	(20)
Rubus idaeus	-	0-40	+	60-200

TABLE 2-4. Cover of herb species at lakeshore forest edges (+/- = greater/less than in the reference data set) and distance of edge influence (DEI) as compared to the adjacent riparian and the upland interior reference data sets. Numbers delimit DEI as a range of two or more consecutive distances with values significantly different from average values in interior forest. Numbers in brackets indicate single distances near the edge with average values that were significantly different from average values in interior forest. Species are subdivided into 'edge-positive' species (with greater cover at edges) and 'edge-negative' species (with lower cover at edges). Only species with significant DEI are included. Average values are tabulated in Appendix 2-1.

	Adjacent riparian		Upland interior	
	+/-	DEI (m)	+/-	DEI (m)
Edge-positive species				
Apocynum androsaemifolium	+	0-60	+	(5)
Aster conspicuus	+	5-40	+	(10,40)
Equisetum arvense	+	0-20	+	0-150
Fragaria virginiana	+	10-20	+ -	(20) (100)
Galium boreale	+	0-10	+	0-10(40)
Lathyrus ochroleucus	+	5-40	+	10-40
Maianthemum canadense	+	5-20(100,200)	+	5-40(100,200)
Orthilia secunda	+	0-20(60)	+	(10)
Petasites palmatus	+	0-20	+	0-20(60)
Pyrola asarifolia	+	5-10	+	5-10
Thalictrum venulosum	+	(20)	+	0-200
Vicia americana	+ -	5-40(100) (200)	+	0-100
Edge-negative species				
Aralia nudicaulis	-	0-10(40)	- +	(0) (20)
Cornus canadensis	- +	(0,10,60) (40)	-	0-10,60-100(200)
Linnaea borealis	-	0-10(40)	-	0-10(40)
Mitella nuda	-	0-10	-	0-10(60)
Rubus pubescens	-	0-5	ns	

ns = no significant DEI.

TABLE 2-5. Results of the best-fit curves to identify an estimate of distance of edge influence for selected response variables. Distance of edge influence was calculated as the intersection of the curve with the critical values determined by randomization tests on the reference data sets (as in Laurance et al. 1998). The method from Chen et al. (1992), applied to the same data sets, uses the best fit exponential equation, and determines the distance along the curve that corresponds to $Y_{0m} +/- 2/3 \times |Y_{0m} - Y_{200m}|$.

Response variable	F	R^2	Equation[a]	Distance of edge influence (m)		
				Reference data set		Method from Chen et al. (1992)
				Adjacent riparian forest	Upland interior forest	
Coarse woody material	10	0.2	$4.6 - 0.1x + 0.001x^2 - 3\times10^{-6}x^3$	33	2	32
Canopy tree density	6.3	0.2	$390 + 16x - 0.17x^2 + 0.0005x^3$	14	10	15
Mid-canopy tree density	7.2	0.1	$460 - 4.2x + 0.016x^2$	55	35	29
Density of *Populus tremuloides* snags	5.6	0.1	$130 + 9.1x - 0.075x^2 + 0.0002x^3$	15	13	14
Density of *P. tremuloides* saplings	9.4	0.1	$0.90 - 0.018x + 0.0002x^2 - 5\times10^{-7}x^3$	51	36	64
Height of *P. tremuloides* saplings	4.0	0.1	$200 - 2.5x + 0.022x^2 - 6\times10^{-5}x^3$	25	18	8
Cover of *Amelanchier alnifolia*	4.6	0.1	$9.3 - 0.08x + 7.2E\text{-}5x^2 + 8\times10^{-7}x^3$	74	92	53
Cover of *Rubus idaeus*	4.3	0.1	$2.0 + 0.0098x + 0.0006x^2 - 3\times10^{-6}x^3$	49	65[b]	78

[a] Units are the same as in Appendices 2-1 and 2-2.

[b] In this case, 70-200m from the lakeshore forest edge is significantly different from the upland interior forest, rather than 0-70m.

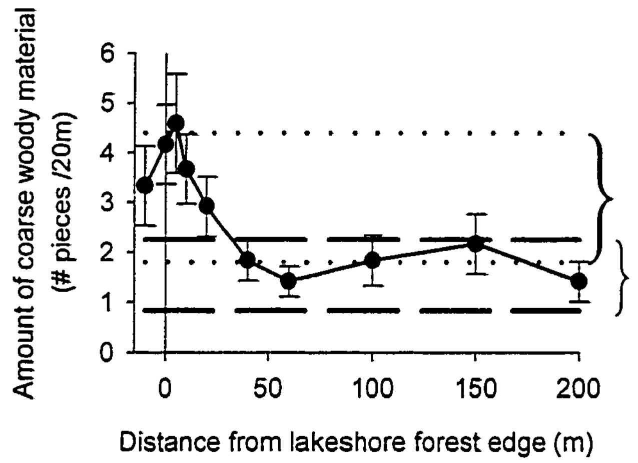


FIGURE 2-1. Average amount of coarse woody material along the lakeshore forest edge-to-interior gradient. Dashed and dotted lines indicate critical values determined by randomization tests of the adjacent riparian and the upland interior reference data sets respectively. Significant values are those that occur outside the critical values. Bars represent ± 1 SE.

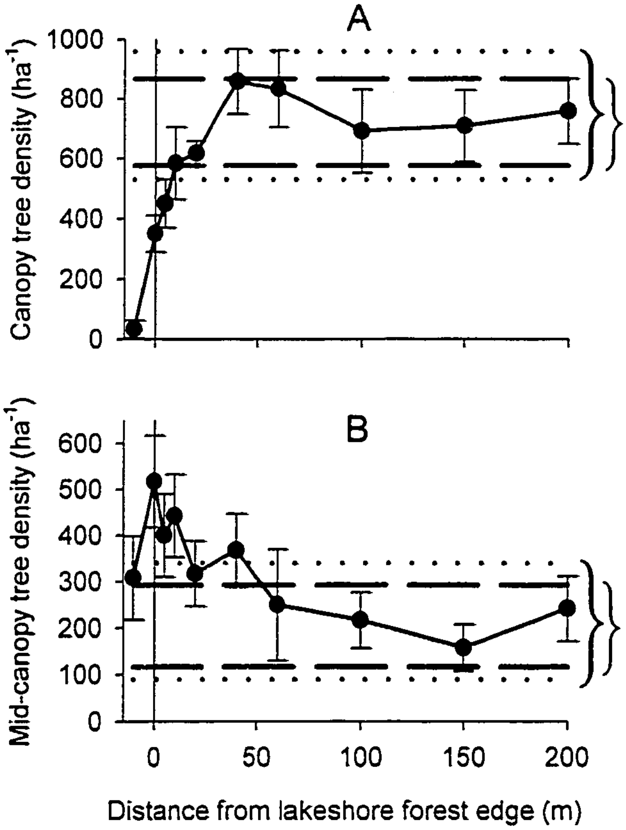


FIGURE 2-2. Average density along the lakeshore forest edge-to-interior gradient for (A) canopy trees and (B) mid-canopy trees. Dashed and dotted lines indicate critical values determined by randomization tests of the adjacent riparian and the upland interior reference data sets respectively. Significant values are those that occur outside the critical values. Bars represent ± 1 SE.

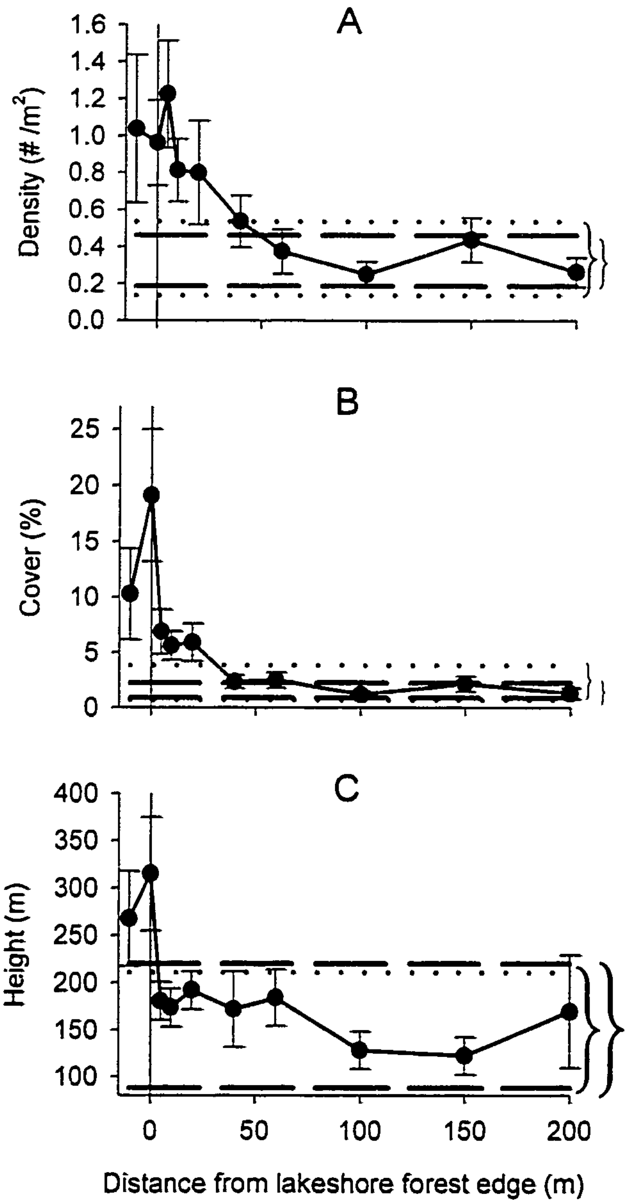


FIGURE 2-3. Average values along the lakeshore forest edge-to-interior gradient for characteristics of *Populus* spp. saplings: (A) density, (B) cover and (C) maximum height. Dashed and dotted lines indicate critical values determined by randomization tests of the adjacent riparian and the upland interior reference data sets respectively. Significant values are those that occur outside the critical values. Bars represent ± 1 SE. Standard error was calculated among all subplots.

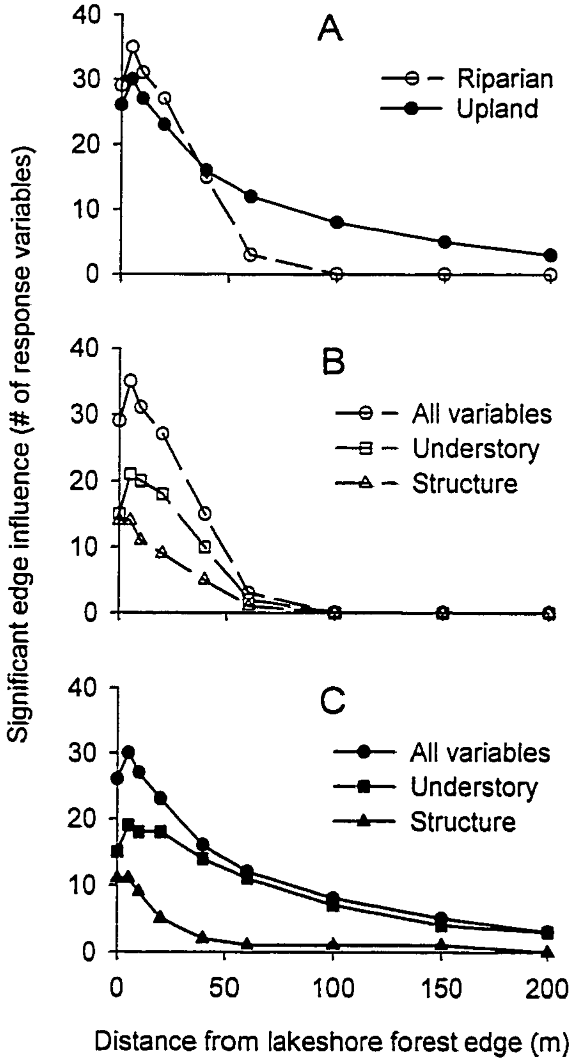


FIGURE 2-4. Summary of distance of edge influence results to determine where edge influence from lakeshore forest edges occurs: number of response variables with significant distance of edge influence for different distances from the lakeshore forest edge. (A) Comparison between the two reference data sets. (B) Comparison between understory composition and forest structure using the adjacent riparian reference data set. (C) Comparison between understory composition and forest structure using the upland interior reference data set.

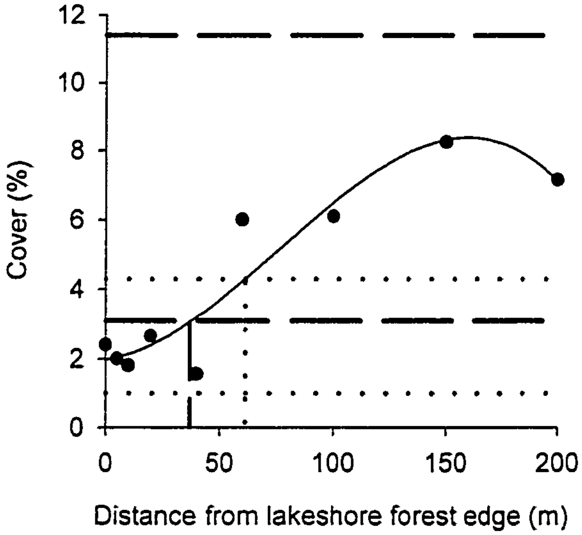


FIGURE 2-5. Average cover of *Rubus idaeus* and the fitted curve (cubic) along the lakeshore forest edge-to-interior gradient. Dashed and dotted lines indicate critical values determined by randomization tests of the adjacent riparian and the upland interior reference data sets respectively. Distance of edge influence is indicated by the extrapolated line from the intersection of the fitted curve with a critical value. Note that in this particular case, within 39m of the edge, the cover of *Rubus idaeus* was significantly different than in the adjacent riparian forest. However, within 70m of the edge, the cover was <u>not</u> significantly different from upland interior forest, but was significantly different from upland interior forest after 70m from the edge.

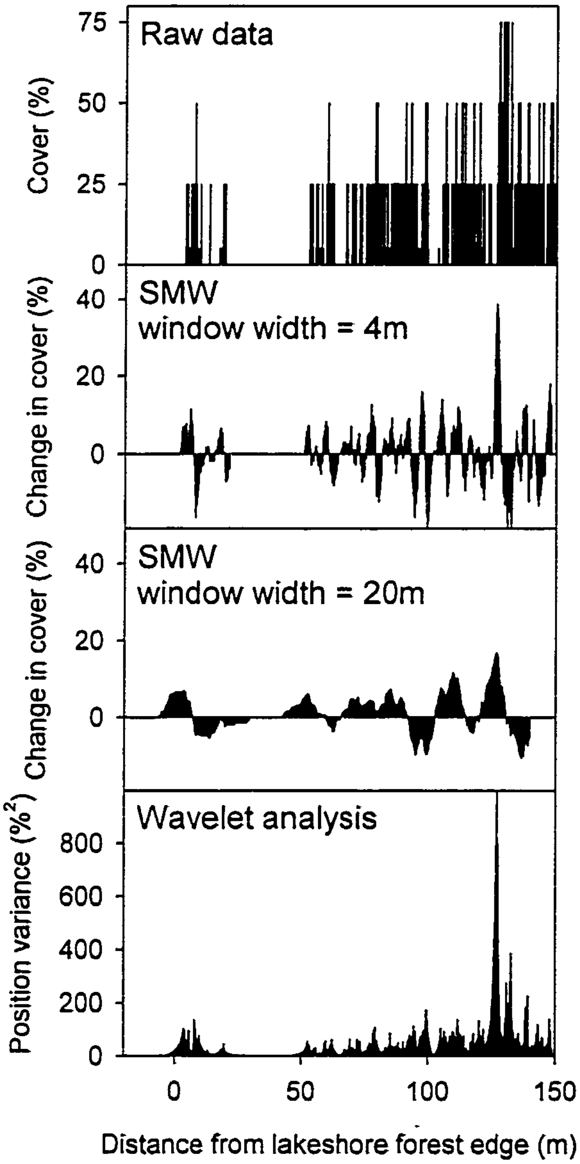


FIGURE 2-6. An example of the pattern of abundance of *Mitella nuda* along a single transect including raw data, results from split moving window analysis (SMW) at scales of 4m and 20m, and position variance from wavelet analysis.

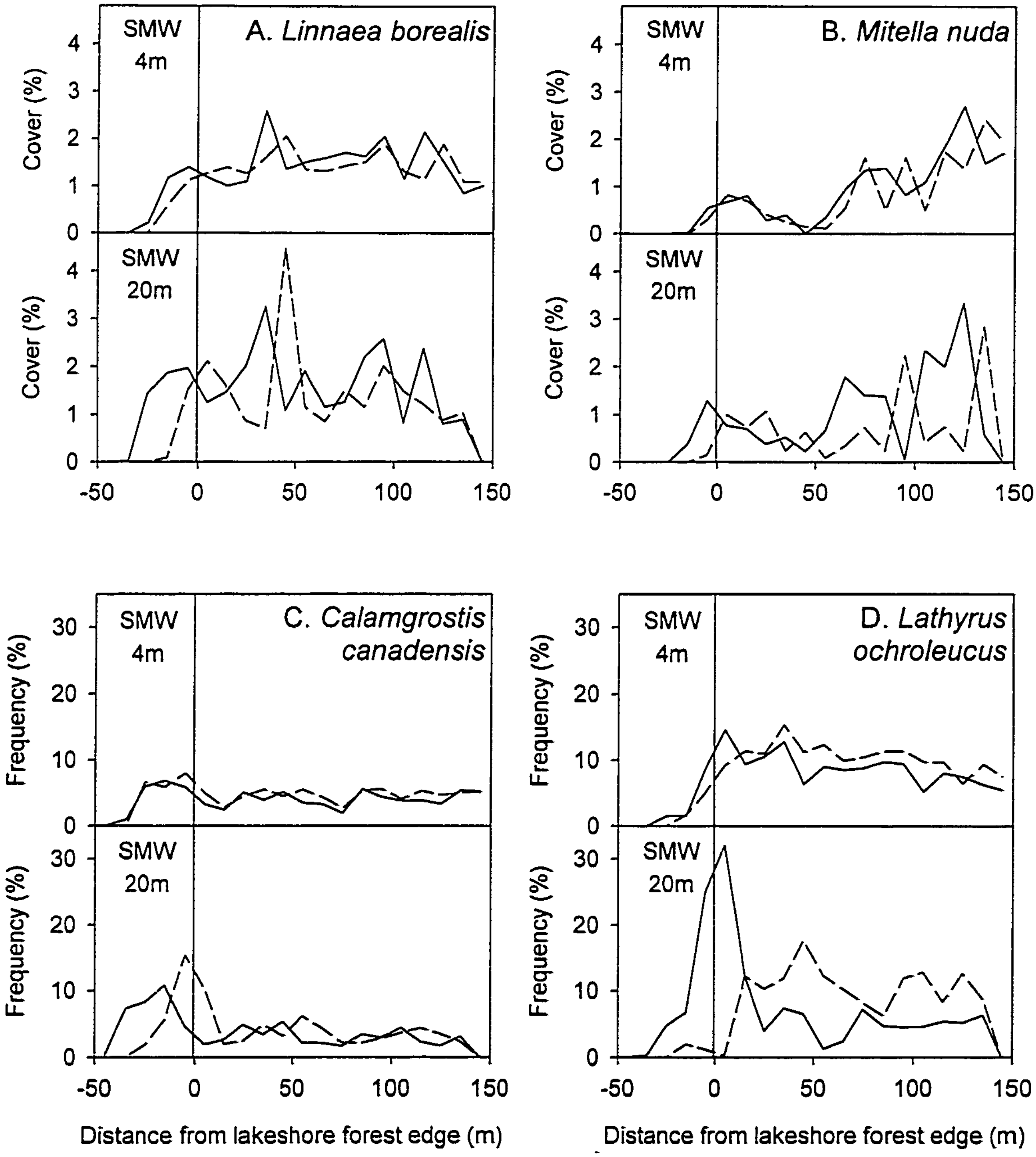


FIGURE 2-7. Change in abundance along the lakeshore forest edge-to-interior gradient using split moving window analysis at two scales (4m, 20m) for (A) *Linnaea borealis*, (B) *Mitella nuda*, (C) *Calamagrostis canadensis*, and (D) *Lathyrus ochroleucus*. Solid lines represent average positive values, or increases in abundance from the edge to the interior. Dashed lines represent average negative values, or decreases in abundance from the edge to the interior. Values are averages for 10m intervals along 6-7 transects. The units represent the average change in % cover or frequency (% of quadrats) from one half of the window to the next.

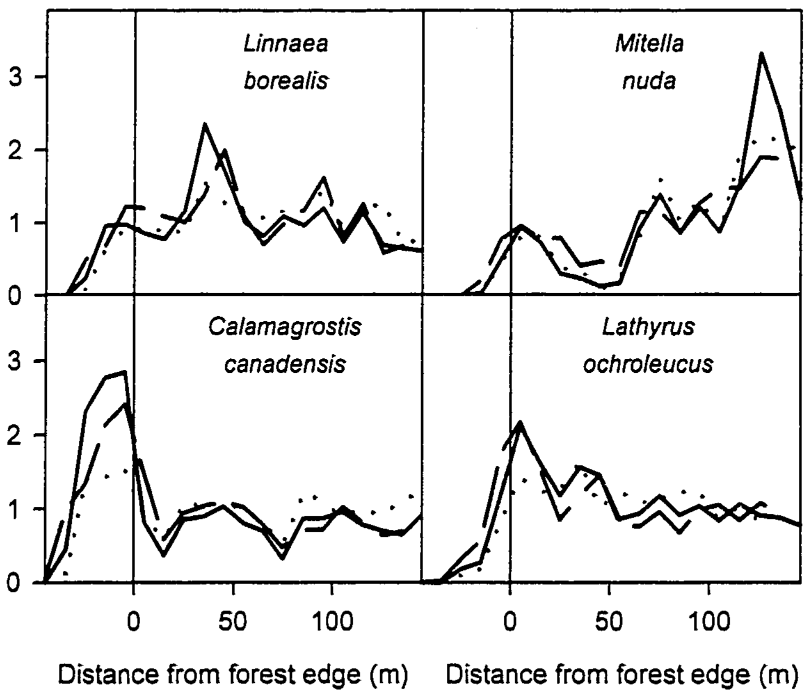


FIGURE 2-8. Comparison of results of change in abundance along the lakeshore forest edge-to-interior gradient from different analyses: split moving window analysis using absolute differences at the 4m scale (dotted line) and at the 20m scale (dashed line), and position variance from wavelet analysis (solid line). Values are averages for 10m intervals along 6-7 transects. Results were standardized for each analysis separately such that the mean equals one.

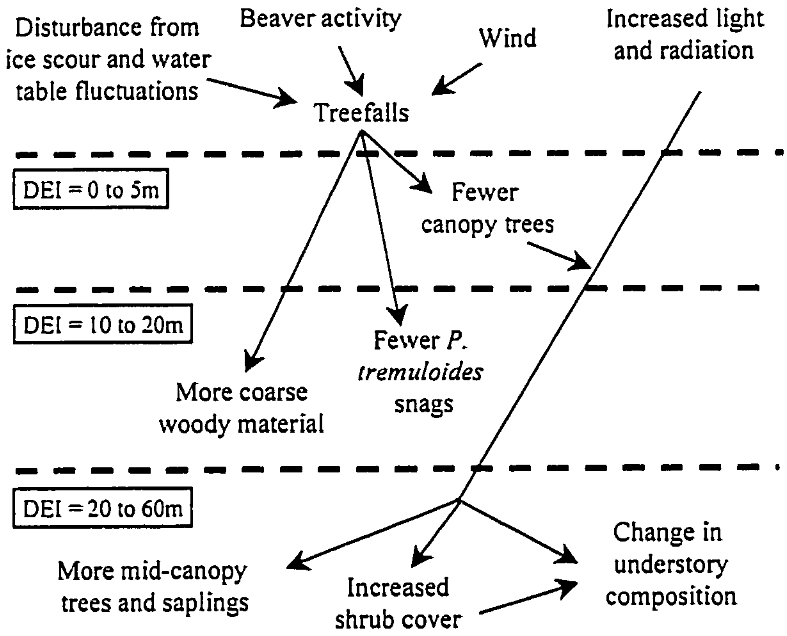


FIGURE 2-9. A proposed conceptual model of the causal factors of edge influence and their relationship to forest structure and composition at lakeshore forest edges. Components of forest structure and composition are organized according to distance of edge influence.

CHAPTER 3. CLEARCUT EDGES: EDGE INFLUENCE AT DIFFERENT AGES OF REGENERATING CUTBLOCKS [1]

In the boreal forest of Alberta, Canada, timber harvesting, fragmentation and edge creation are becoming more common on the landscape. Forest edges in the *Populus*-dominated forest were expected to differ from created edges studied in other forested ecosystems due to rapid regrowth of *Populus* spp. in adjacent regenerating cutblocks. To determine the extent of edge influence on forest structure and composition, I sampled trees, coarse woody material, saplings, shrubs and herbs at different distances from created edges adjacent to 1, 2, 5 and 16 yr old cutblocks, using a combination of pre/post-harvest comparisons (1, 2 yr old edges) and a chronosequence (5, 16 yr old edges). To quantify distance of edge influence, averages of response variables at different distances from the edge were compared to critical values determined by randomization tests of data collected in interior forest. Edge creation led to alterations in structure including increased tree mortality and snag breakage. The resultant increase in downed coarse woody material was evident up to 20m from the edge in the first year post-harvest and was still evident at the 16 yr old edges. The most prominent early response to edge creation was increased regeneration of *Populus* spp. for a distance up to 60m into the forest. Edge influence on understory herb and shrub composition was minimal in the first two years except for a significant decrease in total shrub cover up to 10m from the edge. At the 5 and 16 yr old edges, some individual shrub species had reduced cover, particularly *Viburnum edule*; while several herb species had greater cover, particularly *Lathyrus ochroleucus*. One herb species, *Mitella nuda*, had dramatically lower cover up to 60m and 40m from the 5 and 16 yr old edges, respectively. Distance of edge influence from clearcut edges on forest structure and composition in this *Populus*-dominated boreal forest was not as extensive as demonstrated in other forests. Still, overall forest structure and composition was altered near the edge within approx. 20m, and these changes were still evident at 16 yr old edges.

INTRODUCTION

With increased clearcutting of temperate and tropical forests for fibre production or agriculture, anthropogenically created edges are becoming an increasingly prevalent component of the forest landscape mosaic. The structure and composition of forest adjacent to created edges differs from that of interior forest (see Chapter 1). An assessment of the extent of edge influence on forest structure and composition is important for determining the effective area of interior forest conditions remaining in

---

[1] A version of this chapter has been submitted for publication. Harper, K.A. and S.E. Macdonald. Clearcut edges in *Populus*-dominated boreal forest: edge influence at different ages of regenerating cutblocks. Ecological Applications.

forest fragments. Investigation of the change in forest edges over time, particularly for clearcut edges which are adjacent to regenerating cutblocks, is important for evaluating the long-term impact of edge creation on the landscape. I know of no study that has examined edge development over time next to a rapidly regenerating forest.

Edge influence on forest composition from created edges has been studied mostly in Douglas-fir forests (e.g. Chen et al. 1992) and eastern deciduous forests (e.g. Ranney et al. 1981, Matlack 1993, 1994) of the United States, and in tropical rainforests (e.g. Williams-Linera 1990b, Laurance et al. 1998), but has not yet been explicitly studied in the Canadian boreal forest. Conclusions about edge influence from studies on recently created edges and older, maintained edges in other ecosystems may not be applicable to clearcut edges in the boreal forest of Alberta. The *Populus*-dominated boreal forest is an ideal ecosystem for investigating the early stages of edge development at clearcut edges due to rapid regeneration of *Populus* spp. in the cutblocks. At clearcut edges, edge influence is expected to change over time due to counteracting effects of a lag in vegetation responses, and the abatement of microclimatic gradients as the adjacent forest regenerates. The extent of edge influence in Alberta may differ from other forests because of shorter canopy height, and lower sun angle at these high latitudes. In addition, these forests are dominated by early successional species with relatively high inherent heterogeneity which could affect the ecological significance of edge influence.

My objective was to determine the extent of edge influence on forest structure and composition at created edges in the aspen-dominated boreal forest over time following forest harvesting. I quantified distance of edge influence for changes in different response variables during the first and second years following harvest using matching pre/post-harvest comparisons, and for average values of response variables for two additional times post-harvest: 5 and 16 yr. I defined distance of edge influence as the distance from the clearcut forest edge where averages or changes in forest structure and composition are no longer significantly different from averages or changes in interior forest. I used the critical values approach developed in Chapter 2 to assess distance of edge influence at the older clearcut edges and modified this method for pre/post-harvest comparisons at the younger clearcut edges.

METHODS

Sampling design

I sampled forest edges adjacent to cutblocks of four different ages: 1, 2, 5 and 16 yr post-harvest. All cutblocks were harvested in winter. Most of the older cutblocks were planted with *Picea glauca* seedlings after harvesting; however, *Populus tremuloides* and *P. balsamifera* remained the main regenerative species.

Transects extending from the forest edge to 200m into the forest were established perpendicular to edges with predominantly south-facing aspects (120°-240°). Transects were in upland forest, at least 100m from the nearest corner of a cutblock and from other transects, and were located to avoid conifer-dominated areas and wetlands. For the recent clearcut edges, ten transects (identical to the upland interior reference data set, Chapter 2) were sampled one year pre-harvest (1996), and one and two years post-harvest (1997, 1998), five in each of the South Calling Lake and Lac La Biche study areas (see Chapter 1 for a description of the study sites). The forest edge was defined by the flagged line established to guide the harvest operators, and was found to be accurate within a few metres. Ten transects adjacent to 5 yr old cutblocks were sampled in 1998; five in each of the Calling Lake and Lac La Biche study areas. Also in 1998, I sampled eight transects at edges of 16 yr old cutblocks in the Calling Lake study area, seven of which were adjacent to one very large clearcut (almost 4km long), while the other transect was adjacent to another smaller clearcut. These transects next to the older edges were established such that 0m corresponded to the original clearcut edge (trunks of the furthest snags or live trees towards the clearcut). Slopes within 50m of the edge were generally less than 10%, however, clearcut edges on two of the 1-2 yr old edges were at the top of inclines with downslopes of 21% and 35% over the first 50m from the edge into the forest.

Plots (20m x 5m, length parallel to the forest edge) were established along each transect, centred at the following distances from the edge: 0, 5, 10, 20, 40, 60, 100, 150, and 200m. Distances from edge were considered treatments and were selected to sample more intensively near the edge. Plots were not contiguous since I had no intention of examining spatial pattern. The three plot locations furthest from the edge (100, 150 and 200m) were designated as 'interior forest' and were sampled to provide a measure of variability therein. Because almost all studies in temperate deciduous forest ecosystems have found that edge influence on forest structure and composition is confined to within 100m of the edge (e.g. Wales 1972, Ranney et al. 1981, Matlack 1993), I assumed that 100m from the edge could safely be considered 'interior' forest. Moreover, at natural, inherent lakeshore forest edges, edge influence generally penetrated only 40m into the forest (Chapter 2). On four transects, some of these interior forest plot locations were moved in order to avoid proximity to other edges, but remained at least 100m from any clearcut edge, and 40m from other plots or edges of narrow linear disturbances. I also sampled trees, shrubs and downed coarse woody material in an additional 20m x 5m plot at -10m (10m from the forest edge into the clearcut) to characterize vegetation structure in the adjacent cutblocks. Within all plots, two shrub subplots (2m x 2m) and three herb subplots (0.5m x 0.5m) were established systematically along the major axis of the plot. Subplot sizes were determined based on convenience for visual cover estimation to facilitate more accurate cover estimates for resampling. Multiple subplots were used for better representation of the understory at a given distance from the edge along a given transect.

Data collected

Trees and snags were tallied in the 20m x 5m plots (see Chapter 2 for details of data collected). I recorded diameter at breast height and canopy position for trees and snags (mid-canopy, sub-canopy, canopy). For snags, I also noted the presence of a slightly (diameter at the break: ≤8cm) or majorly (diameter at the break: ≥8cm) broken top, and estimated the height for snags ≤5m tall. I tallied the number of pieces of downed coarse woody material (CWM) intersecting the major axis of the plot (≥8cm diameter at the intersection point, and decay classes 1-3 out of 7, Lee et al. 1995). I assumed that CWM in later stages of decay fell prior to edge creation. Canopy cover was measured at the centre of each plot using a convex spherical densiometer. Within the shrub subplots, cover of all shrub species and *Populus* spp. saplings (<5cm dbh) was estimated, and the number and maximum height of saplings were measured. Sapling density was differentiated into new (< 1 yr, green) and old (≥ 1 yr) saplings for plots near the 5 and 16 yr old edges (except two 5 yr old edge transects due to logistics). Cover of all forbs and dwarf woody plant species was estimated within the herb subplots. Cover was visually estimated to the nearest 1% up to 5%, and to the nearest 10% thereafter. Proportion of plants that were flowering was estimated for *Galium boreale, Cornus canadensis* and *Maianthemum canadense*. Four leaflets each of *Petasites palmatus, Fragaria virginiana* and *Aralia nudicaulis* were collected systematically along the midline of each plot. Measurements of length of the longest leaflet of *A. nudicaulis*, length of the middle leaflet of *F. virginiana*, length of the petiole of *P. palmatus*, and width of the leaf of *P. palmatus* were made for each of the four leaves. Nomenclature follows Moss (1992).

When resampling trees and snags (1 and 2 yr old edges), I noted individual trees that had died and snags that had broken (a detectable change in canopy position, height, or category of broken top) since the previous year. The herb and shrub subplots were resampled each year within a few days of the original sampling date. On one transect, harvesting was done further into the forest than the pre-defined boundary making relocation of some subplots impossible; only data from the remaining herb subplot and shrub subplot were used for analysis. At the end of August, 1998, new shrub and sapling growth was measured within the shrub sub-plots along the transects next to the 2 yr old cutblocks for the three tallest 1 yr old *Populus* spp. saplings and the three longest extensions of new growth of *Rosa acicularis, Viburnum edule* and *Rubus idaeus*.

Data analysis

Response variables were plotted as a function of distance from the clearcut forest edge. Additional response variables included herb and shrub species richness (the total number of herb and shrub species per subplot), and total shrub and herb cover (sum of the cover of all species per subplot). Mortality rate for 1996/97 and 1997/98 was calculated as $r = 1 - (N_t/N_0)$ where N_t = # of living trees in the latter year and N_0 = # of living trees in the initial year (Sheil et al. 1995); trees that were cut in the 0m plots were excluded. Breakage rate for snags was calculated in a similar way using unbroken snags (snags that had not broken during the previous year).

To quantify distance of edge influence at the older edges (and for mortality and breakage rates, shrub and sapling growth at the younger edges), I used the critical values approach introduced in Chapter 2 which uses a randomization test to establish critical values of interior forest conditions, for comparison with average values of response variables at different distances from the edge. Data from the three greatest distances from the edge (100, 150 and 200m) were used to quantify interior forest conditions for each set of transects (adjacent to cutblocks of the same age). Randomization tests were performed using Visual Basic in Microsoft Excel 97 (Microsoft Corporation 1997) following these steps:

1A. For trees and CWM, one ‘interior forest’ response value from each transect was randomly selected (i.e. the value at 100, 150 or 200m) for a total of 10 or 8 (16 yr old edges) values.

1B. For shrubs and saplings, two values were randomly selected from the six ‘interior forest’ subplots (two each at 100, 150 or 200m) along each transect for a total of 20 or 16 (16 yr old edges) values.

1C. For herbs, three values were randomly selected from the nine subplots (three each at 100, 150 or 200m) along each transect for a total of 30 or 24 (16 yr old edges) values.

2. The mean of the data obtained in step 1 was calculated.

3. Steps 1 and 2 were repeated for a total of 5000 permutations.

Critical values were the 2.5 and the 97.5 percentiles of the 5000 permuted averages (2-tailed test, $\alpha=0.05$). Average values at different distances from the forest edge were considered to be significant if they were lower or higher than the critical values. Distance of edge influence was determined as the set of two or more consecutive distances which had values significantly different from values in interior forest.

I modified the critical values approach to evaluate changes in forest structure and composition from pre- to post-harvest (1996-97) and from the first to second year post-harvest (1997-98) and to consider the significance of these changes in the context of the interannual change observed in interior forest:

1A. For trees and CWM, one ‘interior forest’ plot from each transect was randomly selected (at 100, 150 or 200m).

1B. For shrubs and saplings, two subplots were randomly selected among the six ‘interior forest’ subplots (two each at 100, 150 or 200m) along each transect.

1C. For herbs, three subplots were randomly selected among the nine subplots (three each at 100, 150 or 200m) along each transect.

2. The difference (d) in response values between consecutive years was calculated (1996/97 or 1997/98) for each randomly selected plot or subplot.

3. A modified paired t-statistic (T) was performed on the differences from all plots or subplots:

$$T = \frac{\bar{d}}{\sqrt{\sum (d-\bar{d})^2}}$$

T = modified t-statistic

d = difference in values (1997-1996 or 1998-1997)

4. Steps 1-3 were repeated for a total of 5000 permutations.

The 5000 permuted T-values were used to establish a T-distribution for this data set. T-statistics were also calculated for the data at different distances from the forest edge, and then compared to the critical values which were the 2.5 and the 97.5 percentiles of the 5000 permuted T-values (2-tailed test, $\alpha=0.05$). Distance of edge influence for significant change near the clearcut edges in the first two years post-harvest was determined as the set of two or more consecutive distances with T-statistics that were significantly different than the T-distribution of randomized data from interior forest. This is different from DEI for average values that are significantly different from interior forest described above, and will be denoted as DEIc (DEI for change) to distinguish between them.

Points with missing values (missing data, or no breakage or height data available) were excluded from the randomization tests. If there were more than one or two missing values, all the values in the reference data set were pooled. Permuted averages were then calculated from random samples of 10 plots (twice and three times as many for the shrub and herb subplots respectively) from the pooled data.

RESULTS

Forest structure

Structural changes were evident at clearcut edges compared to interior forest. Distance of edge influence for change (DEIc) was based on significant change between years for the 1 and 2 yr old edges, and distance of edge influence for averages (DEI) was based on significant difference for the 5 and 16 yr old edges. Tree mortality rate was greater at the edge (DEIc=0-5m) than in the interior forest during the initial year post-harvest, but not the following year (Figure 3-1). The resulting decrease in live tree density in the first year was only significant at 0m (not shown). Most of the trees that died in the first year were in the sub-canopy and had smaller than average diameter (Table 3-1). Wind damage resulting in a major break accounted for almost half of the mortality, particularly in the 0m edge plots (5 of 7 trees); 23% of all the trees that died broke at the base. At the edges of 5 yr old (0m) and 16 yr old (0-5m) cutblocks, canopy tree density was significantly less than in interior forest (Table 3-2), likely reflecting harvesting in half of the 0m plot and past mortality in the 5m plot. There were also fewer sub-canopy trees at the 16 yr old edges (DEI=0-5m). Canopy cover was also lower near 16 yr old edges (DEI=5-10m). However, there was no trend in canopy cover at the 1, 2 (not shown), or 5 yr old edges (Table 3-2).

Although snag breakage at the edge was prominent in the first year following harvesting, trends of snag densities near older clearcut edges were not consistent. More snags broke at the edge than in interior forest in the first year post-harvest (DEIc=0-40m); but there was no distinct trend for breakage in the second year (Figure 3-1). Snag breakage rates were substantially higher than tree mortality rates. Most of the damaged snags were from the mid or sub-canopy; but about half of the canopy and sub-canopy snags were damaged (Table 3-1). Most of the damage was a major break, and 40% of all damaged snags broke at ground level. Snag densities at the older edges were significantly lower compared to interior forest at 0, 10 and 20m from the 5 yr old edges, but significantly greater at 5m from the 16 yr old edges (Table 3-2). Sixteen yr old edges also had significantly greater numbers of snags with major breaks and snags ≤5m compared to the interior (DEI=5-10m, not shown).

There were greater amounts of downed coarse woody material (CWM) near the edge after the first year, and at the 16 yr old edges. The number of pieces of CWM increased significantly near the edge (DEIc=0-10m) in the first year post-harvest, and then remained unchanged in the second year (Figure 3-2). There was no significant trend in CWM at the 5 yr old edges. At the 16 yr old edges, there were significantly greater amounts of CWM (DEI=0-20m).

The most dramatic change at clearcut forest edges was regeneration of *Populus* spp. by suckering. In the first year following harvest, sucker density increased at the edge (DEIc=0-60m, Figure 3-3A). There was also an increase in *Populus* spp. sapling cover at the edge in the first year (DEIc=0-10m, Figure 3-4A). There were further significant increases in sucker density in the second year post-harvest (DEIc=5-10m, Figure 3-3A), with sapling cover increasing more dramatically (DEIc=0-40m, Figure 3-4A). Also in the second year, sapling growth (average height of the three tallest saplings in each subplot) was greatest in the clearcut and then decreased along the edge-to-interior gradient (Figure 3-4B, DEI could not be determined due to inadequate sample size in the interior forest).

Populus spp. saplings were also a prominent feature of the older edges with greater total sapling densities near the 5 (DEI=0-60m) and 16 yr old edges (significant at 0 and 10m, Figure 3-3A). At the 16 yr old edges, the number of mid-canopy trees was higher at the edge (DEI=0-20m), resulting in a significantly greater total tree density (DEI=0-5m) and lower average tree diameter (DEI=0-10m, Table 3-2). Sapling recruitment continued near the older edges with significantly greater numbers of new (< 1 yr old) *Populus* spp. suckers near the 5 yr old edges (DEI=10-20m, Figure 3-3B). The same trend at the 16 yr old edges was not significant due to high densities in the interior forest. However, the number of new suckers was significantly lower right at (0m) the 5 and 16 yr old edges (0-5m, Figure 3-3B). Older edges had greater sapling cover (DEI=0-60m and 0-20m for the 5 and 16 yr old edges respectively, Figure 3-4A) and maximum height (DEI=0-20m for both 5 and 16 yr old edges, Figure 3-4C).

Overall, in the initial year following harvesting, greater tree mortality and snag breakage at the edge was accompanied by an increase in CWM (Table 3-3). Extensive suckering of the dominant *Populus* spp. trees at the clearcut edge began in the first year following harvest, with new recruitment still evident near the 5 yr old edges. However, the zone of new sucker recruitment was farther away from the edges of the older cutblocks. Sapling cover, which increased significantly near the edge during the first two years, was also high near the older edges. At the 5 yr old edges, the only major structural differences between the edge and interior were lower snag density and greater sapling cover. Increases in CWM and live tree density were prominent at the 16 yr old edges. Distance of edge influence varied considerably among structural components and age of clearcut edges.

Effects on understory composition

Changes in the abundance and composition of shrubs were detectable at all ages of clearcut edges. Total shrub cover decreased near the edge in the first (DEIc=0-5m) and second (DEIc=5-10m) years post-harvest (Figure 3-5A, Table 3-3). Shrub cover was also significantly lower 0-5m from the 5 yr old edges and in the 0m plots at the 16 yr old edges (Fig 3-5B). Shrub richness was significantly lower at the 5 yr old edges (DEI=0-5m, Appendix 3-1). Out of 15 common shrubs (frequency > 10% along at least one set of transects), 12 showed significant DEI for at least one age of edge (Table 3-4, see Appendix 3-1 for average values). Of these, I classified 4 as 'edge-positive' species and 5 as 'edge-negative' species on the basis that they had generally greater and lower cover near the edge, respectively (Table 3-4). Three other species (*Cornus stolonifera, Ribes oxyacanthoides, Salix* spp.) exhibited variable responses at the edges of cutblocks of different ages. There was no significant edge influence on *Alnus crispa, Corylus cornuta* or *Rosa acicularis*. In each of the first two years post-harvest, a few species decreased in cover near the edge with DEIc of up to 40m. At the 5 and 16 yr old edges, there was greater cover for some of the taller shrubs (*Amelanchier alnifolia, Prunus pensylvanica, Salix* spp.), while a couple of shorter species (*Viburnum edule, Ribes triste*) had lower cover. Only one 'edge-negative' species, *V. edule*, had consistently lower cover near the edges of clearcuts of all ages (DEI up to 60m, Figure 3-6A). *Rubus idaeus* had significantly lower new growth in the second year post-harvest 5m from the edge compared to the interior (Figure 3-7). Shrub growth of *Rosa acicularis* and *Rubus idaeus* was significantly greater in the cutblock compared to the interior. There was no significant trend for *Viburnum edule.*

Edge influence on overall herb cover and richness was limited. Total herbaceous cover decreased at the edge (0m) in the first year post-harvest and then increased in the second year (Table 3-5). At the 16 yr old edges, total herb cover was higher at the edge (DEI=0-5m). Herb richness was also significantly greater at the 16 yr old edges (DEI=0-5m, Appendix 3-1). Herb richness increased significantly only at 0m in the first year post-harvest.

Out of 28 common herb species (frequency > 10% along at least one set of transects), 21 showed a significant edge influence for at least one time post-harvest (Table 3-5, see Appendix 3-1 for average values). Seven common species showed no edge influence: *Actaea rubra, Cornus canadensis, Equisetum arvense, Fragaria virginiana, Rubus pubescens,* and *Thalictrum venulosum*. Between pre-harvest and the first year post-harvest, three species with significant DEIc increased in cover at the edge, and none with a significant DEIc decreased in cover. Three species with significant DEIc decreased in cover near the edge between the first and second years post-harvest. At the older edges, many herb species had greater cover (significant DEI for 7 and 12 species at the 5 and 16 yr old edges, respectively); and only some had lower cover (significant DEI for 5 species each at the 5 and 16 yr old edges, respectively). Distances of edge influence for herbs at all clearcut edge ages varied considerably (from 0-5 to 0-60m), and did not always start at 0m (e.g. DEI of 10-20m). I identified 11 'edge-positive' species and only 6 'edge-negative' species (with generally greater and lower cover near the edge, respectively); 4 other species exhibited variable responses at the edges of cutblocks of different ages. Almost all of the 'edge-positive' species had greater cover near the 5 or 16 yr old edges, while only two of these increased in cover in the first year post-harvest (*Aster conspicuus* and *Lathyrus ochroleucus* - Figure 3-6B). Of the 'edge-negative' species, only *Orthilia secunda* and *Mitella nuda* decreased in cover with a significant DEIc in the first two years post-harvest. *Mitella nuda* also had lower cover at both the 5 and 16 yr edges (DEI=0-60 and 0-40m, Figure 3-6C). Leaf sizes showed a few significant decreases in the first and second years post-harvest (Appendix 3-1). There were virtually no significant trends in flowering at edges of cutblocks of all edges (Appendix 3-1).

Most significant changes in forest structure and composition occurred within 20m of the edge in the first year, and between 5 and 20m from the edge in the 2nd year (Figure 3-8A). At the 5 and 16 yr old edges, most response variables were significantly different from interior forest within 20m of the edge (Figure 3-8B). Thus, DEI based on the majority of response variables was relatively constant for different ages of clearcut edges; although there were more response variables with significant DEI at the older edges than at the more recent edges.

Vegetation structure in the adjacent cutblocks

The plots in the cutblocks provided information on remnant vegetation, regeneration, and overall forest structure in the harvested areas. The general harvesting practice is to clearcut, leaving some residual live trees (up to 5% of standing volume as single trees and small clumps). In the plots in the 1-2 yr old cutblocks, almost all trees were harvested and very few snags remained standing except for two small remnant unharvested forest patches with three trees each (Table 3-6). The amount of CWM left after harvesting was high compared to in interior forest (Table 3-6, Figures 3-2 to 3-5 for corresponding data for interior forest). Most suckers in cutblocks appeared in the first year, with further increases in density, cover and height by the second year; 86% of suckers were *Populus tremuloides* with some *P. balsamifera*. Shrubs either left intact after harvesting or regenerated from existing roots increased in cover between the first and second years post-harvest. *Rubus idaeus* had the largest proportional increase in average cover from the first to the second year post-harvest from 2 to 7% (compared to no change in interior forest).

No trees remained in the 5 yr old cutblock plots and only one 2m snag, but there was substantial CWM (significantly greater than in interior forest). Although total *Populus* spp. sapling density was lower than the younger cutblocks, sapling cover and height were greater. Saplings were mostly *P. tremuloides* (75%), with some *P. balsamifera* and *Betula papyrifera*. Total shrub cover was only slightly less than in interior forest.

Many of the regenerated suckers in the 16 yr old cutblocks were classified as trees, resulting in a significantly greater live tree density than in interior forest (Table 3-6, density in interior forest = 1100 per ha). Sapling density, cover and height were still greater than in interior forest, but total shrub cover was, as for the 5 yr old cutblocks, slightly lower. *Picea glauca* that was planted in the clearcuts was 2-4m tall; there were no *P. glauca* in the adjacent interior forest. Half of the saplings were *Populus tremuloides*, with some *P. balsamifera* (25%), *Betula papyrifera* and *Picea glauca*. In these older cutblocks, there was no evidence of any remnant trees or snags from prior to harvesting. Unlike the younger clearcuts, there was no CWM, presumably because all trees and logs were removed during harvesting.

DISCUSSION

Forest structure dynamics

Increased tree mortality and snag breakage were significant factors in the dynamics of forest structure at the studied created edges, resulting in increased downed coarse woody material (CWM) and lower canopy cover. Recently created edges in Douglas-fir forests (Chen et al. 1992) and in tropical forests (Williams-Linera 1990b, Laurance 1991) also had fewer trees and/or lower canopy cover. Tree mortality rates were considerably higher at the clearcut edges in the boreal forest compared to those 50-60m from edges in tropical rain forest fragments (4%, Laurance et al. 1998). However, distance of edge influence (DEI) for mortality rate, canopy cover and canopy tree density were narrow (0-10m or less), compared to other forests (335m for mortality rate in Laurance et al. 1998, 60-120m for tree density and 44m for canopy cover in Chen et al. 1992). Distance of edge influence for snag damage in the first year (0-40m) possibly reflected the zone of increased wind turbulence, which is generally considered to be twice the canopy height. However, increased wind effects in other forests have been observed up to a distance of 5-6 tree heights or more (Chen et al. 1995 and references therein). Wind may not penetrate as deeply into forests with a dense understory (Chen et al. 1995), such as in the *Populus*-dominated boreal forest.

Possible causes for increased tree mortality at created edges include: increased moisture demand due to greater evapotranspiration (Ranney et al. 1981, Kapos 1989), sudden exposure to light (Laurance et al. 1998), and increased wind exposure (Chen et al. 1992, Murcia 1995, Laurance et al. 1998). Since *Populus balsamifera* and *P. tremuloides* are early successional trees adapted to conditions in open areas, changes in temperature and light conditions at the edge are unlikely to kill trees. Most likely, the observed mortality and snag breakage at edges resulted from increased wind turbulence (DeWalle 1983, Laurance et al. 1998). Live and dead trees broken during the first year were probably those most susceptible to wind damage, since there was much less subsequent mortality and breakage in the following year. In the first year, most of trees that died were broken (from wind or possibly from harvesting operations, Chen et al. 1992) rather than left standing (as in a tropical forest, Ferreira and Laurance 1997). Most trees that died were sub-canopy trees that are susceptible to windthrow because of their tall, thin shape (high height:diameter ratio, Ruel 1995). Smaller trees were also more affected by edge influence in Douglas-fir forest (Chen et al. 1992). Death of sub-canopy trees immediately following harvesting could have contributed to the lower canopy tree densities at the 5 and 16 yr old edges.

Snag breakage at edges following harvest could potentially result in a decrease in total availability of snags or of tall snags, or an increase in the availability of shorter snags with major breaks. At the 16 yr old clearcut edges, there were greater numbers of snags with major breaks and snags <5m height. Decreases in total snag availability could be offset by recruitment of snags from tree mortality. Higher snag density 5m in from the 16 yr old edges may have been the result of increased mortality in the years following edge creation. Other studies have reported more snags at edges in 10-15 yr old Douglas-fir stands (Chen et al. 1992) and maintained edges (Young and Mitchell 1994). Additionally, regeneration of *Populus* spp. saplings in the 16 yr old cutblocks to a height of up to 10m could have diminished wind effects at the edge and thus reduced blowdown of snags over time. At maintained edges, however, regeneration in the adjacent area is suppressed, allowing continued wind turbulence and a constant tree damage rate for at least two decades (Laurance et al. 1998), until the eventual formation of a sidewall of regrowth reduces wind effects (Brothers and Spingarn 1992).

Structural changes have several potential impacts on the edge environment. Although snag breakage did not result in an overall decrease in snag density, snag availability would be more dynamic at edges. An effect of lower canopy tree density and canopy cover is increased exposure to light and wind, effectively extending the structural edge (e.g. up to 10m from the 16 yr old clearcut edges). Another major consequence of tree mortality and snag breakage is an increase in CWM, detectable after the first year post-harvest and at the 16 yr old edges. Chen et al. (1992) also found higher amounts of CWM at 10-15 yr old Douglas-fir clearcut edges. The lack of this trend at the 5 yr old clearcut edges in my study may have been due to low amounts of CWM prior to harvest. Low live tree and snag densities suggest that these edges also experienced greater snag breakage and mortality, which could have resulted in an increase in CWM since edge creation. At the 16 yr old edges, increased CWM from tree mortality could be partially the result of crown asymmetry of trees growing at the edges. Tree canopies can develop away from neighbouring trees (as at gap edges), leading to crown asymmetry and more frequent treefalls (Young and Hubbell 1991).

With the removal of the adjacent forest and increased tree mortality at the edge, *Populus* spp. regenerated rapidly at clearcut edges through suckering. This effect extended well into the forest with a DEI of up to 60m in the first year and at 5 yr old edges. Increased tree recruitment has been observed at many types of edges, as evidenced by greater seedling (Chen et al. 1992), sapling or tree densities (e.g. Wales 1972, Ranney et al. 1981, Young and Mitchell 1994). For *Populus balsamifera* and *P. tremuloides*, regeneration after harvesting is almost exclusively through suckering from a well-developed underground clonal rhizome system, rather than seedling establishment. At clearcut edges, removal of apical dominance likely initiates suckering from the roots of harvested trees; this process could be accelerated by increased soil temperature (Maini and Horton 1966, Steneker 1974). Continued tree mortality may have produced ongoing suckering near the edge after two and five years. Shade from saplings which established at the edge in the first year may have precluded further suckering in subsequent years.

Saplings grew rapidly after establishment. After the first year, sapling cover and maximum height at the edge were greater than in interior forest. Distance of edge influence for sapling cover was greatest at the 5 yr old edges (0-60m). At the 16 yr old edges, some of the saplings had become small trees (diameter at breast height ≥5cm). However, compared to the adjacent cutblocks, sapling density and cover were considerably less at forest edges. Growth and height were similar at edges and in the clearcut, except for 16 yr old edges. Lower cover at the edge compared to in cutblocks could be due to fewer saplings, and/or fewer resources for growth due to competing trees.

Effects on understory composition

Both the initial decrease in total shrub cover at clearcut edges and the reduced shrub cover at the 5 yr old edges were unexpected. Edges are often characterized by greater abundance (Matlack 1993, Young and Mitchell 1994) or growth (Williams-Linera 1990a) of shrubs. I observed greater shrub growth (stem elongation) of *Rosa acicularis* and *Viburnum edule* in the clearcut where there was no residual canopy; however, cover of these same species decreased near the edge. Although initial decreases in shrub cover could be accounted for by damage during harvest operations, shrub cover continued to decrease in the second year up to 10m from the edge. Lower shrub cover could have been caused by herbivore browsing and/or competition from *Populus* spp. suckers. Deer and snowshoe hares could have browsed the palatable regrowth more intensively at the edge while still under the shelter of the adjacent forest (K. Ozeroff and S. E. Macdonald unpublished data). Alternatively, I hypothesize that the decrease in shrub cover was due to competition by new *Populus* spp. suckers that could have responded more quickly to edge influence; once the saplings grew taller than the shrubs, shrub cover may have been reduced due to shading. In the clearcut, both shrubs and *Populus* spp. were damaged by harvesting and therefore responded with increased growth by taking advantage of increased light. At the edge, only *Populus* spp. responded more quickly following harvesting by suckering from the extensive rhizome system, and could therefore gain the competitive advantage to take advantage of increased light.

Most individual shrub species followed the same trend as total shrub cover, with lower abundance at the edge. I found that *Viburnum edule*, for example, showed consistently lower abundance at all edges, and might thus be considered an indicator of negative edge influence. Even *Rubus idaeus*, commonly found on disturbed sites, was classified as an 'edge-negative' species due to a significant decrease in cover near the edge in the second year, and had lower growth 5m from the edge. I speculate that *R. idaeus* was shaded by *Populus* spp. suckers. In the clearcut where *R. idaeus* increased in abundance in the second year, competition would be only from regenerating vegetation, and not any pre-existing vegetation.

The herb layer also seemed to be suppressed by regeneration of *Populus* spp. at the edge. There was no dense herbaceous understory as predicted (Ranney et al. 1981) for the first stage of edge development. Instead, the only trend in total herbaceous cover was an increase and decrease at 0m in the first and second years, respectively, and greater abundance at the 16 yr old edges. In the mixedwood boreal forest, response to greater light at the edges may have been too slow relative to the onset of shading from rapidly regenerating *Populus* spp.

Most individual herb species did show significant responses to edge influence, particularly at the older edges. Herbaceous understory composition may have responded to changes in microclimate (including light, nutrient availability, moisture), structure (increased *Populus* spp. suckering) or both. Over time, with decreased canopy and shrub cover, and self-thinning of saplings, light levels at the herbaceous layer may have increased, resulting in the increased abundance of some herb 'edge-positive' species. In gaps in young eastern boreal forest dominated by *Populus tremuloides* and *Betula* *papyrifera*, understory composition did not change drastically in the first four years; but there was an increase in cover of some early successional understory species and an increase in species richness (De Grandpré and Bergeron 1997).

Previous studies have found contrasting results of edge influence on individual herb species. Shade-tolerant interior species have had lower (Ranney et al. 1981, Young and Mitchell 1994) or similar (Williams-Linera 1990b) abundance at edges compared to interior forest, and shade-intolerant species have been more abundant at some edges (Wales 1972, Ranney et al. 1981, Palik and Murphy 1990), but not others (Williams-Linera 1990b). In this study, two species that were previously considered to be shade-tolerant 'understory obligates' (*Aralia nudicaulis*, *Linnaea borealis*, Lieffers 1995) were surprisingly classified as 'edge-positive' and 'other', suggesting that light conditions underneath the sapling layer at the edge could be similar to or even lower than conditions in interior forest. I did, however, classify another 'understory obligate', *Mitella nuda* (Lieffers 1995), as an 'edge-negative' species. These interior forest species could be responding in different ways to the changes in forest structure and microclimatic conditions at the clearcut edges. *Mitella nuda,* the most negatively affected at the older edges, was also less abundant at lakeshore forest edges (Chapter 2), and therefore could be considered one of the most susceptible boreal forest species to edge influence. The pioneer grass species, *Calamagrostis canadensis*, had greater cover only at the 5 yr old edges where shrub cover was particularly low. This was unexpected as *Calamagrostis canadensis* often dominates the herbaceous cover in clearcuts (Lieffers et al. 1993), has greater cover with increased light (Lieffers and Stadt 1994), and is a serious competitor for regeneration of *Populus* spp. and *Picea glauca* (Lieffers et al. 1993). *Epilobium angustifolium* which also has increased cover with greater light (Lieffers and Stadt 1994), had greater cover at the 16 yr old edges.

Greater diversity at edges is a fundamental principle in ecology (Wiens 1976, Harris 1988), and greater species richness has been generally found at maintained created edges (Ranney et al. 1981, Fraver 1994, Fox et al. 1997). I found an increase in herb richness only at 0m in the first year and greater herb richness at the edges of 16 yr old cutblocks. Ecotones or edges may have higher diversity only if they are stable for long periods (Risser 1995). The general lack of edge influence on species richness at the younger edges may also be an effect of suppression of the herb layer through *Populus* spp. suckering. Unlike some maintained edges (Brothers and Spingarn 1992, Fraver 1994), I saw no invasion of non-native species at these clearcut edges, although non-native and non-forest species are common along maintained edges of right-of-ways in the study area (pers. obs.). Only one introduced species, *Taraxacum officinale*, was found in only one plot in interior forest. *Populus* spp. regeneration, or a lack of an appropriate germination substrate (as in Williams-Linera 1990a) may have limited invasion by weedy species.

Synthesis and implications to management

The 1, 2, 5 and 16 yr old clearcut edges represent a chronosequence from which inferences on edge development can be made. Edge influence might also differ among the different data sets due to other reasons such as location and harvesting practise. However, I always compared values at the edge to values in the adjacent interior forest, thus providing a 'control' for determining edge influence.

I propose a general model of forest succession at clearcut edges in the aspen-dominated boreal forest (Figure 3-9). After edge creation, increased exposure to wind results in damage to live trees and snags, increasing CWM. Opening of the canopy and release from apical dominance induces prolific suckering of *Populus* spp. near the edge. Shrubs are unable to respond immediately to changes in microclimate, and thus they decrease in cover as a result of competition from new suckers. As suckering continues, cover increases, accompanied by a further decrease in overall shrub cover. Over time, canopy trees continue to fall at edges, creating an accumulation of CWM near the edge. Sucker recruitment continues near the edge for at least five years. Saplings grow and self-thin; by 16 yr some develop into mid-canopy trees. Competition from suckers keeps shrub cover low even after 5 yr. Consequently, many understory herbs increase in cover by 5 and/or 16 yr after relatively few changes in understory composition in the initial post-harvest years. *Mitella nuda*, a key 'edge-negative' species, is virtually eliminated from the edge community.

Even after 16 yr, clearcut edges in the boreal forest were still in the first stage of development prior to canopy closure (Ranney et al. 1981, Matlack 1994), with a dense understory formed by increased sapling density. I predict that as trees in the adjacent cutblocks approach the height of the uncut forest canopy, edges will have increased tree density, more CWM, decreased abundance of shrubs (particularly *Viburnum edule*), and different (greater or lower) abundances of some herbs (such as *Lathyrus ochroleucus*) compared to the interior of the mature forest. There will likely be no species replacement except perhaps the disappearance (and possible reappearance after canopy closure) of a few understory edge-negative forest species such as *Mitella nuda*.

At the forest edge, the plant community responds to gradients of increased light, wind and related microclimatic variables in both space and time (Figure 3-10). Vegetation changes at the edge following harvest result from: a time lag in responding to different microclimatic conditions, changing light and wind accompanying regrowth in the adjacent clearcut and at the edge, or both. Microclimatic gradients diminish through time as saplings increase in height, narrowing the window between the saplings and the canopy, and shading the understory. Concurrently, edge influence in the understory takes time to develop, particularly in boreal forests with shorter growing seasons and low productivity, and may persist following relaxation of edge-induced gradients. Fast regeneration of the dominant species at the edge and in the clearcut, coupled with slow response of the understory, results in minimal edge response of the understory before microclimatic gradients dissipate. The adjacent forest stand also develops at the same time, which could affect the contrast between the edge community and interior forest.

With time, edge influence can penetrate farther into the forest, widening the effective edge, particularly if there is a continued decrease in canopy trees at the edge. However, I only detected this effect in the increase in DEI for *Populus* spp. sapling cover up to 5 yr old edges, and in the movement of DEI further into the forest for *Populus* spp. sapling recruitment after the first year. Edge influence can also diminish with time as vegetation growth at the edge weakens microclimatic gradients (Forman 1997). At the studied clearcut edges, I saw little evidence of reduced edge influence on herb species at older edges compared to younger ones, a trend that was observed by Matlack (1994). Over time, the edges I studied will become sheltered by regeneration in the adjacent cutblock, rather than the formation of a side canopy of woody vegetation as for maintained edges (Wales 1972, Lovejoy et al. 1986, Williams-Linera 1990b). Indeed, reduction of edge influence because of regeneration could prevent the formation of a side canopy. Trends in forest structure and composition along the edge-to-interior gradient may dissipate after the regenerating forest reaches the canopy height of the adjacent forest. In a two-pass harvesting system, however, the residual forest would normally be harvested before that time.

Edge influence varies with ecosystem type, time since disturbance and maintenance at the edge. Not surprisingly, responses to edge influence at these clearcut edges in the boreal forest differed from those found for other ecosystems. Unlike tropical forests and other temperate forests, regeneration of the dominant *Populus* spp. trees at the edge and in the clearcut generally suppressed growth of the understory. At clearcut edges in the *Populus*-dominated boreal forest, edge influence for most response variables extended 20m into the forest, although some significant effects were detected at greater distances. My estimate of DEI falls within the range of DEI reported from older temperate and tropical maintained forest edges (20m, Wales 1972; 15m, Ranney et al. 1981; 5-45m, Palik and Murphy 1990; 4-16m, Fox et al. 1997). However, it falls well below DEI results from recent tropical forest edges (85-335m, Laurance et al. 1998) and recent clearcut edges in Douglas-fir forests (16-137m, Chen et al. 1992), particularly for structural damage.

Edge influence may not be as extensive or dramatic in the boreal forest since it is a disturbance-adapted ecosystem with many inherent edges, and a relatively open, shorter, deciduous canopy. In most ecosystems, edges resemble an early stage in succession (Whitney and Runkle 1981). However, the disturbance-adapted forest stands in my study area already contained a lot of early successional species including the dominant tree. It has been hypothesized that regions with more frequent natural disturbance, like the boreal forest, are more resistant to fragmentation (Bierregaard et al. 1997). For example, the magnitude of fragmentation and edge effects on bird communities is relatively small in this area (Schmiegelow et al. 1997, Song 1998), perhaps due in part to the small DEI of forest structure and composition at clearcut edges.

Based on my results (DEI=20m), square forest fragments of 40, 100 and 500 ha would be composed of 12, 8 and 4% edge habitat, respectively. Irregularly shaped 40, 100 and 500 ha fragments might have 34, 21 and 10% edge habitat respectively (Core-Area Model, shape index of 3, Laurance and Yensen 1991). These estimates are considerably lower than those from other studies which showed 30-85% edge habitat for fragments larger than 200 ha (Laurance 1991, Chen et al. 1996, Ferreira and Laurance 1997, Laurance et al. 1998). Given that forest harvesting in my study area consists of irregularly shaped 40 ha blocks in a two pass system, the proportion of the area with forest structure and composition significantly affected by edge influence is still substantial, up to one-third. Edge influence on forest structure and composition is a significant and dynamic component on the harvested boreal forest landscape that persists for at least 16 years, and should be considered in forest management (see Chapter 5).

LITERATURE CITED

Bierregaard, R. O., Jr., W. F. Laurance, J. W. Sites Jr., A. J. Lynam, R. K. Didham, M. Andersen, C. Gascon, M. D. Tocher, A. P. Smith, V. M. Viana, T. E. Lovejoy, K. E. Sieving, E. A. Kramer, C. Restrepo, and C. Moritz. 1997. Key priorities for the study of fragmented tropical ecosystems. Pages 515-525 *in* W. F. Laurance and R. O. Bierregaard Jr., editors. Tropical forest remnants: Ecology, management and conservation of fragmented communities. The University of Chicago Press, Chicago.

Brothers, T. S., and A. Spingarn. 1992. Forest fragmentation and alien plant invasion of central Indiana old-growth forests. Conservation Biology **6**:91-100.

Chen, J., J. F. Franklin, and T. A. Spies. 1992. Vegetation responses to edge environments in old-growth Douglas-fir forests. Ecological Applications **2**:387-396.

Chen, J., J. F. Franklin, and T. A. Spies. 1995. Growing-season microclimatic gradients from clearcut edges into old-growth douglas-fir forests. Ecological Applications **5**:74-86.

Chen, J., J. F. Franklin, and J. S. Lowe. 1996. Comparison of abiotic and structurally defined patch patterns in a hypothetical forest landscape. Conservation Biology **10**:854-862.

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

DeWalle, D. R. 1983. Wind damage around clearcuts in the ridge and valley province of Pennsylvania. Journal of Forestry **81**:158-159, 172.

Esseen, Per-A. 1994. The mortality patterns after experimental fragmentation of an old-growth conifer forest. Biological Conservation **68**:19-28.

Ferreira, L. V., and W. F. Laurance. 1997. Effects of forest fragmentation on mortality and damage of selected trees in central Amazonia. Conservation Biology **11**:797-801.

Forman, R. T. T. 1997. Land mosaics: The ecology of landscapes and regions. Cambridge University Press, Cambridge.

Fox, B. J., J. E. Taylor, M. D. Fox, and C. Williams. 1997. Vegetation changes across edges of rainforest remnants. Biological Conservation **82**:1-13.

Fraver, S. 1994. Vegetation responses along edge-to-interior gradients in the mixed hardwood forests of the Roanoke River basin, North Carolina. Conservation Biology **8**:822-832.

Harris, L. D. 1988. Edge effects and conservation of biotic diversity. Conservation Biology **2**:330-332.

Kapos, V. 1989. Effects of isolation on the water status of forest patches in the Brazilian Amazon. Journal of Tropical Ecology **5**:175-185.

Kapos, V., E. Wandelli, J. L. Camargo, and G. Ganade. 1997. Edge-related changes in environment and plant responses due to forest fragmentation in central Amazonia. Pages 33-44 *in* W. F. Laurance and R. O. Bierregaard Jr., editors. Tropical forest remnants: Ecology, management and conservation of fragmented communities. The University of Chicago Press, Chicago.

Laurance, W. F. 1991. Edge effects in tropical forest fragments: application of a model for the design of nature reserves. Biological Conservation **57**:205-219.

Laurance, W. F., and E. Yensen. 1991. Predicting the impacts of edge effects in fragmented habitats. Biological Conservation **55**:77-92.

Laurance, W. F., L. V. Ferreira, J. M. Rankin-de Merona, and S. G. Laurance. 1998. Rain forest fragmentation and the dynamics of Amazonian tree communities. Ecology **79**:2032-2040.

Lee, P. C., S. Crites, K. Sturgess, and J. B. Stelfox. 1995. Changes in understory composition for a chronosequence of aspen mixedwood stands in Alberta. Pages 63-80 *in* J. B. Stelfox, editor. Relationships between stand age, stand structure and biodiversity in aspen mixedwood forests in Alberta. Jointly published by Alberta Environment Centre, Vegreville, Alberta, and Canadian Forest Service, Edmonton, Alberta, Canada.

Lieffers, V. J. 1995. Ecology and dynamics of boreal understory species and their role in partial-cut silviculture. Pages 33-39 *in* C. R. Bamsey, editor. Innovative silviculture systems in boreal forests. Clear Lake Ltd., Edmonton, Canada.

Lieffers, V. J., S. E. Macdonald. and E. H. Hogg. 1993. Ecology of and control strategies for Calamagrostis canadensis in boreal forest sites. Canadian Journal of Forest Research **23**:2070-2077.

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

Lovejoy, T. E., R. O. Bierregaard, A. B. Rylands, J. R. Malcolm, C. E. Quintela, L. H. Harper, K. S. Brown, A. H. Powell, G. V. N. Powell, H. O. R. Schubart, and M. B. Hays. 1986. Edge and other effects of isolation on Amazon forest fragments. Pages 257-285 *in* M. E. Soule, editor. Conservation Biology. Sinauer Associates, Inc, Sunderland, Massachusetts.

Maini, J. S., and K. W. Horton. 1966. Vegetative propagation of *Populus* spp. I. Influence of temperature on formation and initial growth of aspen suckers. Canadian Journal of Botany **44**:1183-1189.

Matlack, G. R. 1993. Microenvironment variation within and among forest edge sites in the eastern United States. Biological Conservation **66**:185-194.

Matlack, G. R. 1994. Vegetation dynamics of the forest edge - trends in space and successional time. Journal of Ecology **82**:113-123.

Moss, E. H. 1992. Flora of Alberta. Second Edition. Revised by J. G. Packer. University of Toronto Press, Toronto, Canada.

Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. Trends in Ecology and Evolution **10**:58-62.

Palik, B. J., and P. G. Murphy. 1990. Disturbance versus edge effects in sugar-maple/beech forest fragments. Forest Ecology and Management **32**:187-202.

Ranney, J. W., M. C. Bruner, and J. B. Levenson. 1981. The importance of edge in the structure and dynamics of forest islands. Pages 67-95 *in* R. L. Burgess and D. M. Sharpe, editors. Forest Island Dynamics in Man-Dominated Landscapes. Springer-Verlag, New York.

Risser, P. G. 1995. The status of the science examining ecotones. BioScience **45**:318-325.

Ruel, Jean-C. 1995. Understanding windthrow: silvicultural implications. The Forestry Chronicle **71**:434-445.

Schmiegelow, F. K. A., C. S. Machtans, and S. J. Hannon. 1997. Are boreal birds resilient to forest fragmentation? An experimental study of short-term community responses. Ecology **78**:1914-1932.

Sheil, D., D. F. R. P. Burslem, and D. Alder. 1995. The interpretation and misinterpretation of mortality rate measures. Journal of Ecology **83**:331-333.

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. dissertation, University of Alberta, Edmonton, Canada.

Steneker, G. A. 1974. Factors affecting the suckering of trembling aspen. The Forestry Chronicle **50**:32-34.

Wales, B. A. 1972. Vegetation analysis of north and south edges in a mature oak-hickory forest. Ecological Monographs **42**:451-471.

Whitney, G. G., and J. R. Runkle. 1981. Edge versus age effects in the development of a beech-maple forest. Oikos **37**:377-381.

Wiens, J. A. 1976. Population responses to patchy environments. Annual Review of Ecology and Systematics **7**:81-120.

Williams-Linera, G. 1990a. Origin and early development of forest edge vegetation in Panama. Biotropica **22**:235-241.

Williams-Linera, G. 1990b. Vegetation structure and environmental conditions of forest edges in Panama. Journal of Ecology **78**:356-373.

Young, T. P., and S. P. Hubbell. 1991. Crown asymmetry, treefalls, and repeat disturbance of broad-leaved forest gaps. Ecology **72**:1464-1471.

Young, A., and N. Mitchell. 1994. Microclimate and vegetation edge effects in a fragmented podocarp-broadleaf forest in New Zealand. Biological Conservation **67**:63-72.

TABLE 3-1. Number of live trees and snags by canopy position, and average diameter: pre-harvest total (1996), and those that died or were damaged during the first year post-harvest (1996-97); also, condition of broken top for pre-harvest and post-harvest snags as a result of mortality or snag damage during the first year post-harvest. Values are totals (except for average diameter) for all 90 plots (5 x 20m) along the ten transects.

	Live trees		Snags	
	Total 1996	Died 1996-97	Total 1996	Damaged 1996-97
Total # trees or snags	1049	26	576	156
# canopy trees or snags	676	2	31	14
# sub-canopy trees or snags	180	16	78	40
# mid-canopy trees or snags	193	8	241	78
# snags ≤ 5m tall	-	-	226	24
Average diameter (cm)	16.3	10.6	9.2	10.3
# snags broken at ground level	-	6	-	62
# snags with no broken top	-	12	230	-
# snags with slight broken top	-	2	138	58
# snags with major broken top	-	12	208	98

TABLE 3-2. Density of all trees, canopy trees, sub-canopy trees, mid-canopy trees and snags, average tree diameter, and canopy cover along the edge-to-interior gradient for transects perpendicular to 5 yr old and 16 yr old clearcuts. Shaded values are significantly different from values in interior forest (by randomization test). Data are means ± 1 SE.

		Distance from forest edge (m)						
		0	5	10	20	40	60	Interior
5 yr	All trees (# per ha)	700 ± 130	1090 ± 200	1280 ± 290	1160 ± 190	1120 ± 240	1250 ± 180	1140 ± 90
	Canopy trees (# per ha)	410 ± 70	710 ± 140	690 ± 90	890 ± 140	680 ± 110	860 ± 120	760 ± 70
	Sub-canopy trees (# per ha)	130 ± 70	100 ± 50	270 ± 90	130 ± 40	110 ± 50	150 ± 60	140 ± 20
	Mid-canopy trees (# per ha)	160 ± 40	280 ± 90	320 ± 160	140 ± 50	330 ± 120	240 ± 70	240 ± 50
	Snags (# per ha)	450 ± 50	530 ± 80	400 ± 80	460 ± 110	660 ± 110	480 ± 100	610 ± 60
	Diameter (cm)	18 ± 2	19 ± 2	19 ± 2	21 ± 1	18 ± 1	19 ± 1	19 ± 1
	Canopy cover (%)	78 ± 4	82 ± 2	81 ± 3	80 ± 3	80 ± 3	81 ± 4	81 ± 2
16 yr	All trees (# per ha)	1240 ± 150	1350 ± 170	1010 ± 140	1300 ± 220	1160 ± 270	1180 ± 150	1040 ± 70
	Canopy trees (# per ha)	200 ± 50	500 ± 110	560 ± 110	840 ± 200	750 ± 170	800 ± 180	680 ± 80
	Sub-canopy trees (# per ha)	20 ± 20	60 ± 40	160 ± 60	120 ± 60	210 ± 70	150 ± 70	180 ± 30
	Mid-canopy trees (# per ha)	1010 ± 180	790 ± 230	290 ± 120	340 ± 120	200 ± 80	220 ± 100	190 ± 50
	Snags (# per ha)	320 ± 70	790 ± 170	610 ± 110	620 ± 100	550 ± 130	420 ± 100	490 ± 90
	Diameter (cm)	10 ± 1	15 ± 2	17 ± 1	17 ± 2	19 ± 1	17 ± 1	19 ± 1
	Canopy cover (%)	84 ± 4	75 ± 3	78 ± 4	80 ± 3	7 ± 4	82 ± 2	82 ± 1

TABLE 3-3. Summary of distance of edge influence results for structural changes at the edge for the 1st and 2nd yr post-harvest, and for average values of structural components for edges adjacent to 5 and 16 yr old cutblocks. Numbers delimit DEI as a range of two or more consecutive distances with values or changes that were significantly different from average values or changes in interior forest. Numbers in brackets indicate single distances near the edge with changes or average values that were significantly different from changes or average values in interior forest. Values at different distances from the edge and in interior forest are in Figures 3-1 to 3-5 and Table 3-2.

	Changes		Average values	
	1st yr	2nd yr	5 yr old	16 yr old
Tree mortality (greater mortality rate for changes, lower canopy tree density for average values)	0-5	ns	(0)	0-5
Snag damage (greater damage rate for changes, lower snag density for average values)	0-40	(40)	(0)10-20	ns
Greater abundance of coarse woody material	0-10	ns	ns	0-20
Populus spp. sapling recruitment (increases in sapling density for changes, greater density of new saplings for average values)	0-60	5-10	10-20	ns
Greater *Populus* spp. sapling cover	0-10	0-40	0-60	0-20(60)
Greater mid-canopy tree density	ns	ns	ns	0-20
Lower total shrub cover	0-5	5-10	0-5	(0)

ns = No significant DEI.

TABLE 3-4. Cover of shrub species at clearcut edges (+/- = increase/decrease relative to changes in interior forest for the 1st and 2nd yr, and greater/less than in interior forest for the 5 and 16 yr old edges) and distance of edge influence (DEI). Numbers delimit DEI as a range of two or more consecutive distances with values or changes that were significantly different from average values or changes in interior forest. Numbers in brackets indicate single distances near the edge with changes or average values that were significantly different from changes or average values in interior forest. Species are subdivided into 'edge-positive' species (with mostly increases or greater cover at edges) and 'edge-negative' species (with mostly decreases or lower cover at edges) and other species (with different responses at edges at different times post-harvest). Only species with significant DEI are included. Average values are tabulated in Appendix 3-1.

	Changes				Average values			
	1st yr		2nd yr		5 yr old		16 yr old	
	+/-	DEIc (m)	+/-	DEIc (m)	+/-	DEI (m)	+/-	DEI (m)
Edge-positive species								
Amelanchier alnifolia	ns		ns		+	10-60	+	(5)
Lonicera dioica	ns		+ -	(0) (5,20,60)	ns		+	5-10
Prunus pensylvanica	+	(0,20)	ns		+	0-60	+	(10)
Symphoricarpos albus (could include *S. occidentalis*)	-	0-5	+	(0)	+	20-40	+	0-5
Edge-negative species								
Alnus rugosa	+	(10)	ns		-	20-40	ns	
Lonicera involucrata	-	(40)	-	0-10	-	(5,20,60)	-	(0)40-60
Ribes triste	ns		-	(5)	- +	0-10 40-60	ns	
Rubus idaeus	ns		-	5-20(60)	-	(5)	-	(5)20-40
Viburnum edule	-	0-40	- +	(10) 40-60	-	0-5	-	0-5
Other species								
Cornus stolonifera	-	0-20	+	(0)	ns		+	0-20(60)
Ribes oxyacanthoides[1]	-	0-5(20)	+	10-20	-	(40)	ns	
Salix spp.	-	0-5	ns		+	(20)	+	0-10

ns = No significant DEI.

[1] *Ribes oxyacanthoides* includes *R. lacustre*.

TABLE 3-5. Cover of herb species at clearcut edges (+/- = increase/decrease relative to changes in interior forest for the 1st and 2nd yr, and greater/less than in interior forest for the 5 and 16 yr old edges) and distance of edge influence (DEI). Numbers delimit DEI as a range of two or more consecutive distances with values or changes that were significantly different from average values or changes in interior forest. Numbers in brackets indicate single distances near the edge with changes or average values that were significantly different from changes or average values in interior forest. Species are subdivided into 'edge-positive' species (with mostly increases or greater cover at edges), 'edge-negative' species (with mostly decreases or lower cover at edges) and other species (with different responses at edges at different times post-harvest). Only species with significant DEI are included. Average values are tabulated in Appendix 3-1.

	Changes				Average values			
	1st yr		2nd yr		5 yr old		16 yr old	
	+/-	DEIc (m)	+/-	DEIc (m)	+/-	DEI (m)	+/-	DEI (m)
Total herb cover	-	(0)	+	(0)	ns		+	0-5(20)
Edge-positive species								
Achillea millefolium	ns		ns		+	0-5	+	0-5
Aster conspicuus	+	10-20	+ -	(60) (10)	-	(60)	+	0-20(60)
Disporum trachycarpum	ns		ns		+	0-5,20-60	ns	
Epilobium angustifolium	ns		+	(20)	+	(0)10-40	+	5-10
Galium boreale	+	(10,60)	ns		+	(0,40)	+	0-20
Lathyrus ochroleucus	+	5-10	ns		+	0-10	+	0-10
Linnaea borealis	-	(10)	+	(0,40)	+	(40)	+	(0,10)40-60
Maianthemum canadense	-	(0)	ns		+	(10)	+	0-5(20,60)
Petasites palmatus	ns		+	(10)	+	0-20(60)	+ -	0-10 (40)
Pyrola asarifolia	-	(0,60)	+	(60)	ns		+	(0)20-60
Vicia americana	+	(0,20)	+	(10)	+	(0)	+	0-10
Edge-negative species								
Equisetum pratense	+	(0)	ns		ns		-	5-10
Equisetum sylvaticum	ns		ns		-	(5,20,60)	-	5-10
Mertensia paniculata	-	(0,10)	-	(20)	-	(0)10-20	- +	(10) (5)

Mitella nuda	-	(0)	-	10-40	-	0-60	-	0-40
	+	(10)						
Orthilia secunda	-	(0,10)	-	0-5(20)	+	(20)	+	(20)
	+	(5)	+	(60)				
Viola spp. (mostly *V. canadensis*)	ns		ns		-	5-10(40)	+	(0)
Other species								
Aralia nudicaulis	ns		+	(20)	-	0-10	+	20-40
			-	(60)				
Aster ciliolatus	ns		-	10-40	+	10-20	+	(0)
Calamagrostis canadensis	+	(5)	+	(0)	+	0-5	-	0-5(60)
Galium triflorum	+	0-5,20-40	+	(0)	-	0-5	-	0-5(20)
			-	(60)				

ns = no significant DEI.

TABLE 3-6. Coarse woody material, sapling characteristics and shrub abundance for plots in the adjacent 1, 2, 5 and 16 yr old clearcuts. Data for the 1 and 2 yr old clearcuts are for the same plots, sampled in the 1st and 2nd yr post-harvest. Data are means ± 1 SE; standard error for sapling characteristics and total shrub cover was calculated among all subplots. Data for interior forest can be found in Figures 3-2 to 3-5.

	1st yr	2nd yr	5 yr old	16 yr old
Coarse woody material (# pieces / 20m)	6 ± 1	6 ± 1	5 ± 1	0 ± 0
Populus spp. sapling density (m^{-2})	7.7 ± 2.3	8.1 ± 1.2	4.7 ± 0.5	1.7 ± 0.3
Populus spp. sapling cover (%)	6 ± 2	25 ± 4	43 ± 5	36 ± 5
Height of *Populus* spp. saplings (cm)	70 ± 10	160 ± 10	280 ± 20	720 ± 50
Total shrub cover (%)	23 ± 3	29 ± 5	35 ± 5	50 ± 6
Total live tree density (# per ha)	60 ± 4	60 ± 4	0 ± 0	1900 ± 300

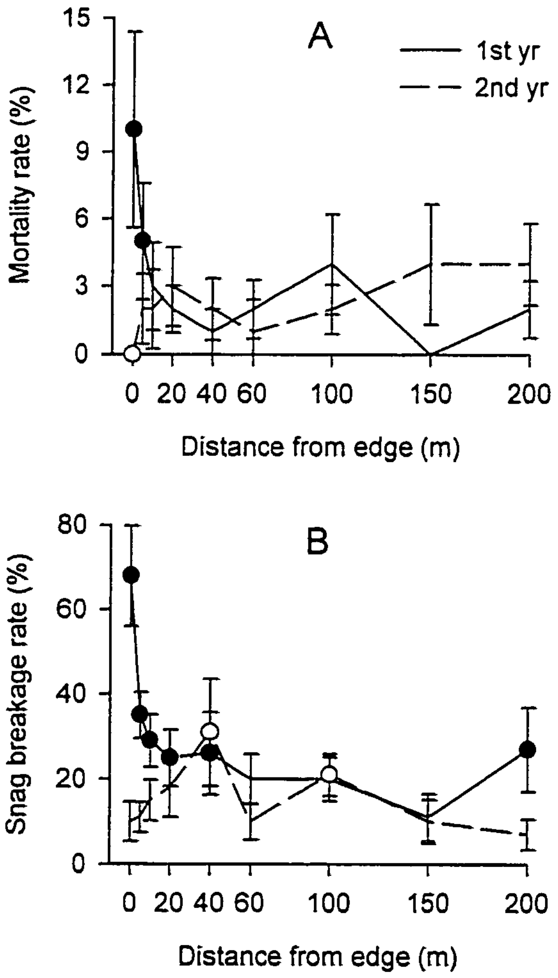


Figure 3-1. Average tree mortality (A) and snag breakage (B) rates between pre-harvest and the first year post-harvest (1st yr), and between the first and second years post-harvest (2nd yr), along the clearcut edge-to-interior gradient. Symbols represent rates that were significantly greater (filled symbols) or less (open symbols) than those in interior forest (plots 100-200m from the edge). Bars represent ± 1 SE.

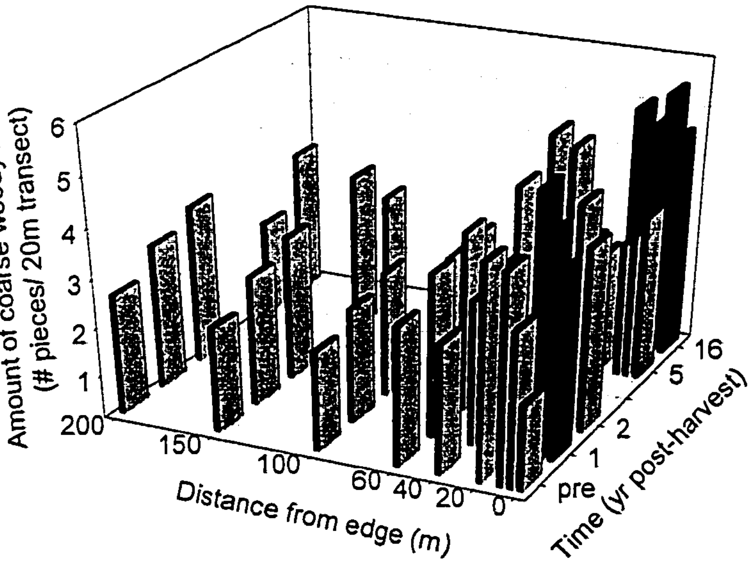


Figure 3-2. Average abundance (# pieces/ 20m transect) of coarse woody material along the clearcut edge-to-interior gradient for pre-harvest and 1, 2, 5 and 16 yr post-harvest. Dark gray bars for 1 and 2 yr represent significant changes between pre-harvest and the first year post-harvest, and between the first and second years post-harvest, respectively, compared to changes in interior forest (plots 100-200m from the edge). Dark gray bars for 5 and 16 yr represent averages that were significantly different from averages in interior forest. Standard error, which was not shown due to clarity, ranged from 0.5 to 1.3. The x-axis has been reversed for clarity.

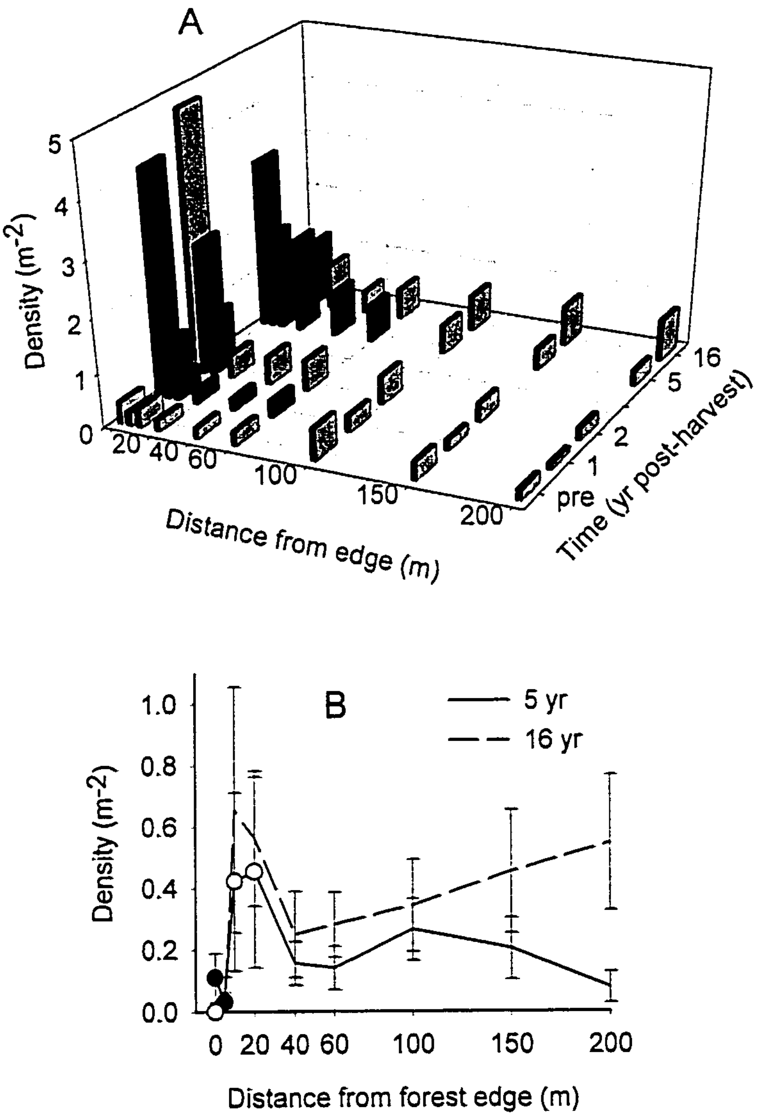
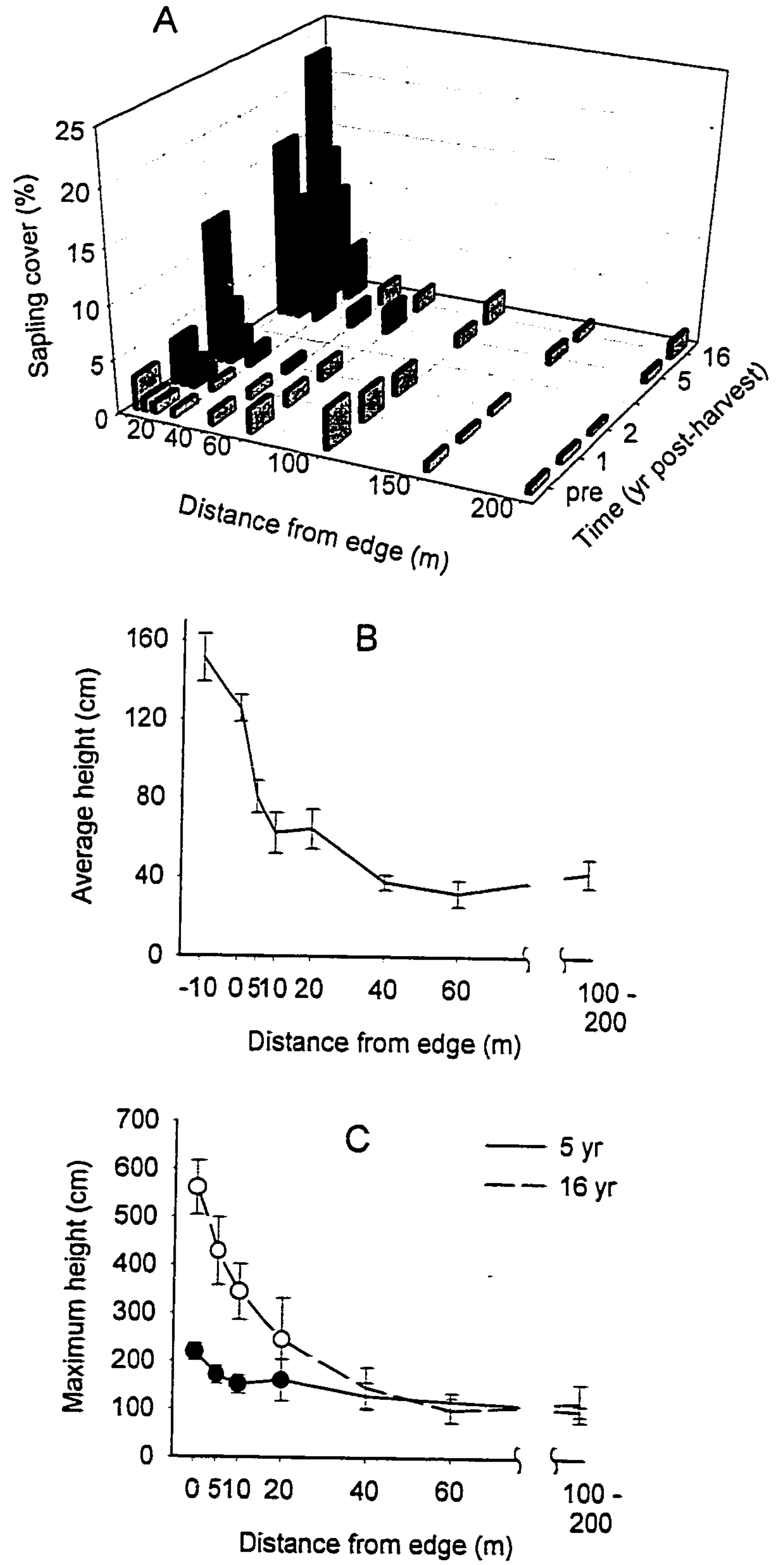
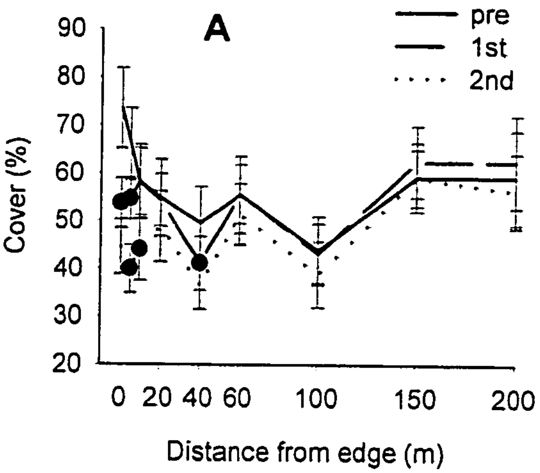


Figure 3-3. Average sapling density along the clearcut edge-to-interior gradient. A. Total density for pre-harvest and 1, 2, 5 and 16 yr post-harvest. Dark gray bars for 1 and 2 yr represent significant changes between pre-harvest and the first year post-harvest, and between the first and second years post-harvest, respectively, compared to changes in interior forest (plots 100-200m from the edge). Dark gray bars for 5 and 16 yr represent averages that were significantly different from averages in interior forest. Standard error, which was not shown due to clarity, ranged from 0.04 to 0.25 in the interior forest, and up to 1.6 at the edge. B. Density of new saplings (< 1 yr) for 5 and 16 yr post-harvest; symbols represent densities which were significantly different compared to densities in the interior forest. Bars represent ± 1 SE. Standard error was calculated among all subplots.

Figure 3-4. Average sapling abundance and growth along the clearcut edge-to-interior gradient. A. *Populus* spp. sapling cover for pre-harvest and 1, 2, 5 and 16 yr post-harvest. Dark gray bars for 1 and 2 yr represent significant changes between pre-harvest and the first year post-harvest, and between the first and second years post-harvest, respectively, compared to changes in interior forest (plots 100-200m from the edge). Dark gray bars for 5 and 16 yr represent averages that were significantly different from averages in interior forest. Standard error, which was not shown due to clarity, ranged from 0.1 to 2.2 in the interior forest, and up to 4.9 at the edge. B. Sapling growth (average height of three tallest 1 yr old saplings in each subplot) in the second year post-harvest. The first point at -10m was located 10m into the cutblock. A randomization test could not be performed due to an inadequate sample size (n=7) in the interior forest. C. Maximum height of saplings for 5 and 16 yr post-harvest. Symbols represent heights that were significantly greater than those in interior forest. Bars for B and C represent ± 1 SE. Standard error was calculated among all subplots.


A
Sapling cover (%)
0
5
10
15
20
25
20
40
60
100
150
200
Distance from edge (m)
pre
1
2
5
16
Time (yr post-harvest)
B
Average height (cm)
0
40
80
120
160
-10
0
5
10
20
40
60
100 - 200
Distance from edge (m)
C
Maximum height (cm)
0
100
200
300
400
500
600
700
5 yr
16 yr
0
5
10
20
40
60
100 - 200
Distance from edge (m)



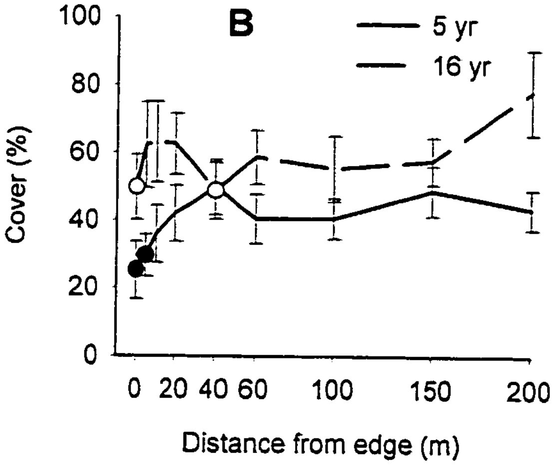
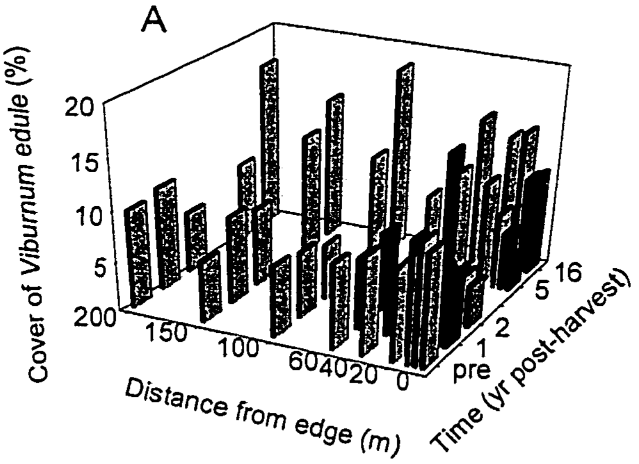
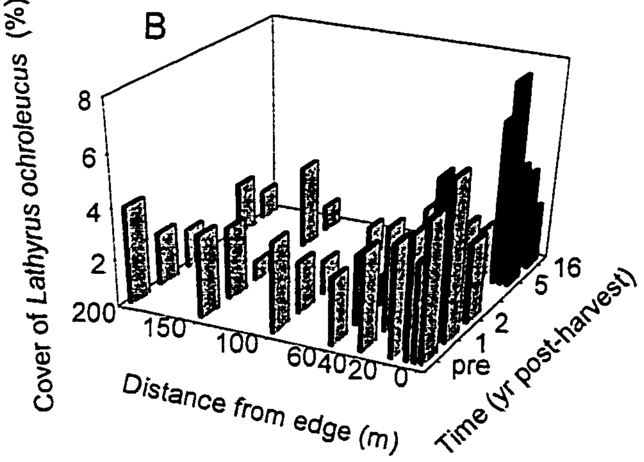
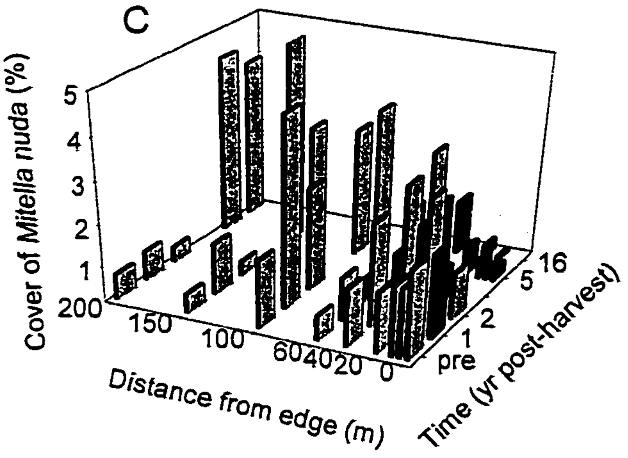


Figure 3-5. Total shrub cover along the clearcut edge-to-interior gradient. A. Pre-harvest, 1st and 2nd yr post-harvest. Symbols represent significant decreases between pre-harvest and the first year post-harvest, and between the first and second years post-harvest, compared to changes in interior forest (plots 100-200m from the edge). B. Five and 16 yr post-harvest. Symbols (filled for 5 yr and open for 16 yr post-harvest) represent averages that were significantly lower than averages in interior forest. Bars represent ± 1 SE; standard error was calculated among all subplots.

Figure 3-6. Average cover of selected species along the clearcut edge-to-interior gradient for pre-harvest and 1, 2, 5 and 16 yr post-harvest: A. *Viburnum edule*, B. *Lathyrus ochroleucus*, and C. *Mitella nuda*. Dark gray bars for 1 and 2 yr represent significant changes between pre-harvest and the first year post-harvest, and between the first and second years post-harvest, compared to changes in interior forest (plots 100-200m from the edge). Dark gray bars for 5 and 16 yr represent averages that were significantly different from averages in interior forest. Standard errors are in Appendix 3-1. The x-axis has been reversed for clarity.


A
Cover of *Viburnum edule* (%)
20
15
10
5
200
150
100
60
40
20
0
Distance from edge (m)
pre
1
2
5
16
Time (yr post-harvest)


B
Cover of *Lathyrus ochroleucus* (%)
8
6
4
2
200
150
100
60
40
20
0
Distance from edge (m)
pre
1
2
5
16
Time (yr post-harvest)


C
Cover of *Mitella nuda* (%)
5
4
3
2
1
200
150
100
60
40
20
0
Distance from edge (m)
pre
1
2
5
16
Time (yr post-harvest)

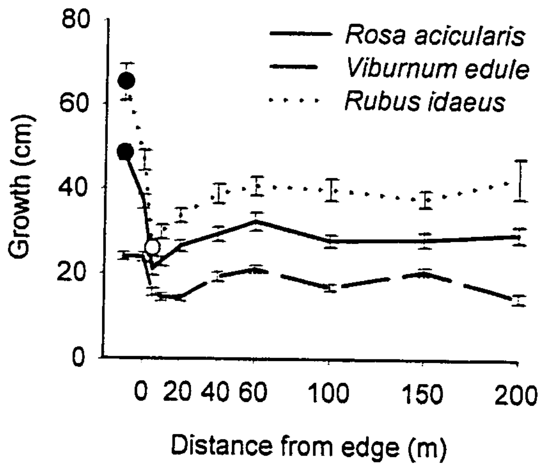


Figure 3-7. Growth of *Rosa acicularis, Viburnum edule* and *Rubus idaeus* along the clearcut edge-to-interior gradient (average length of new growth of three tallest stems in each subplot) in the second year post-harvest. Symbols represent values that were significantly greater (filled) or lower (open) than values in the adjacent interior forest (plots 100-200m from the edge). The first point at -10m was located 10m into the cutblock. Bars represent ± 1 SE; standard error was calculated among all subplots.

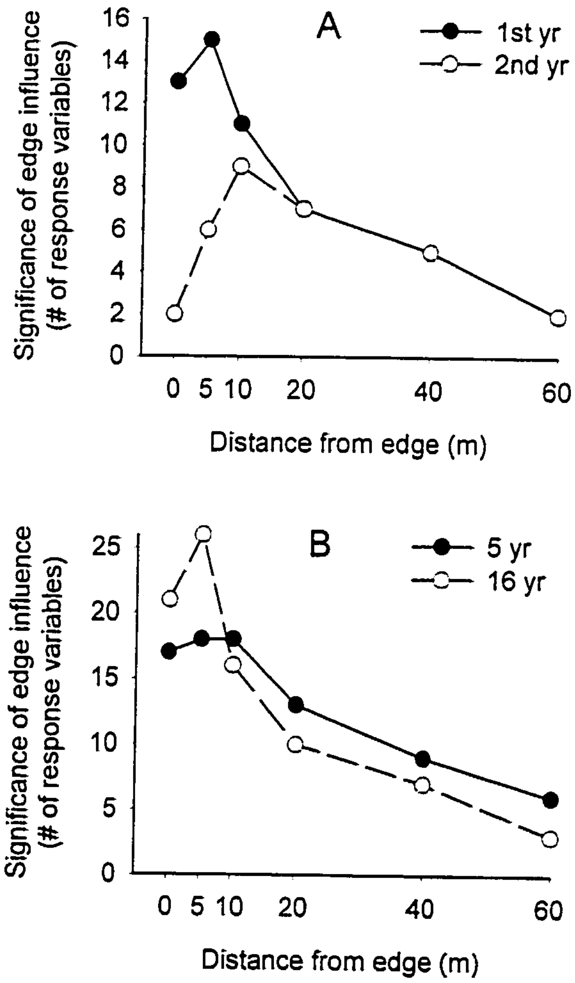


FIGURE 3-8. Summary of distance of edge influence results to determine where edge influence from clearcut edges occurs: response variables with significant distance of edge influence for different distances from the edges of cutblocks of different ages. A. Changes in the 1st and 2nd yr post-harvest. B. Differences from interior forest for 5 and 16 yr old edges.

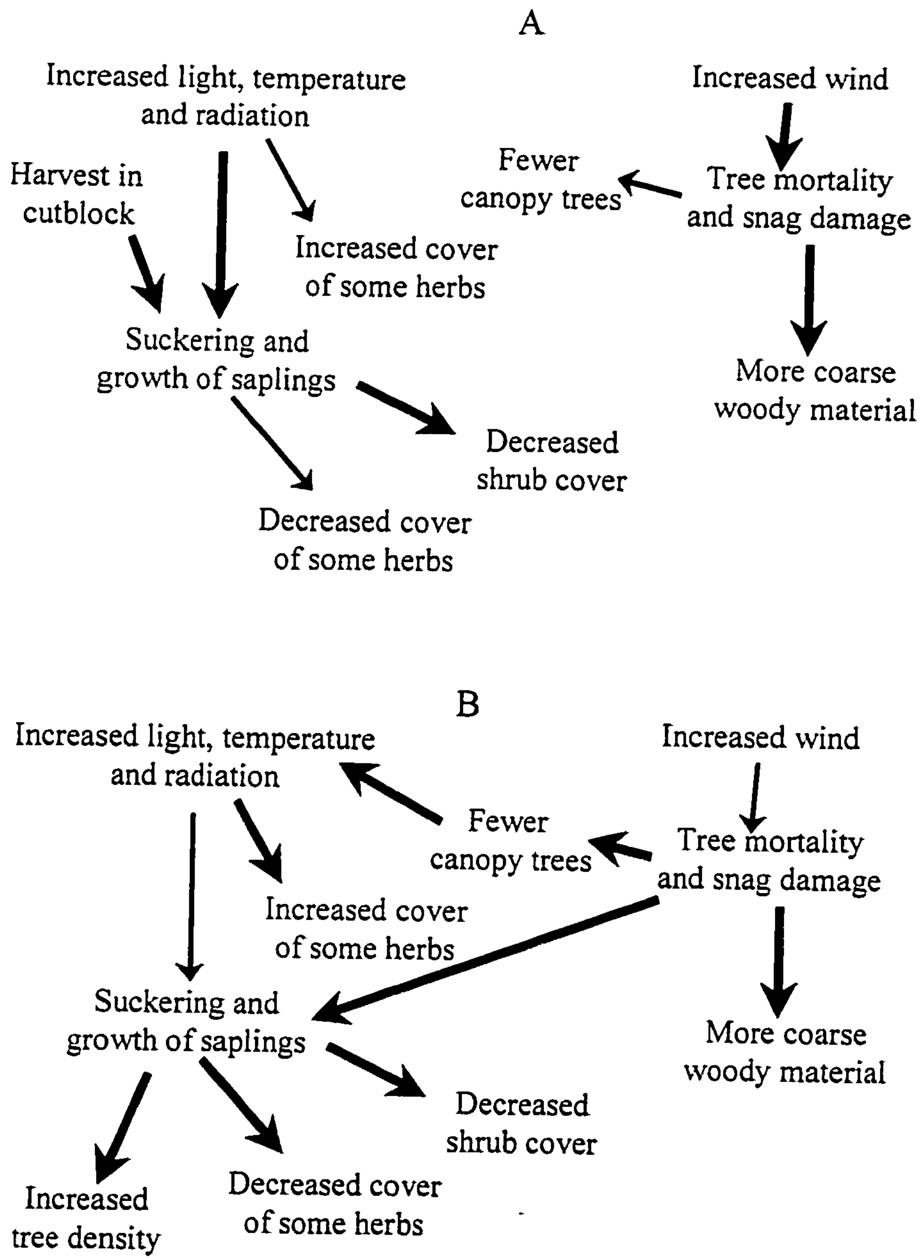


FIGURE 3-9. A proposed conceptual model of the causal factors of edge influence and their relationship to forest structure and composition at clearcut forest edges. A. Initial changes in the first two years post-harvest, B. Later stages after 5 or 16 yr post-harvest.

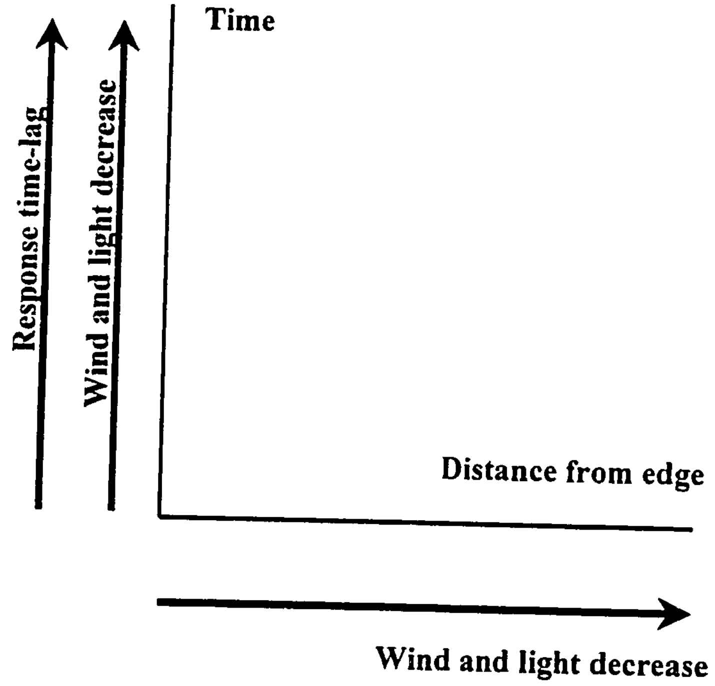


FIGURE 3-10. Gradients in space and time which affect edge influence at clearcut edges.

CHAPTER 4. EDGE INFLUENCE IN BUFFER ZONES: MODELS, PREDICTIONS AND EMPIRICAL RESULTS

Forest structure and composition in remnant buffer zones around lakes following harvesting are influenced by two types of edge: lakeshore and clearcut. Models of magnitude of edge influence (MEI) in buffer zones of three different widths (25, 100 and 200m) were developed which incorporated different interactions of edge influence: 1) edge influence limited to the strongest influence from either the lakeshore or clearcut edge, 2) combined edge influence from both lakeshore and clearcut edges, 3) resistance of the riparian forest to clearcut edge influence and 4) combined edge influence modified by resistance. The models predicted greater MEI in buffers with combined edge influence, and less MEI with resistance; these effects were greatest in narrow buffers. Using distance of edge influence (DEI) from both types of edge, I predicted the amount of interior forest habitat within 1 yr old and older buffers with the three different widths, following the limitation model. Predictions included: no interior forest remaining in 25m buffers, varying amounts of interior forest (depending on response variables) in 100m buffers, and a considerable width (approx. 100m) of interior forest in 200m buffers. To test my models and predictions for 1 yr old buffers, forest structure and composition were sampled across 25, 100 and 200m buffers. Empirical results did not fit the model very well, but lower MEI and DEI for structural changes at clearcut edges in narrow buffers compared to wider buffers, provided some evidence for the resistance model. The predictions of interior forest width were generally validated by empirical results for forest structure, but not for understory composition, most likely due to inadequate sample sizes. Over time, the 200m buffer width is predicted to be the only one of the three widths considered that will contain substantial interior forest habitat.

INTRODUCTION

In many forested landscapes, a narrow strip of forest is left around water bodies to protect aquatic ecosystems following timber harvest or agricultural development. Such buffers have been shown to moderate effects of disturbance in upland areas (particularly from agriculture) on riparian ecosystems by reducing sediment and nutrient input to aquatic ecosystems (Lowrance et al. 1984, Peterjohn and Correll 1984, Hubbard and Lowrance 1995). Buffers also maintain aesthetic values, provide shade, moderate riparian microclimate and provide organic material to water bodies (Gregory et al. 1991, O'Laughlin and Belt 1995).

Following commercial harvest of forests in Alberta, the required practice is to leave a 100m wide strip of forest around most lakes. Such buffer width designations are usually arbitrary, but recent studies in the United States have resulted in recommendations for various buffer width requirements depending on the management objectives. Widths of

10-90m (Castelle et al. 1994), and 4-250m (O'Laughlin and Belt 1995) have been recommended for reducing excess sedimentation and nutrient input, and protecting water quality. For maintaining riparian microclimate, forested buffer widths of 20-30m (Castelle et al. 1994), two tree heights (O'Laughlin and Belt 1995) or at least 45m (Brosofske et al. 1997) have been proposed.

In addition to their importance for protecting aquatic ecosystems, riparian forests within buffer zones may also provide wildlife habitat, complementing other unharvested areas, and provide connectivity in the landscape (Castelle et al. 1994, Brosofske et al. 1997). In order to determine whether a given buffer width will provide wildlife habitat, edge influence on forest structure and composition, and the associated wildlife responses, must be considered. Buffer zones around lakes are composed of two edges: an inherent lakeshore forest edge and a created clearcut edge. Due to these combined influence of these two edges, buffer zones may be too narrow to provide enough interior forest habitat for some edge-averse wildlife species (Hobbs 1992).

In buffer zones, edge influence from the two different types of edges could be combined. Such additive effects could be more prevalent in narrow buffers where there is overlap in the distance of edge influence (DEI) from the two edges. Malcolm (1994) included additive effects in a model which considered total edge influence as the sum of edge influence from all nearby edges. Malcolm (1994) suggested testing his model on linear forest fragments. Extending this theory to narrow remnant forest buffers, we would expect that edge influence at points within buffers would be the sum of edge influence from both clearcut and lakeshore edges. Combined effects caused by greater light, wind or related edge conditions from more than one edge could result in a greater edge influence than if just one edge was considered. Clearcut edge influence may be modified within riparian forest buffers, however. Riparian forest that is already exposed to edge influence from a natural, inherent edge could be more resistant to change following establishment of a created edge, due to wind-resistant canopy trees and an understory already exposed to edge conditions. In this case, edge influence from created edges could be lower in riparian forest than in upland forest.

The overall objective of the research described in this chapter was to evaluate edge influence on forest structure and composition within 25, 100 and 200m buffer zones, and to predict the width of interior forest habitat within the three widths of buffer zones. Specifically, my objectives were:

A. To develop models to predict the magnitude of edge influence in buffer zones of different widths (25, 100, 200m) for 1 yr old and older (5 or 16 yr old) buffers using data from Chapters 2 and 3. Four models were developed to incorporate different interactions of edge influence: 1) edge influence limited to the strongest influence from either the lakeshore or clearcut edge, 2) combined edge influence from both lakeshore and clearcut edges, 3) resistance of the riparian forest to clearcut edge influence and 4) combined edge influence modified by resistance.

B. To predict the amount of interior forest in buffer zones of different widths for 1 yr old and older buffers.

C. To test the models and predictions of interior forest for 1 yr old buffer zones using empirical data.

In addition, I asked the following questions:

1. Is distance of edge influence for north-facing edges different than distance of edge influence for south-facing edges?
2. Are changes in forest structure and composition greater at clearcut edges of narrow buffers, compared to wider buffers?

For the first question, I used empirical data to test an assumption of the models that aspect does not affect edge influence. I addressed the second question which was asked to test a prediction of the combination model, by empirically using response variables that were not included in the models.

METHODS

Construction of models

The dependent variable in the models, magnitude of edge influence (MEI), was the proportional increase or decrease (assumed to be due to edge influence) in the value of a response variable compared to interior forest:

$$MEI = x_d / x_i$$

x_d = fitted value of the response variable at distance d from the edge

x_i = average value of the response variable in the interior forest (for lakeshore edges or buffer zones: adjacent riparian forest reference data set, Chapter 2; clearcut edges: plots 100-200m from the clearcut forest edge in the same stands, Chapter 3)

If MEI = 1, there is no edge influence. Edge influence is negative when MEI < 1, and positive when MEI > 1.

In the models, I assumed that edge influence is the same for north-facing and south-facing edges. Buffer strips composed of one south-facing edge must also have a north-facing edge, yet edge influence from lakeshore and clearcut edges was determined for south-facing edges only (Chapters 2 and 3). Distance of edge influence has been shown to be greater at south aspects than at north aspects (Palik and Murphy 1990, Brothers 1993, Fraver 1994). Thus, using data all from south-facing edges should provide an idea of maximum edge influence in buffers. I tested the assumption that there was no difference in DEI among edges with different aspects by assessing whether aspect affected clearcut DEI.

Four models were developed for magnitude of edge influence in buffers of three different widths (25, 100, 200m) that incorporated different ways in which edge influence from the two edges might operate:

1) edge influence limited to the strongest influence from either the lakeshore or clearcut edge
2) combined edge influence from both lakeshore and clearcut edges
3) resistance of the riparian forest to clearcut edge influence
4) combined edge influence modified by resistance

For the first model, MEI at a given distance was the greatest MEI from either the lakeshore or clearcut edge:

Model 1) Limitation: B_d = {Max. or Min.} (L_d, $C_{w\text{-}d}$)

if $L_d < 1$ and $C_{w\text{-}d} > 1$ or vice versa, the greatest MEI was selected by comparing L_d to $1/C_{w\text{-}d}$ to determine the strongest edge influence

d = distance from the lakeshore forest edge

w = width of the buffer zone

B_d = MEI in the buffer zone at distance d from the lakeshore edge

L_d = MEI at lakeshore edges, at distance d from the lakeshore edge

$C_{w\text{-}d}$ = MEI at clearcut edges, at distance w - d from the clearcut edge

According to this model, the response is limited to the strongest edge influence; edge influence from both edges is not combined. This could occur if MEI is so high due to the influence of one edge that additional response due to combined effects of both edges is unlikely. For example, if the cover of a particular species is already close to 100%, additional edge influence would be unlikely to increase it further.

The second model combines edge influence from both edges by multiplying the lakeshore and clearcut MEIs:

Model 2) Combination: $B_d = L_d \times C_{w\text{-}d}$

In effect, this represents an additional clearcut edge influence on the value of a response variable at distance x from the lakeshore edge after lakeshore edge influence has been accounted for. Additive effects of light and wind from both edges would likely contribute to combined edge influence within buffers.

The next two models represent the situation in which the riparian forest is resistant to clearcut edge influence, thereby reducing MEI. This is expected to be the case if the riparian forest is already adapted to the edge environment. At a given distance x from the lakeshore edge, resistance is defined in relation to the strongest (max. or min.) MEI from the lakeshore edge:

if $L_0 < 1$, $R = (1 - L_d) / (1 - L_{min})$

if $L_0 > 1$, $R = (L_d - 1) / (L_{max} - 1)$

if $R < 0$, set to 0

R = resistance of the riparian forest to clearcut edge influence

L_0 = MEI at the lakeshore forest edge

L_{max} = maximum L_d for that variable

L_{min} = minimum L_d for that variable

Resistance ranges from 0 to 1 (maximum resistance).

The third model was constructed using the following conditions: 1) if R = 0, then $B_d = C_{w\text{-}d}$, and 2) if R = 1, then $B_d = L_d$. Assuming a linear function between these two conditions, the equation for the third model is:

Model 3) Resistance: $B_d = C_{w\text{-}d} \times (1\text{-}R) + L_d \times R$

Thus, with no resistance, MEI is only due to the clearcut edge; and with maximum resistance, MEI is only due to the lakeshore edge.

In the final model, combined edge influence from the two types of edges is modified by resistance of the riparian forest to clearcut edge influence. The first condition described above is changed to: 1) if R = 0, then $B_d = L_d \times C_{w\text{-}d}$:

Model 4) Combination modified by resistance: $B_d = L_d \times C_{w\text{-}d} \times (1\text{-}R) + L_d \times R$

For this model, with no resistance, MEI is the same as for the combination model.

A simple, hypothetical case was used to illustrate the predictions of these four models. A linear response to edge influence was assumed along both the lakeshore and clearcut edge-to-interior gradients, with MEI = 5 at the edge, and MEI = 1 in interior forest at distances greater than 50m from the lakeshore forest edge or greater than 25m from the clearcut edge. This case approximates overall edge influence from lakeshore and clearcut edges based on similar DEIs (Chapters 2 and 3) and a linear response model. The equations for MEI from both lakeshore and clearcut edges for this simple, linear response were:

if $d < 50$, $L_d = 5 - 0.08 \times d$ if $d \geq 50$, $L_d = 1$

if $w\text{-}d < 25$, $C_{w\text{-}d} = 5 - 0.16 \times d$ if $d \geq 25$, $C_{w\text{-}d} = 1$

These four models were built using empirical data. Models for 1 yr old and older (5 or 16 yr old) buffer zones were constructed using data from the transects perpendicular to lakeshore (Chapter 2) and clearcut edges (Chapter 3). For 1 yr buffer zones, average values in the first year post-harvest were used rather than changes between consecutive years. For older buffer zones, I used data from either 5 or 16 yr old edges, whichever had the larger distance of edge influence (DEI). I selected a set of variables that covered most sampled components of forest structure and composition: amount of coarse woody material; canopy, sub-canopy and mid-canopy tree density; snag density; *Populus* spp. sapling density and cover; total shrub and herb cover; and cover of individual shrub and herb species that were common (> 10% frequency) in data sets used for Chapters 2 and 3.

Curves were fit to data along the edge-to-interior gradient in order to estimate values for distances that were not sampled. To construct the models, values at all distances from both lakeshore and clearcut edges were needed, and empirical data were only available for some distances. (For example, to model edge influence in 100m buffers, empirical data were available for 5m from clearcut edges, but no data were collected 95m from lakeshore edges). I tried a variety of polynomial, rational, sigmoidal, exponential and logistic curves; and then used the curve with the highest R^2. Only variables with significant regressions ($p<0.05$) with R^2 greater than 0.1 were included. Curves were fit using SigmaPlot Version 4 (SPSS Inc. 1997).

Predicting the width of interior forest.—To model the effective width of interior forest remaining in buffer zones for a particular response variable, the simple solution is to subtract the lakeshore DEI and the clearcut DEI from the actual buffer width (limitation model). However, if the combined MEI from both edges in a buffer zone results in an average value which falls outside the critical values of interior forest conditions, DEI may be extended from the two edges, resulting in a narrower width of interior forest (combination models). Alternatively, there could be a greater width of interior forest if resistance to additional edge influence is great enough to reduce the MEI near clearcut edges such that the average value is no longer significantly different from interior forest, thereby reducing clearcut DEI (resistance models).

With the subset of variables used in the MEI models (those that could be fit to regression curves with $R^2 > 0.1$), I determined DEI for the four models. Distance of edge influence was determined by comparing the predicted MEI from the models to critical values from randomization tests of data in the adjacent riparian forest data set used in Chapter 2 (1996 pre-harvest data from 100-200m along the transects perpendicular to lakeshore forest edges). The width of interior forest in each buffer was determined as the difference between the buffer width and the DEIs from both edges.

Since the width of interior forest using all models could only be determined for five variables (those that could be fit to regression curves with $R^2 > 0.1$), I applied the limitation model to predict interior forest for a wider set of variables in 1 yr old and 5 or 16 yr old buffer zones. Average values did not need to be fit to curves for the limitation model which only uses maximum DEI from the lakeshore and clearcut edges. I selected variables that covered most measured aspects of forest structure and composition (amount of coarse woody material; canopy, sub-canopy and mid-canopy tree density; snag density; *Populus* spp. sapling density and cover; total shrub and herb cover; and cover of common shrub and herb species). The amount of interior forest in buffers was determined by subtracting DEI from each edge. Distance of edge influence from lakeshore forest edges were the results presented in Chapter 2. Clearcut DEI for 1 yr old buffer zones was based on data for the 1st yr post-harvest at clearcut edges (Chapter 3). I performed new randomization tests (described in Chapter 3) to determine whether they had a significant DEI at a 1 yr old clearcut edge (rather than DEI for changes from pre-harvest to the first year post-harvest as in Chapter 3). For modeling the amount of interior forest in the older buffer zones, I used the larger of the two DEI values from 5 or 16 yr old clearcut edges (Chapter 3).

Empirical data collection

I sampled forest structure and composition along transects across three different widths of buffer strips: 25m, 100m, and 200m. Buffer zones were sampled at two lakes (with 100m and 200m buffers) in the South Calling Lake TROLS study region, and at three lakes (with 25m, 100m and 200m buffers) in the Lac La Biche TROLS study region (Figure 4-1). The buffer zone at the lake with a 25m buffer zone in the TROLS South Calling Lake region was not sampled due to a different canopy tree composition (stands were not dominated by *Populus* spp.). Buffers with designated widths of 20m, 100m, and 200m, had measured widths 25m, 75-110m, and 157-207m respectively (Table 4-1). Although the narrowest buffer width was designated to be 20m, I refer to a 25m wide buffer zone since the buffer was always 25m at my transect locations. Harvesting did not always follow the prescribed clearcut edge: two 100m buffer transects were cut 5m narrower than prescribed, and one 25m and two 200m buffer transects were cut 5m wider than prescribed.

Data on forest structure and composition were collected on 3, 4 and 5 transects across 25m, 100m and 200m buffer zones respectively (Table 4-1). Trees and downed coarse woody material (CWM) were sampled on one additional 100m and one additional 200m transect. Transects were established prior to harvest and were sampled one year pre-harvest (1996) and one year post-harvest (1997). They spanned the widths of the buffer zones, perpendicular to both the lakeshore and clearcut forest edges. Transects were all approximately north-south oriented; either the lakeshore or the clearcut forest edge had a predominantly south-facing aspect (120°-240°). This criterion for selecting transect locations severely limited the number of potential transect locations. Transects were at least 100m apart, and were at least 100m from the nearest corner of a cutblock. Most of the buffer transects with south-facing lakeshore forest edges were also used for the characterization of lakeshore forest edges (Chapter 2, pre-harvest data). Therefore, the models were tested using part of the same data which were used to develop them; this was not ideal, but was necessary given time constraints. Consequently, the models would be expected to fit the data better than expected. Slopes along transects at lakeshore forest edges generally ranged from 0 to 42%, except for one at 73%; and at clearcut edges were less than 10%.

Plots (20m x 5m) were established along each transect (length parallel to the forest edge) at the following distances from each edge (where possible): 0, 5, 10, 20, 40, 60 and 100m (Table 4-2). Occasionally the midpoint between the two edges was used instead of 40 or 60m (100m buffers), or 100m (200m buffers). When harvesting did not follow the prescribed edge (either no trees or all trees were cut in the 0m plot), plot distances changed. In these situations, plots were re-assigned to one of the distances listed above for analysis. Along one transect where relocation of some herb and shrub subplots was impossible due to the installment of a haul road, only data from the remaining two herb subplots and one shrub subplot were used for analysis.

In the pre-harvest year, all trees and snags were counted within the 20m x 5m plots (see Chapter 2 for details of data collection). Canopy position (mid-canopy, sub-canopy, canopy) was recorded for all trees and snags, and presence of a broken top was noted for all snags. I tallied the number of pieces of downed CWM intersecting the major axis of the plot (≥8cm diameter at the intersection point, and decay classes 1-3 out of 7, Lee et al. 1995). Canopy cover was measured at the centre of each plot. I estimated the cover of all shrubs and *Populus* spp. saplings (<5cm dbh), and counted the number of *Populus* spp. saplings within two 2m x 2m subplots. Cover of all forbs and dwarf woody species was estimated within three 0.5m x 0.5m subplots. Cover was visually estimated to the nearest 1% up to 5%, and to the nearest 10% thereafter. Nomenclature follows Moss (1983). Plots were resampled the following year. For resampling of trees and snags, death of trees and snag breakage (a detectable change in canopy position, height, or category of broken top) were noted. The herb and shrub subplots were resampled within a few days of the original sampling date. Additional response variables included total shrub and herb cover (sum of the cover of all species in the subplots). Mortality and snag breakage rates were calculated as in Chapter 3.

Analyses.–To test the models, MEI was calculated using the empirical data at each distance in the buffer zones. To determine significant edge influence at different distances within the 1 yr old buffers, average values at different distances from the lakeshore and clearcut edges within each of the three buffer widths were compared to the critical values from randomization tests of data from the adjacent riparian forest data set used in Chapter 2 (1996 pre-harvest data from 100-200m along the transects perpendicular to lakeshore forest edges). Randomization tests (described in Chapter 2) were repeated using identical sample sizes as the buffer data sets. For example, step 1A (Chapter 2) was changed to: 1.

One value each from n random transects was randomly selected (1 of 3 possible values at 100, 150, 200m). For CWM, trees and snags, n = 3, 5, 6 for the 25m, 100m and 200m buffers respectively; for all other variables, n = 3, 4, and 5. Distance of edge influence was determined from each edge as the set of two or more consecutive distances which had values that were significantly different from the riparian forest data set. The width of interior forest was the set of distances within the buffers with values that were within the range of variation in interior forest.

In order to test the prediction of the combination model that changes would be greater at the clearcut edges of narrower buffers compared to clearcut edges of wider buffers, I quantified changes in forest structure and composition in buffer zones from pre-harvest to the first year post-harvest. Modified T-statistics (see Chapter 3) calculated on differences between pre-harvest and post-harvest values, were compared with results of the randomized T-distribution of differences in interior forest (using pre- to 1st yr post-harvest data at 100-200m from clearcut edges, Chapter 3). These randomization tests using modified T-statistics (described in Chapter 3) were done using identical sample sizes as the buffer data sets. For example, step 1A (Chapter 3) was changed to: 1. One value each from n random transects was randomly selected (i.e. the value at 100, 150 or 200m). For CWM, trees and snags, n = 3, 5, 6 for the 25m, 100m and 200m buffers respectively; for all other variables, n = 3, 4, and 5. Distance of edge influence for significant change in the buffers was determined as the set of two or more consecutive distances with T-statistics that were significantly different than the T-distribution of randomized data from interior forest. This is different from DEI for average values that are significantly different from interior forest described above, and will be denoted as DEIc (DEI for change) to distinguish between them. Mortality and snag breakage rates were analyzed using the methods in the previous paragraph.

Testing effect of aspect.–To test the assumption of no effect of aspect on DEI, DEIc was compared between clearcut edges with north- and south-facing aspects. This assumption was not tested for lakeshore forest edges because sample sizes were too small. A total of six 100m and 200m buffer transects had north-facing clearcut forest edges (100m buffer transects 1-3 and 200m buffer transects 1, 2 and 5, Table 4-2); and these were compared to south-facing clearcut forest edges from Chapter 3. Only response variables with significant DEIc at south-facing clearcut forest edges in the first year post-harvest were analyzed (total CWM, mortality and breakage rates, *Populus* spp. sapling density and cover, total shrub cover, and cover of: *Cornus stolonifera, Ribes oxyacanthoides, Salix* spp., *Symphoricarpos albus; Viburnum edule, Aster conspicuus, Galium triflorum, Lathyrus ochroleucus*). Differences between pre-harvest and the first year post-harvest were determined for distances from the edge up to 40m (since 60m from the clearcut edge along the 100m buffer transects was only 40m from the lakeshore forest edge). Modified T-statistics were calculated and then compared to randomized T-distributions (using n = 6) to determine significant DEIc for changes associated with edge creation. The same analysis was repeated on six randomly selected south-facing clearcut edge transects from Chapter 3.

RESULTS

Model predictions

The predictions of the model are illustrated using the simple hypothetical case of linear trends in magnitude of edge influence along the edge-to-interior gradient up to distances of 25m from the clearcut edge and 50m from the lakeshore forest edge (Figure 4-2). Predicted magnitude of edge influence (MEI) was identical for Models 1, 2 and 4 in the 100 and 200m buffer zones, but differed dramatically in the 25m buffers. The greatest MEI was predicted by the combination model throughout the entire 25m buffer zone, particularly near the cut edge. Resistance decreased predicted MEI in the 25m buffers, particularly in model 4 where combined edge influence was modified by resistance. In the wider buffers, Model 3 predicted lower MEI near the lakeshore edges. This could be an artifact of the model; resistance lowered MEI even though there was no additional edge influence from clearcut edges at those distances.

The combination model predicted greater MEI at clearcut edges in the narrower buffers, as compared to the wider; whereas the resistance model predicted lower MEI at clearcut edges in the narrower buffers. These predictions were tested using changes in forest structure and composition in the first year post-harvest at clearcut edges in buffers of different widths (see changes in buffer subsection below).

Models were constructed using results from Chapters 2 and 3 for only five response variables (coarse woody material, density of mid-canopy and canopy trees, density and cover of *Populus* spp. saplings) that could be fit to curves along the lakeshore forest edge-to-interior gradient with $R^2>0.1$ (Table 4-3). Three of these variables (density of mid-canopy trees, density and cover of *Populus* spp. saplings) were used for the models of 1 yr old buffers (the other two could not be fit to curves with $R^2>0.1$). For older buffers, two variables (density and cover of *Populus* spp. saplings) were modeled in 5 yr old buffers, and three variables (coarse woody material, and density of mid-canopy and canopy trees) were modeled in 16 yr old buffers.

Predicted MEI was generally similar in the models for the response variables (Figures 4-3 to 4-10) as for the hypothetical case (Figure 4-2). Results among models differed dramatically in the 25m buffers only. For almost all response variables, the greatest MEI was predicted by the combination model throughout the entire 25m buffer zone (e.g. Figure 4-3B). Large differences among models were found at the cut edges of the 25m buffers where predicted MEI was often twice as great using the combination model (and sometimes the modified combination model) vs. either of the other two models (Figures 4-4A, 4-6A, 4-7A, 4-10A). Resistance often decreased predicted MEI, particularly in the 25m buffers and at the lakeshore edges of the 100m and 200m buffers. Differences between the combination and modified combination models were generally greater than between the limitation and resistance models (e.g. Figures 4-4A and 4-10A). The resistance model almost always predicted the lowest MEI throughout all buffers. Results with unusual trends (e.g. Figures 4-3A, 4-5C, 4-6C, 4-8B) were often associated with MEIs that were in opposite directions (i.e. increase vs. decrease) for the lakeshore and clearcut edges. For most response variables, as in the hypothetical case, the combination model predicted greater MEI at clearcut edges in the narrower buffers, as compared to the wider buffers (Figures 4-4 to 4-8); whereas the resistance model predicted lower MEI at clearcut edges in the narrower buffers.

Predicting the width of interior forest.–There were few consistent differences in the predicted width of interior forest among the four models in the 25m and 100m buffers (Table 4-4). However, particularly within 200m buffers, the resistance model often predicted the greatest amount of interior forest.

To predict the amount of interior forest remaining in buffers using a more complete set of response variables, distance of edge influence (DEI) from lakeshore forest edges and clearcut edges was combined using the limitation model (Figures 4-11 and 4-12). Since the limitation model uses only maximum DEI, predictions could be made for more response variables. In 1 yr old 25m buffers, many variables were predicted to be significantly different from interior forest throughout most of the buffer width, thereby leaving no interior forest (Figure 4-11). Forest structure and composition variables in 100 and 200m buffers were predicted to be significantly different from interior forest within about 40m from the lakeshore forest edge; but some variables had DEI beyond this distance or near the clearcut edge. Eight response variables had significant DEI from both lakeshore and 1 yr old clearcut edges (coarse woody material; canopy and mid-canopy tree density; *Populus* spp. sapling density; cover of *Amelanchier alnifolia, Prunus* spp., *Aralia nudicaulis, Lathyrus ochroleucus*).

Twenty-two response variables were predicted to have significant DEI from both edge types in older buffers (5-16 yr post-harvest); twenty-three additional variables had significant DEI from only one type of edge. No remaining interior forest was predicted within 25m older buffers (Figure 4-12). In 100m older buffers, some response variables were predicted to be significantly different from interior forest throughout most or all of the buffer width. A considerable amount of interior forest (approx. 100m wide) was predicted within 200m older buffers. For all buffers, the estimated width of interior forest depends on the response variables.

Empirical results

Testing models of magnitude of edge influence.–Empirical results generally differed greatly from model predictions, making it difficult to assess the fit of the data to the different models (Figures 4-3 to 4-5). Mid-canopy tree density did not appear to match any of the models in the 25m buffer, but instead had greater MEI at both edges (Figure 4-3A). *Populus* spp. sapling density in the 25m buffers was most similar to predictions from the resistance model (Figures 4-4A). Average values of *Populus* spp. sapling cover were generally lower than any of the predicted values in the 25m buffer (Figure 4-5A). In the 100m buffer, MEI for mid-canopy tree density was much greater than the predictions from any model (Figure 4-3B). The cover of *Populus* spp. saplings in the 100m buffer generally matched the predicted values for the limitation model, except at the lakeshore edge (0m) where it was more similar to the combination model (Figure 4-5B). In the 100m buffer for *Populus* spp. sapling density, and in all of the 200m buffers, predictions from the various models were very similar (Figures 4-3C, 4-4B and C, 4-5C), thereby making it difficult to assess fit of the empirical data to the models.

Testing predictions of interior forest width.–The models rarely predicted the width of interior forest correctly for mid-canopy tree density, *Populus* spp. sapling density or cover in the 1 yr old buffers (Table 4-4). Often the empirical results were quite different from the predicted DEI for any of the models.

In terms of predicting the width of interior forest using all the selected response variables (Figures 4-11 and 4-12), DEI was similar to predicted DEI in 1 yr old buffers for some structural variables. Canopy tree density was predicted to be lower 0-5m from both lakeshore and clearcut edges, but it was only significantly lower at the clearcut edges of the 25 and 100m buffers and at the lakeshore forest edge of the 200m buffers (Figure 4-13). Mid-canopy tree density had similar DEI as predicted at the lakeshore edges, but not the clearcut edges, of the 100m and 200m buffers; and it was within the range of variation in interior forest throughout most of the 25m buffers (Figure 4-14). There was no edge influence on sub-canopy tree density (not shown). The amount of downed coarse woody material was greater near the lakeshore edges of the 25m and 200m buffers, and the clearcut edges of the 100 and 200m buffers, although DEI was different than predicted for both edges (Figure 4-15). At the clearcut edges of buffers, post harvest densities of *Populus* spp. saplings were higher than in interior forest, with similar DEI as predicted (Figure 4-16). Sapling densities were also greater at lakeshore edges with significant DEI in the 100m and 200m buffers, but not in the 25m buffers. *Populus* spp. sapling cover was greater near the lakeshore edges of buffers of all widths, but with narrower DEI than predicted (Figure 4-17).

Distance of edge influence on the cover of individual species was rarely similar to predicted DEI. The cover of most species was not significantly different from interior forest (Appendix 4-1). Some species had either greater or lower cover at edges than in interior forest, with different DEI than predicted (*Ribes triste* and *Orthilia secunda* in the 25m buffers; *Amelanchier alnifolia, Prunus* spp., *Salix* spp, *Symphoricarpos albus, Aralia nudicaulis, Equisetum arvense, Lathyrus ochroleucus* and *Maianthemum canadense* in the 100m buffers; *Equisetum arvense* and *Galium boreale* in the 200m buffers). For cover of *Salix* spp. in the 200m buffers, empirical results matched the predictions.

Changes in buffers.–Changes in forest structure and composition in the buffers following harvest were assessed using differences between pre- and post-harvest values. Within the 25m buffer zone, there was significantly greater mortality between pre-harvest and the first year post-harvest 5-10m from the lakeshore edge (15-20m from the clearcut edge), as compared to interior forest. Snag breakage was greater near the clearcut edge, but not significantly (Figure 4-18). Both 100m and 200m buffers had greater mortality and snag breakage near the cut edges, as compared to interior forest (DEIc=0-5 or 0-10m). Decreases in canopy cover were significantly greater than in interior forest at the clearcut edges of all buffers (significant at 0m in the 25m buffer, DEIc=0-5m in the 100 and 200m buffers, Figure 4-19). The accumulation of downed coarse woody material from the pre-harvest year to the first year post-harvest was high throughout the 25m buffer and at the cut edges of the other buffers; however, these changes were not significantly different than in interior forest (Figure 4-20). At the cut edges of buffers of all widths, *Populus* spp. sapling density increased significantly compared to interior forest (DEIc=0-5m, 0-10m and 0-5m for the 25m, 100m and 200m buffers, respectively, Figure 4-21). Only four structure variables had significant DEIc (significant for two or more consecutive distances) for changes near the clearcut edges following harvest (mortality rate, snag breakage rate, canopy cover and *Populus* spp. sapling density, Table 4-5). For these variables, DEIc was generally narrower in the 25m buffers than in the 100m and 200m buffers. In addition, the amount of change in these variables (directly related to MEI) was usually lower at the clearcut edges of 25m buffers, as compared to the edges of wider buffers, except for *Populus* spp. sapling density (Figures 4-18 to 4-21). There was little significant change in total shrub and herb cover, and few consecutive distances with significant changes in the cover of individual species (Appendix 4-1).

Testing effect of aspect.–There were few differences in DEI between north and south-facing edges when equal sample sizes were used (Table 4-6). The only differences were: significant DEI for mortality rate at north-facing edges but no edge influence at south-facing edges, wider DEI for *Populus* spp. sapling density at north-facing edges than at south-facing edges, and significant DEI for cover of *Galium triflorum* at south-facing edges but no edge influence at north-facing edges. For south-facing edges, DEI was considerably lower with the smaller sample size used in the analysis vs. the larger sample size used in Chapter 3. For eleven of the fourteen variables, DEI was not significant using the smaller sample size. Only density of *Populus* spp. saplings, cover of *Symphoricarpos albus*, and cover of *Galium triflorum* had significant DEI at south-facing edges with a sample size of six.

DISCUSSION

Magnitude of edge influence on forest structure and composition in buffers

The magnitude of edge influence (MEI) on forest structure and composition in narrow buffers is predicted to be greater if lakeshore and clearcut edge influence are combined. This is especially true at the cut edges of narrow buffers where changes due to edge influence are manifest upon riparian forest that is already significantly different from interior forest. Within narrow buffers, increased light and wind come from two edges, creating the potential for greater structural damage and understory development than at a single edge. However, resistance to additional edge influence from clearcut edges could ameliorate this combination, or decrease MEI if there are no additive effects. Resistance had a greater effect on reducing MEI when combination was also considered (Model 4 compared to Model 2). Trees in riparian forest have grown under edge conditions and are likely more windfirm, and would therefore be more resistant to increased wind following the creation of the clearcut edge. Likewise, the understory would already be exposed to the edge environment, and might not respond much to greater light in buffers following harvest of the adjacent cutblocks. Thus, combination of edge influence from two edges and resistance of riparian forest are two key factors in determining MEI, especially in narrow buffers.

In general, the empirical results for MEI for the three response variables (mid-canopy tree density, *Populus* spp. sapling density and cover) did not fit well to any model. Possible reasons for this lack of fit include: too small a sample size to observe trends (discussed below), similarities in predicted MEI among models, and inappropriateness of the adjacent riparian forest data set for determining MEI. The adjacent riparian forest data were not all from the same forest stands where the buffer transects were located, and therefore may not have been a good reference for edge influence on a stand level scale.

Results of the changes in the first year following harvesting provide some evidence to distinguish among models. The combination model predicts that MEI will be greater in narrow buffers than in wider buffers, particularly at the clearcut edge; whereas the resistance model predicts the opposite trend. For three of the four structural variables that changed significantly following harvest (mortality rate, snag breakage, canopy cover), there was little evidence of greater magnitude of change in 25m buffers compared to other buffers. Also, distance of edge influence for change (DEIc) was not as great for the 25m buffers as for the wider buffers. This evidence is difficult to assess, however, because the narrowest buffers also had the lowest sample size. Less change in narrower buffers provides some evidence that edge influence from the two edge types is not combined in buffers. Instead, resistance to edge influence could minimize edge influence at the clearcut edges in the narrow buffers. This may not be true for *Populus* spp. sapling density which increased more at clearcut edges of 25m buffers than at edges of 100 and 200m buffers. *Populus* spp. suckering is initiated by the interruption of apical dominance following harvesting in the adjacent cutblock, and may not be as sensitive to changes in microclimatic conditions at the edge.

Edge influence along the 25m buffer transects was not that strong; but the three transects, all located at the same lake, may not well represent changes in 25m buffers. Throughout a large portion of the buffer zones at this same lake (but not at the sampled transects), almost all of the living and dead trees fell over following harvest of the adjacent cutblocks (Plate 4-1). Only one of my 25m buffer transects experienced mortality; and this mortality was due to an extensive treefall event that occurred prior to, and following pre-harvest sampling. This mortality appeared to be the result of flooding rather than a consequence of harvesting (the water level rose 1-2m from 1995-1996, pers. obs.). Overall, (in areas without substantial blowdown following harvest), my data provide little evidence of combination of edge influence from two different types of edge within 25m buffers. Instead, I hypothesize that edge influence in these narrow buffers could be acting as a threshold response: either very little edge influence due to resistance of the riparian forest, or very high interaction if the threshold of resistance is exceeded.

Distance of edge influence for forest structure and composition in buffers

Although the models predicted quite different patterns for MEI in buffers, there were few differences in the predicted width of interior forest (Table 4-4). The resistance model sometimes predicted greater width in the 200m buffers, as compared to other models. However, this could be the result of an artifact of the resistance model since predicted MEI is lower than in the other models even near the lakeshore edge where there is no additional edge influence from clearcut edges (Figure 4-2).

For the limitation model using more variables (Figures 4-11 and 4-12), predictions for interior forest width were generally validated by the empirical results for forest structure (usually with lower distance of edge influence), but not understory composition. Differences between observed and expected results can partly be explained by sample size. Sample sizes, particularly for the 25m buffer, appeared to be inadequate given the amount of variation in the boreal forest. This was evident in the general lack of edge influence on species composition from the lakeshore forest edge in the pre-harvest year (compared to the results from Chapter 2 using a larger sample size), and in the differences in DEI using different sample sizes for south-facing edges.

Another possible explanation for discrepancies between predictions and empirical results could be lower DEI for north-facing (vs. south-facing) edges. Understory composition could be particularly affected by aspect due to differences in solar angle between south- and north-facing edges. However, when I tested this assumption for clearcut edges using the small sample size, I found an almost complete lack of edge influence at both south- and north-facing edges. The lack of significance was probably due to sample size rather than aspect. Other studies have found greater DEI at south-facing vs. north-facing older edges for canopy density and ground layer composition (Palik and Murphy 1990), tree density and species richness (Brothers 1993), and species composition (Fraver 1994). However, at more recently created edges, Matlack (1993, 1994) found no effect of aspect on edge influence on shrub cover or understory composition. Due to low sample sizes, I cannot conclusively validate or refute the assumption of no effect of aspect on DEI. I recommend retaining the conservative assumption that DEI from north-facing edges is the same as DEI from south-facing edges.

Managing buffers for wildlife habitat

In addition to protecting aquatic ecosystems, preserving riparian forests as buffers could serve various functions for wildlife habitat: conserving unique lakeshore forest edge habitat, serving as reserves of interior forest habitat, and providing corridors for wildlife. For the first function, the minimum buffer width would need to encompass the width of lakeshore edge forest that is significantly different from interior forest - the lakeshore DEI (40m, Chapter 2). In order to prevent changes in the lakeshore edge forest community from clearcut edge influence, clearcut DEI (20m, Chapter 3) should be added to the lakeshore DEI, leading to a recommended minimum buffer width of 60m for riparian buffers in the study area. If there is combination between edge influence from lakeshore and clearcut edges, buffer width may need to be even greater. Alternatively, buffers may not need to be as wide if the riparian forest is resistant to edge influence. A more cautious estimate should include maximum penetration of edge influence (Laurance and Bierregaard 1997), which in this study would be a buffer width of at least 100m to encompass the maximum DEI of all variables (Figure 4-12B).

In addition to protecting aquatic ecosystems, one of the goals of buffer management may be to provide connected interior forest habitat on the landscape for species sensitive to edge influence. To achieve this objective, buffers would need to be even wider. The width would depend on how wide a strip of interior forest habitat is desired, and which response variables are considered important for wildlife. Of the three studied buffer widths, only the 200m buffers were predicted to contain interior forest habitat over time for all response variables. In the first year following harvest there were few predicted or observed changes in buffers, but forest structure and composition are expected to be substantially different in older buffer zones. A study in eastern boreal forest, however, showed no decline in bird populations in a 60m-wide buffer next to a river for the first three years following harvest (Darveau et al. 1995); and buffers of 100m have been shown to act as corridors for the movement of juvenile songbirds following harvest in a study area near one of the TROLS sites (Machtans et al. 1996).

Applying a fixed buffer width equal to the sum of the lakeshore and clearcut DEI to all lakes is not the only possible management scenario. Another option could be a narrower unharvested buffer adjacent to an area of selective harvesting which could mitigate edge influence, and perhaps decrease DEI (Brosofske et al. 1997). An alternative to applying a fixed-width buffer everywhere is a variable-width buffer system which would be based on several criteria. This would provide greater flexibility in meeting landscape level objectives, but could be more difficult and expensive to implement (O'Laughlin and Belt 1995). In this variable buffer system, my predictions could be used to estimate the amount of interior forest remaining in various widths of buffer, and to determine which response variables would be most affected. Buffers could be provided for other hydrological features such as important wetlands instead of or in addition to lakeshore buffers. Buffer width could depend on the level of resistance in the riparian forests (which could be lower for some species of trees, steeper slopes, and buffers oriented perpendicular to the prevailing wind). In forest management, as in other decision-making processes, it is usually imperative to make 'best-bet judgements' rather than waiting for adequate data (Hobbs 1992). With the results of this chapter, predictions of the interior forest habitat within buffers of different widths can be combined with information (from TROLS) for other buffer functions such as protecting aquatic ecosystems, in order provide our best-bet judgement on an appropriate buffer width.

Although models of MEI and predictions of DEI within 1 yr old buffers were generally not validated by empirical results, other important findings were made in this chapter. First of all, my predictions provide important guidelines for buffer management, particularly for estimating the amount of interior forest left in buffers sixteen years following harvest. Second, the results of the models show that combination of edge influence in buffers would increase MEI, and resistance of the riparian forest would decrease MEI. Third, variables that showed significant DEI in 1 yr old buffers despite small sample sizes (mid-canopy tree density, amount of coarse woody material, *Populus* spp. sapling density and cover) may be particularly susceptible to edge influence. Understory composition is more heterogeneous than forest structure and thus probably requires a greater sample size to assess edge influence which may be less in the context of inherent heterogeneity. Fourth, virtually no evidence of combination in edge influence in the sampled 25m buffers, and personal observation of extensive blowdown following harvesting in other 25m buffers suggests a threshold response to edge influence in narrow buffers. Finally, there was generally no overall effect of aspect on edge influence, although this needs to be confirmed using larger sample sizes. These findings are important in developing an overall plan for buffer management, one of the objectives of the TROLS project.

LITERATURE CITED

Brosofske, K., J. Chen, R. J. Naiman, and J. F. Franklin. 1997. Harvesting effects on microclimatic gradients from small streams to uplands in western Washington. Ecological Applications 7:1188-1200.

Brothers, T. S. 1993. Fragmentation and edge effects in central Indiana old-growth forests. Natural Areas Journal **13**:268-275.

Castelle, A. J., A. W. Johnson, and C. Conolly. 1994. Wetland and stream buffer size requirements - a review. Journal of Environmental Quality **23**:878-882.

Darveau, M., P. Beauchesne, L. Bélanger, J. Huot, and P. LaRue. 1995. Riparian forest strips as habitat for breeding birds in boreal forest. Journal of Wildlife Management **59**:67-78.

Fraver, S. 1994. Vegetation responses along edge-to-interior gradients in the mixed hardwood forests of the Roanoke River basin, North Carolina. Conservation Biology **8**:822-832.

Gregory, S. V., F. J. Swanson, W. A. McKee, and K. W. Cummins. 1991. An ecosystem perspective of riparian zones. BioScience **41**:540-551.

Hobbs, R. J. 1992. The role of corridors in conservation: solution or bandwagon? Trends in Ecology and Evolution **7**:389-392.

Hubbard, R. K., and R. R. Lowrance. 1994. Riparian forest buffer system research at the coastal plain experiment station, Tifton, GA. Pages 409-432 *in* C. C. Trettin, W. M. Aust and J. Wisniewski, editors. Wetlands of the Interior Southeastern United States. Kluwer Academic Publishers, Dordrecht, Netherlands.

Laurance, W. F., and R. O. Bierregaard Jr., editors. 1997. Tropical forest remnants: ecology, management, and conservation of fragmented communities. The University of Chicago Press, Chicago.

Lee, P. C., S. Crites, K. Sturgess, and J. B. Stelfox. 1995. Changes in understory composition for a chronosequence of aspen mixedwood stands in Alberta. Pages 63-80 *in* J. B. Stelfox, editor. Relationships between stand age, stand structure and biodiversity in aspen mixedwood forests in Alberta. Jointly published by Alberta Environment Centre, Vegreville, Alberta, and Canadian Forest Service, Edmonton, Alberta, Canada.

Lowrance, R., R. Todd, J. Frail Jr., O. Hendrickson Jr., R. Leonard, and L. Asmussen. 1984. Riparian forests as nutrient filters in agricultural watersheds. BioScience **34**:374-377.

Machtans, C. S., Marc-A. Villard, and S. J. Hannon. 1996. Use of riparian buffer strips as movement corridors by forest birds. Conservation Biology **10**:1366-1379.

Malcolm, J. R. 1994. Edge effects in central Amazonian forest fragments. Ecology **75**:2438-2445.

Matlack, G. R. 1993. Microenvironment variation within and among forest edge sites in the eastern United States. Biological Conservation **66**:185-194.

Matlack, G. R. 1994. Vegetation dynamics of the forest edge - trends in space and successional time. Journal of Ecology **82**:113-123.

Moss, E. H. 1983. Flora of Alberta. Second Edition. Revised by J. G. Packer. University of Toronto Press, Toronto, Canada.

O'Laughlin, J., and G. H. Belt. 1995. Functional approaches to riparian buffer strip design. Journal of Forestry **93**:29-32.

Palik, B. J., and P. G. Murphy. 1990. Disturbance versus edge effects in sugar-maple/beech forest fragments. Forest Ecology and Management **32**:187-202.

Peterjohn, W. T., and D. L. Correll. 1984. Nutrients dynamics in an agricultural watershed: observations on the role of a riparian forest. Ecology **65**:1466-1475.

SPSS Inc. 1997. SigmaPlot for Windows Version 4.00.

Table 4-1. Number of buffer transects sampled in each TROLS study area, subdivided by buffer width, aspect, and by whether all data were collected or only data on trees and coarse woody material. Lake edge or cut edge refers to which edge was south-facing.

	Calling Lake		Lac La Biche		Total	
Buffer width	All data	Trees only*	All data	Trees only*	All data	Trees only*
25m - lake edge	0	0	3	3	3	3
100m - lake edge	1	1	2	2	3	3
100m - cut edge	0	0	1	2	1	2
200m - lake edge	2	2	1	1	3	3
200m - cut edge	1	2	1	1	2	3

* Total number, not the number of additional transects.

Table 4-2. Plot locations and actual buffer widths along the buffer transects. Plot distances (in m) are from the nearest forest edge: lakeshore (lake) or clearcut (cut). Since harvesting did not follow the planned edge, plot distances changed, thus creating unequal sample sizes. Underlined pairs of distances indicate that the same plot was used for both distances.

	0 Lake	5	10	20	40	60	100	100	60	40	20	10	5	0 Cut	Buffer width
25m buffers															
1	0	5	10									10	5	#	25
2	0	5	10									10	5	0	25
3	0	5	10									10	5	0	25
100m buffers															
1	0	5	10	20	40					40	15	#	5	0	71
2	0	5	10	20	40					40	20	10	5	0	88
3	0	5	10	20	40					35	#	15	5	0	105
4*	0	5	10	20	40					40	20	10	5	0	100
5	0	5	10	20	38					38	20	10	5	0	75
200m buffers															
1	0	5	10	20	40	60	100	100	60	40	20	10	5	0	200
2	0	5	10	20	40	60	97.5	97.5	60	40	20	10	5	0	195
3*	0	5	10	20	40	60	89.5	95.5	65	45	25	10	5	#	184
4	0	5	10	20	40	60	104	104	60	40	20	10	5	0	207
5	0	5	10	20	40	60			65	45	25	10	5	#	162
6	0	5	10	20	40	60	100	79	60	40	20	10	5	0	179

No plot since harvesting did not follow the planned edge and plot distances had to be adjusted accordingly.

* Trees and coarse woody material sampled only.

[1] Herbs and shrubs sampled only.

Table 4-3. Results of the best-fit curves along edge-to-interior gradients from lakeshore edges, and from 1, 5 and 16 yr old clearcut edges. Only response variables that had curves with $R^2>0.1$ are included.

Edge type and age	Response variable	Curve	F	R^2	p
Lakeshore	Coarse woody material	Cubic	9.96	0.22	<0.0001
	Canopy tree density	Cubic	6.32	0.15	0.0006
	Mid-canopy tree density	Quadratic	7.23	0.12	0.0011
	Density of *P. tremuloides* saplings	Cubic	16.2	0.16	<0.0001
	Cover of *P. tremuloides* saplings	Rational	36.5	0.24	<0.0001
1 yr old clearcut	Mid-canopy tree density	Cubic	4.38	0.13	0.01
	Density of *P. tremuloides* saplings	Logistic	38.8	0.4	<0.0001
	Cover of *P. tremuloides* saplings	Exponential	17.3	0.23	<0.0001
5 yr old clearcut	Density of *P. tremuloides* saplings	Exponential	22.4	0.28	<0.0001
	Cover of *P. tremuloides* saplings	Logistic	23.7	0.29	<0.0001
16 yr old clearcut	Coarse woody material	Cubic	4.76	0.17	0.0045
	Canopy tree density	Sigmoidal	4.39	0.16	0.01
	Mid-canopy tree density	Logistic	14.7	0.39	<0.0001

TABLE 4-4. (for 1 yr old buffers only). Widths (in m) of interior forest were calculated by subtracting the lakeshore and clearcut Predicted width of interior forest in buffers of different widths and age for the four alternative models (M1: limitation, M2: combination, M3: resistance, M4: combination modified by resistance), and actual width based on empirical results DEIs from the designated buffer widths (see methods for more details and Figures 4-2 to 4-9).

	25m buffer					100m buffer					200m buffer				
	M1	M2	M3	M4	Actual	M1	M2	M3	M4	Actual	M1	M2	M3	M4	Actual
1 yr old buffers															
Mid-canopy tree density	---	10	10	5	15	40	---	40	20	20	140	140	160	150	140
Populus sapling density	---	---	---	---	20	---	---	20	---	90	100	80	120	80	195
Populus sapling cover	---	---	---	---	20	---	---	---	---	60	---	---	90	---	160
5 yr old buffers															
Populus sapling density	---	---	---	---		---	---	---	---		---	---	20	---	
Populus sapling cover	---	---	---	---		---	---	---	---		40	---	100	---	
16 yr old buffers															
Coarse woody material	---	---	---	---		20	20	20	20		100	100	100	100	
Canopy tree density	---	---	5	---		70	80*	80	70*		170	180*	180	170*	
Mid-canopy tree density	---	---	---	---		50	30	70	30		150	130	170	130	

--- There was no interior forest remaining, or only one distance was not significantly different from interior forest.

* Within part of this width of interior forest, the predicted values were above the critical values for interior forest, whereas the predicted values at the edges were below the critical values.

Table 4-5. Summary of distance of edge influence results for structural changes between the pre-harvest year and the first post-harvest year within buffers of three different widths. Numbers delimit DEI as a range of two or more consecutive distances with changes that were significantly different from changes in interior forest; distances in the table are from the clearcut edge. Numbers in brackets indicate single distances near the edge that were significantly different from interior forest. Values at different distances from the edge are in Figures 4-10 to 4-13.

	25m buffer	100m buffer	200m buffer
Mortality rate	15-20	0-5	(0)
Snag breakage rate	ns	0-5	0-10
Canopy cover	(0)	0-5	0-5
Populus spp. sapling density	0-5	0-10	0-5

Table 4-6. Significant distance of edge influence (DEI) for changes between the pre-harvest year and the first post-harvest year for south and north-facing clearcut forest edges, subdivided by sample size for south-facing edges (see methods). Numbers delimit DEI as a range of two or more consecutive distances with changes that were significantly different from changes in interior forest. Only response variables with significant distance of edge influence for south-facing edges (n=10, Chapter 3) are included. Numbers in brackets indicate single distances near the edge that were significantly different from interior forest. The maximum distance measured was 40m.

	South-facing n=10	South-facing n=6	North-facing n=6
Coarse woody material	0-10	ns	ns
Mortality rate	0-5	ns	0-10
Damage rate	0-40	(0,40)	(0,10)
Density of *Populus* spp. saplings	0-40	0-5(40)	0-10
Cover of *Populus* spp. saplings	0-10	ns	ns
Total shrub cover	0-5(40)	ns	ns
Cornus stolonifera	0-20	ns	(5,10)[1]
Ribes oxyacanthoides[2]	0-5(20)	ns	ns
Salix spp.	0-5	ns	(0)
Symphoricarpos albus	0-5	0-5	ns
Viburnum edule	0-40	(5,40)	(0)
Aster conspicuus	10-20	(10)	ns
Galium triflorum	0-5,20-40	0-5(20)	ns
Lathyrus ochroleucus	0-5	ns	(10)[3]

ns = no significant DEI

[1] *Cornus stolonifera* decreased significantly at 5m, and increased significantly at 10m.

[2] *Ribes oxyacanthoides* includes *R. lacustre*.

[3] *Lathyrus ochroleucus* decreased significantly at 10m, while it increased significantly near the south-facing edges.

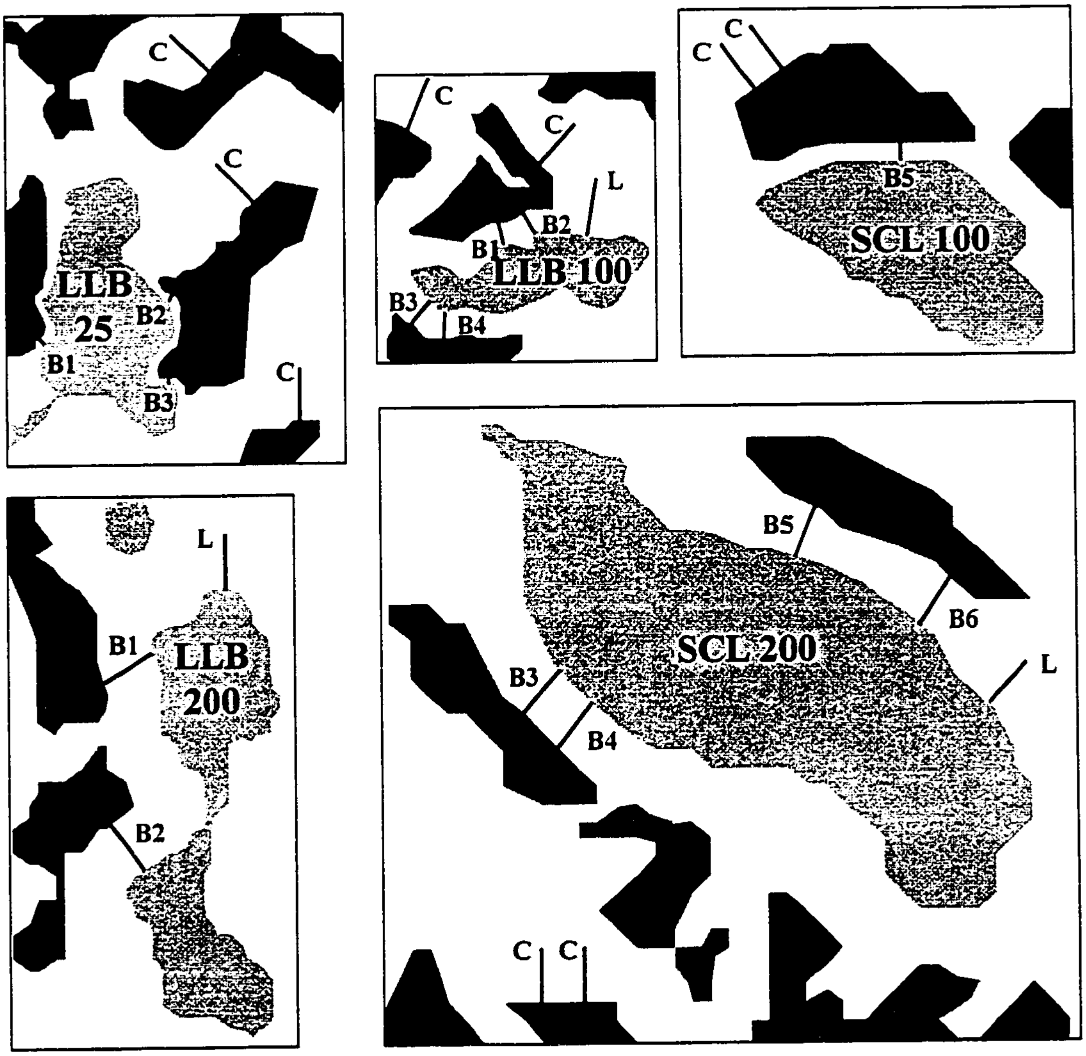


Figure 4-1. Maps showing locations of the buffer transects (B) in the South Calling Lake (SCL) and Lac La Biche (LLB) TROLS study regions around lakes with 25, 100 and 200m buffer zones. Transect numbers are the same as those in Table 4-2. Lakeshore edge transects (L, from Chapter 2) and clearcut edge transects (C, from Chapter 3) in the nearby areas are also indicated on the maps.

Figure 4-2. Predicted trends in the magnitude of edge influence for a simple hypothetical case (Model 1: Limitation, Model 2: Combination, Model 3: Resistance, Model 4: Combination modified by resistance) across 1 yr old buffers of three different widths: A. 25m, B. 100m, C. 200m. Magnitude of edge influence is the proportional increase or decrease compared to interior forest (see methods). The hypothetical case assumes linear trends in magnitude of edge influence along the edge-to-interior gradient up to distances of 25m from the clearcut edge and 50m from the lakeshore forest edge.

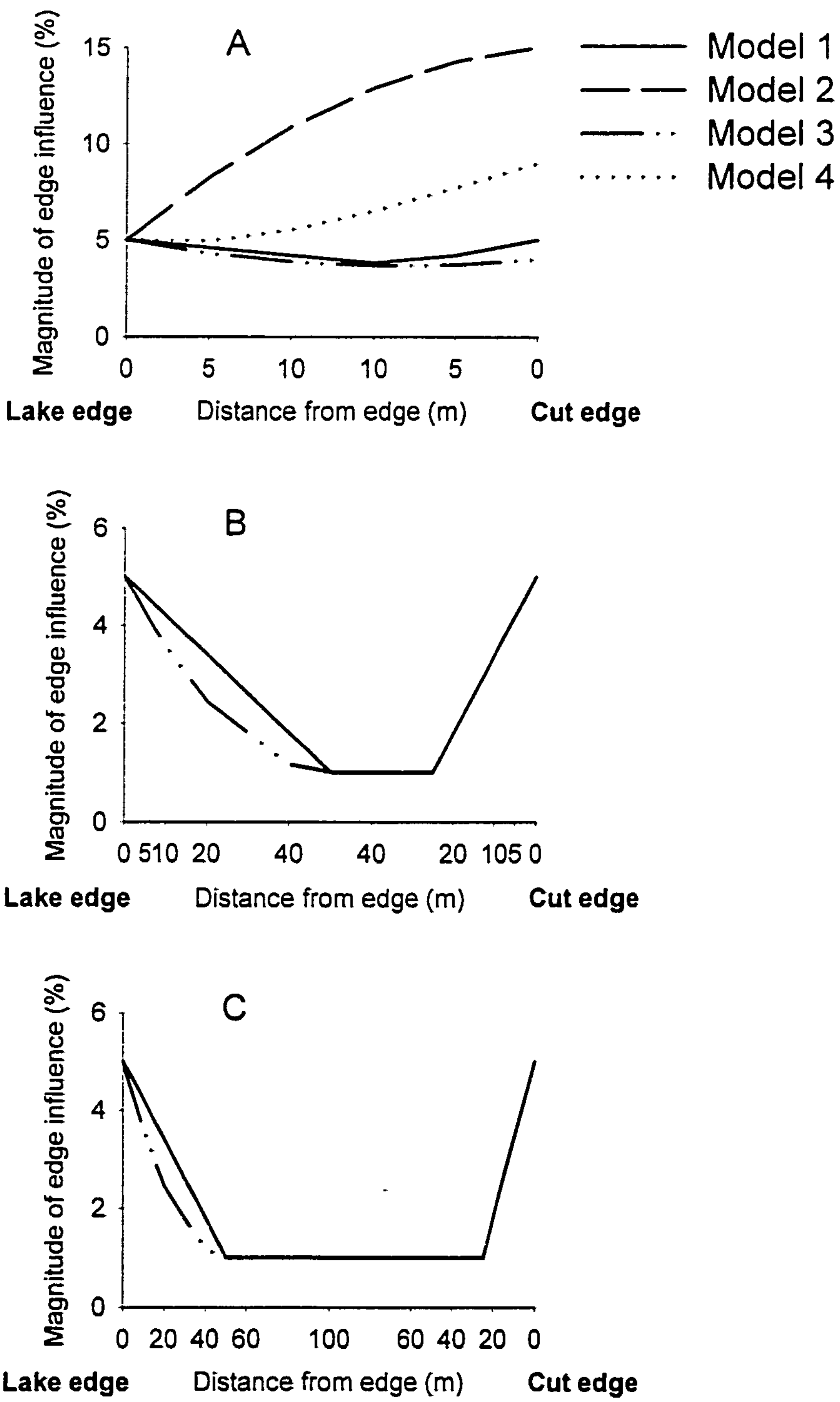

A
Model 1
Model 2
Model 3
Model 4
Magnitude of edge influence (%)
15
10
5
0
0
5
10
10
5
0
Lake edge
Distance from edge (m)
Cut edge
B
Magnitude of edge influence (%)
6
4
2
0
0 510 20
40
40
20 105 0
Lake edge
Distance from edge (m)
Cut edge
C
Magnitude of edge influence (%)
6
4
2
0
0 20 40 60
100
60 40 20 0
Lake edge
Distance from edge (m)
Cut edge

Figure 4-3. Predicted trends in the magnitude of edge influence on mid-canopy tree density (Model 1: Limitation, Model 2: Combination, Model 3: Resistance, Model 4: Combination modified by resistance), and empirical results across 1 yr old buffers of three different widths: A. 25m, B. 100m, C. 200m. Magnitude of edge influence is the proportional increase or decrease compared to interior forest (see methods). Parallel lines (long dash) correspond to the critical values of interior forest conditions (using sample size of n=10), for comparison with the predicted trends. Values outside these critical values are significantly different from the range of variation in interior forest, and thus exhibit a significant edge influence. Circles represent average magnitude of edge influence for empirical data used to test the models. Filled circles are values that were significantly different from interior forest (using sample sizes of n=3, 5 and 6 for 25, 100 and 200m buffers). Error bars for the empirical data are in Figure 4-14.

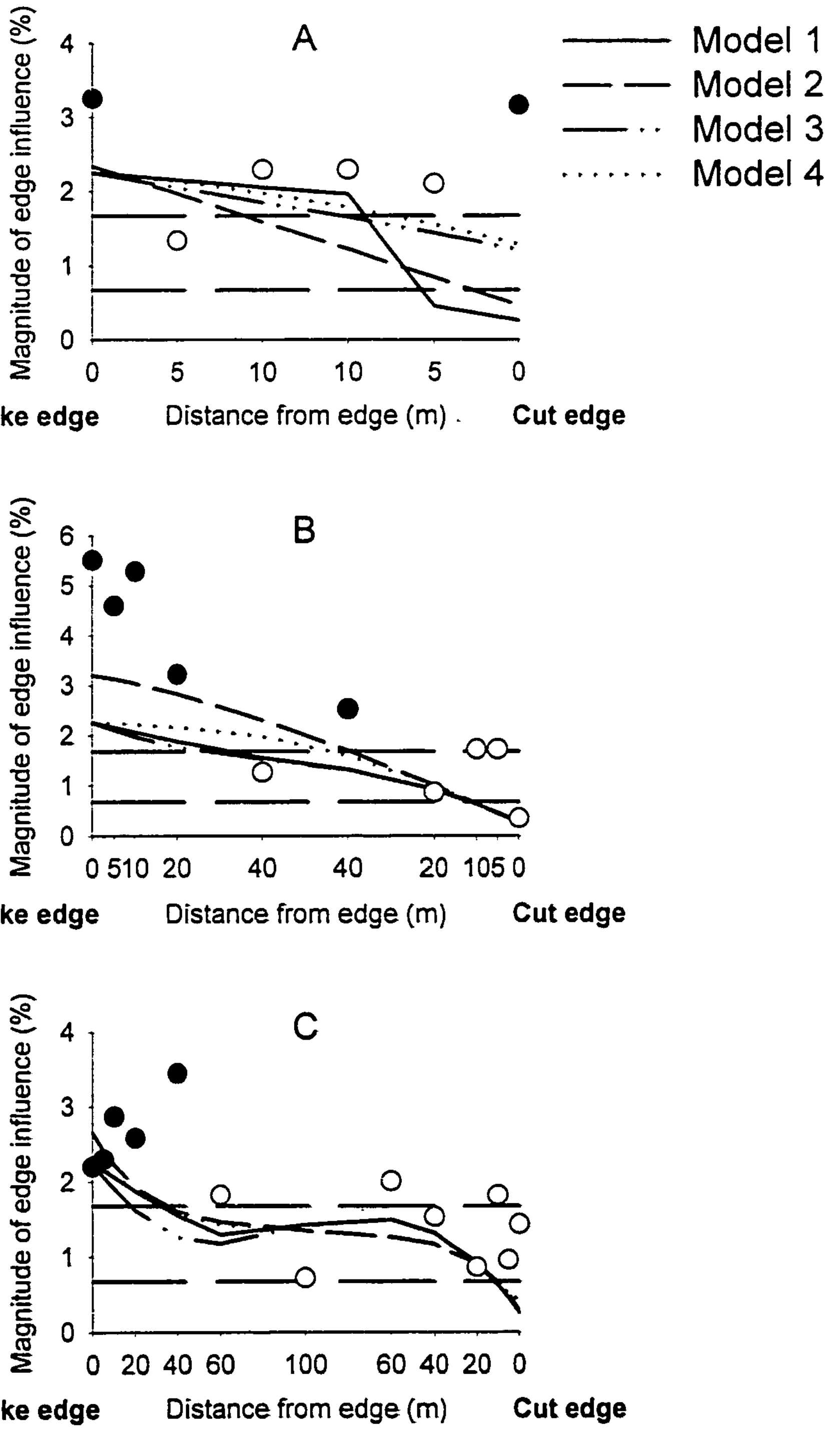

A
Model 1
Model 2
Model 3
Model 4
Magnitude of edge influence (%)
0
1
2
3
4
0
5
10
10
5
0
Lake edge
Distance from edge (m)
Cut edge
B
Magnitude of edge influence (%)
0
1
2
3
4
5
6
0 510 20
40
40
20 105 0
Lake edge
Distance from edge (m)
Cut edge
C
Magnitude of edge influence (%)
0
1
2
3
4
0 20 40 60
100
60 40 20 0
Lake edge
Distance from edge (m)
Cut edge

Figure 4-4. Predicted trends in the magnitude of edge influence on *Populus* spp. sapling density (Model 1: Limitation, Model 2: Combination, Model 3: Resistance, Model 4: Combination modified by resistance), and empirical results across 1 yr old buffers of three different widths: A. 25m, B. 100m, C. 200m. Magnitude of edge influence is the proportional increase or decrease compared to interior forest (see methods). Parallel lines (long dash) correspond to the critical values of interior forest conditions (using sample size of n=10), for comparison with the predicted trends. Values outside these critical values are significantly different from the range of variation in interior forest, and thus exhibit a significant edge influence. Circles represent average magnitude of edge influence for empirical data used to test the models. Filled circles are values that were significantly different from interior forest (using sample sizes of n=3, 4 and 5 for 25, 100 and 200m buffers). Error bars for the empirical data are in Figure 4-16.

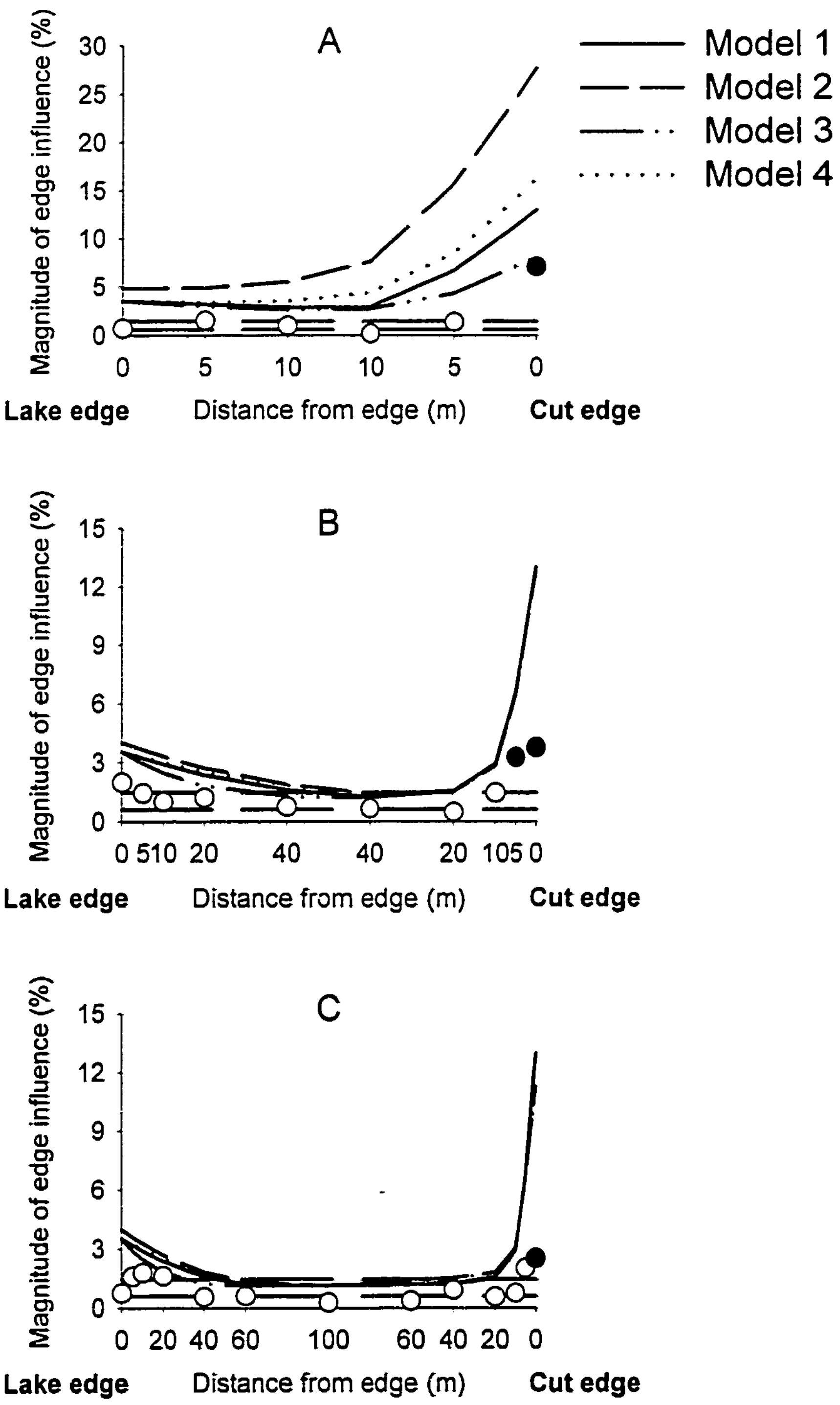

A
Model 1
Model 2
Model 3
Model 4
Magnitude of edge influence (%)
30
25
20
15
10
5
0
0 5 10 10 5 0
Lake edge
Distance from edge (m)
Cut edge
B
Magnitude of edge influence (%)
15
12
9
6
3
0
0 5 10 20 40 40 20 10 5 0
Lake edge
Distance from edge (m)
Cut edge
C
Magnitude of edge influence (%)
15
12
9
6
3
0
0 20 40 60 100 60 40 20 0
Lake edge
Distance from edge (m)
Cut edge

Figure 4-5. Predicted trends in the magnitude of edge influence on *Populus* spp. sapling cover (Model 1: Limitation, Model 2: Combination, Model 3: Resistance, Model 4: Combination modified by resistance), and empirical results across 1 yr old buffers of three different widths: A. 25m, B. 100m, C. 200m. Magnitude of edge influence is the proportional increase or decrease compared to interior forest (see methods). Parallel lines (long dash) correspond to the critical values of interior forest conditions (using sample size of n=10), for comparison with the predicted trends. Values outside these critical values are significantly different from the range of variation in interior forest, and thus exhibit a significant edge influence. Circles represent average magnitude of edge influence for empirical data used to test the models. Filled circles are values that were significantly different from interior forest (using sample sizes of n=3, 4 and 5 for 25, 100 and 200m buffers). Error bars for the empirical data are in Figure 4-17.

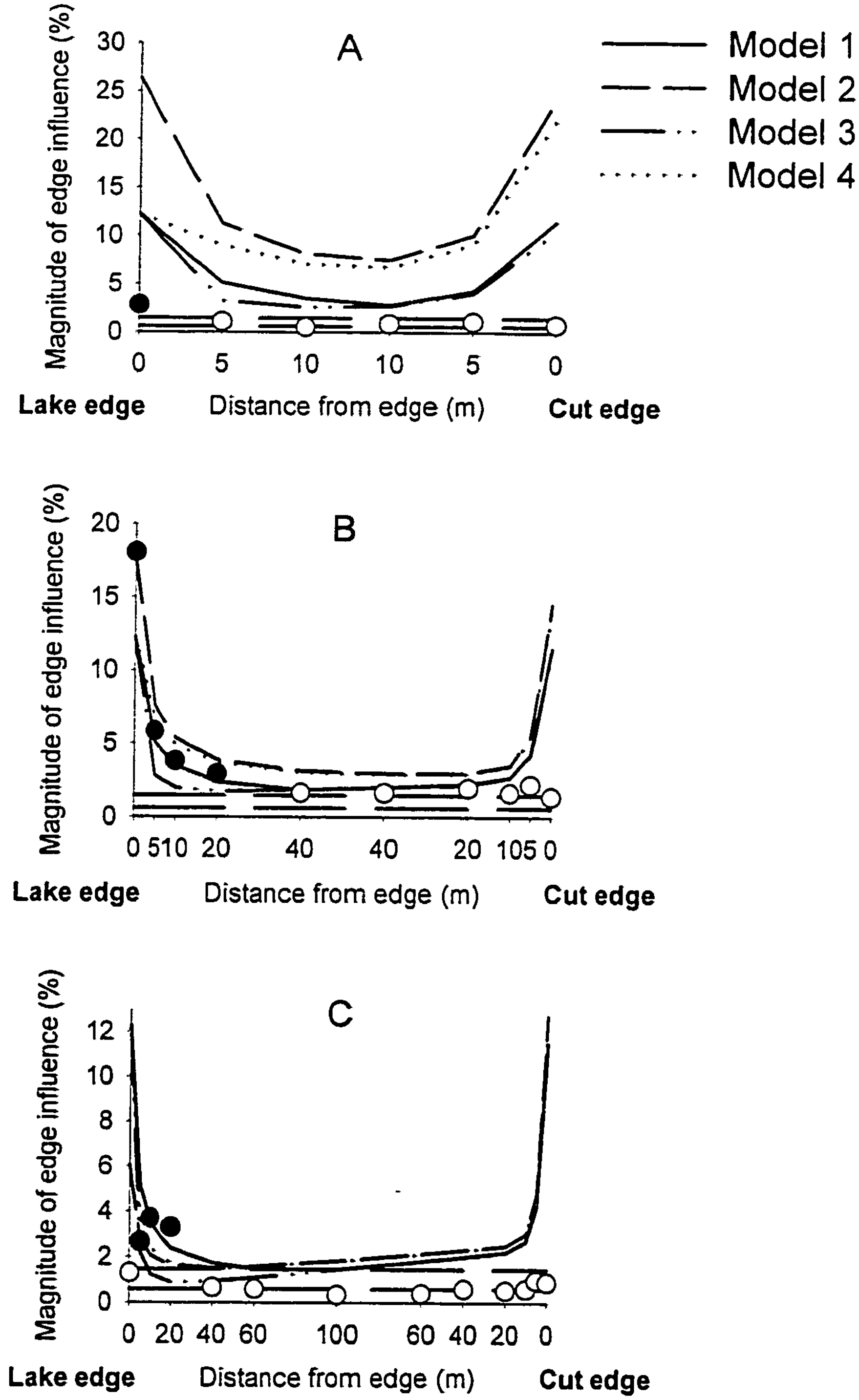

A
Model 1
Model 2
Model 3
Model 4
Magnitude of edge influence (%)
30
25
20
15
10
5
0
0
5
10
10
5
0
Lake edge
Distance from edge (m)
Cut edge
B
Magnitude of edge influence (%)
20
15
10
5
0
0 510 20
40
40
20 105 0
Lake edge
Distance from edge (m)
Cut edge
C
Magnitude of edge influence (%)
12
10
8
6
4
2
0
0 20 40 60
100
60 40 20 0
Lake edge
Distance from edge (m)
Cut edge

Figure 4-6. Predicted trends in the magnitude of edge influence on *Populus* spp. sapling density (Model 1: Limitation, Model 2: Combination, Model 3: Resistance, Model 4: Combination modified by resistance) across 5 yr old buffers of three different widths: A. 25m, B. 100m, C. 200m. Magnitude of edge influence is the proportional increase or decrease compared to interior forest (see methods). Parallel lines (long dash) correspond to the critical values of interior forest conditions (using sample size of n=10), for comparison with the predicted trends. Values outside these critical values are significantly different from the range of variation in interior forest, and thus exhibit a significant edge influence.

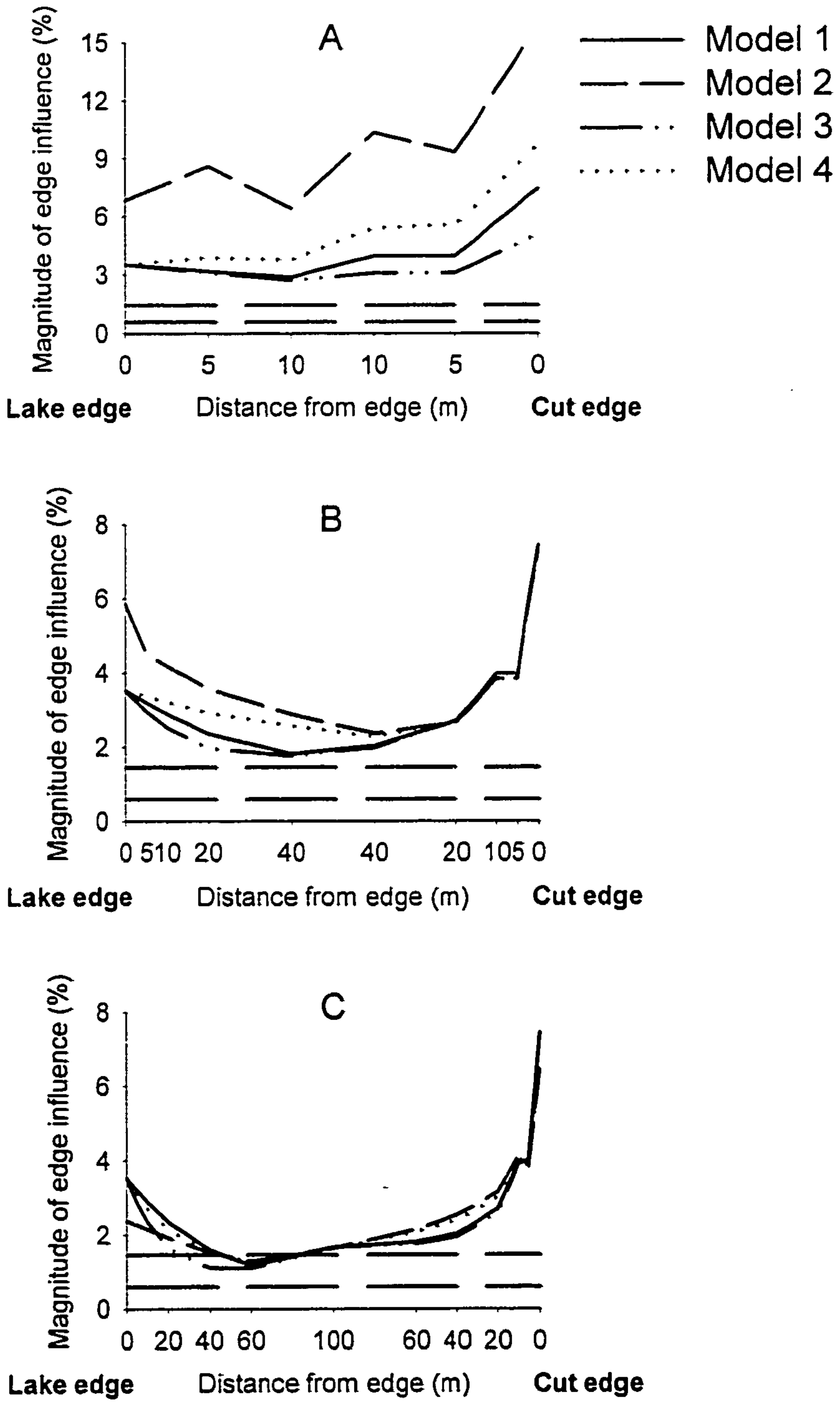

A
Model 1
Model 2
Model 3
Model 4
Magnitude of edge influence (%)
15
12
9
6
3
0
0
5
10
10
5
0
Lake edge
Distance from edge (m)
Cut edge
B
Magnitude of edge influence (%)
8
6
4
2
0
0 510 20
40
40
20 105 0
Lake edge
Distance from edge (m)
Cut edge
C
Magnitude of edge influence (%)
8
6
4
2
0
0 20 40 60
100
60 40 20 0
Lake edge
Distance from edge (m)
Cut edge

Figure 4-7. Predicted trends in the magnitude of edge influence on *Populus* spp. sapling cover (Model 1: Limitation, Model 2: Combination, Model 3: Resistance, Model 4: Combination modified by resistance) across 5 yr old buffers of three different widths: A. 25m, B. 100m, C. 200m. Magnitude of edge influence is the proportional increase or decrease compared to interior forest (see methods). Parallel lines (long dash) correspond to the critical values of interior forest conditions (using sample size of n=10), for comparison with the predicted trends. Values outside these critical values are significantly different from the range of variation in interior forest, and thus exhibit a significant edge influence.

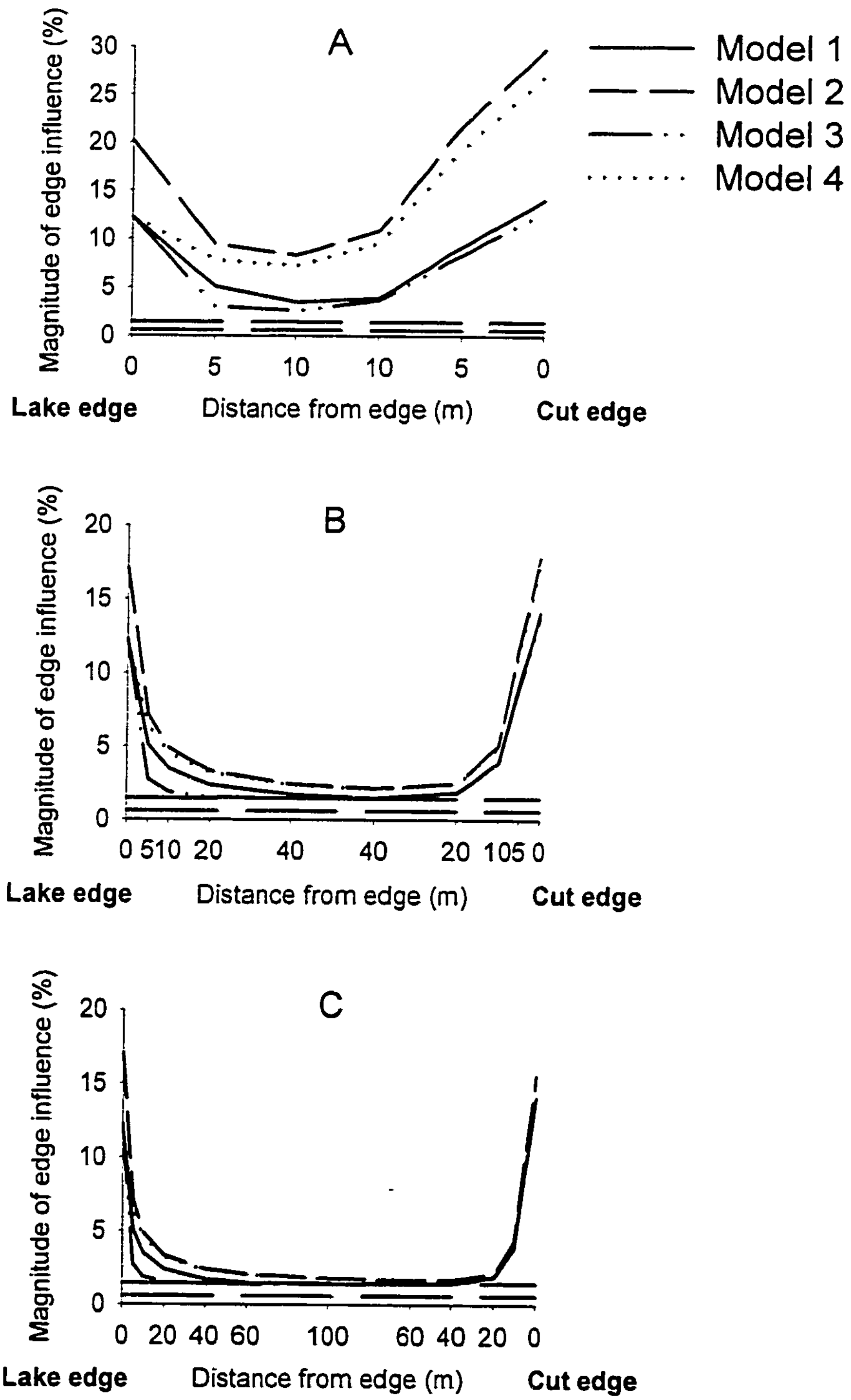

A
Model 1
Model 2
Model 3
Model 4
Magnitude of edge influence (%)
30
25
20
15
10
5
0
0
5
10
10
5
0
Lake edge
Distance from edge (m)
Cut edge
B
Magnitude of edge influence (%)
20
15
10
5
0
0 510 20 40 40 20 105 0
Lake edge
Distance from edge (m)
Cut edge
C
Magnitude of edge influence (%)
20
15
10
5
0
0 20 40 60 100 60 40 20 0
Lake edge
Distance from edge (m)
Cut edge

Figure 4-8. Predicted trends in the magnitude of edge influence on the amount of coarse woody material (Model 1: Limitation, Model 2: Combination, Model 3: Resistance, Model 4: Combination modified by resistance) across 16 yr old buffers of three different widths: A. 25m, B. 100m, C. 200m. Magnitude of edge influence is the proportional increase or decrease compared to interior forest (see methods). Parallel lines (long dash) correspond to the critical values of interior forest conditions (using sample size of n=10), for comparison with the predicted trends. Values outside these critical values are significantly different from the range of variation in interior forest, and thus exhibit a significant edge influence.

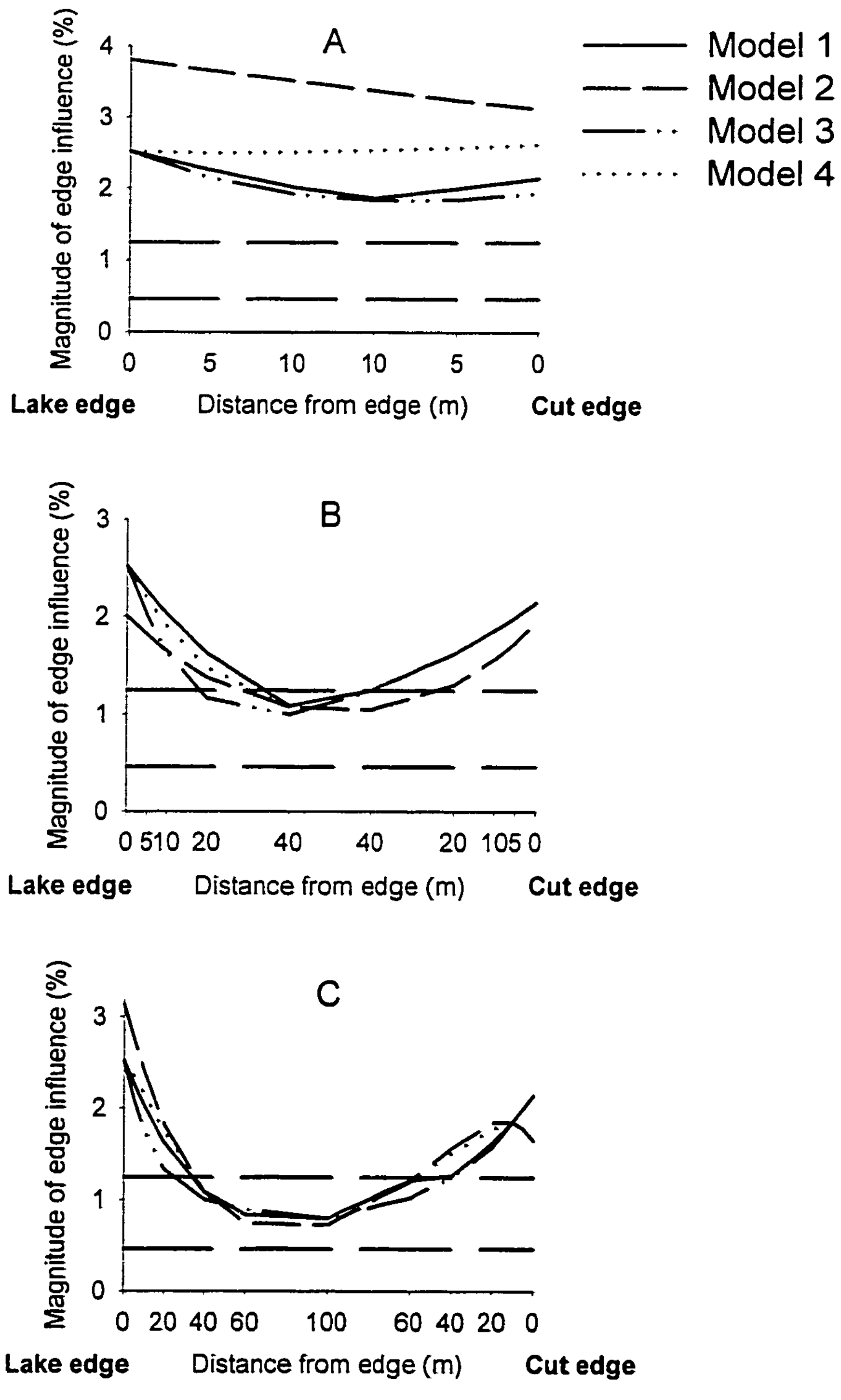

A
Model 1
Model 2
Model 3
Model 4
Magnitude of edge influence (%)
0
1
2
3
4
0 5 10 10 5 0
Lake edge
Distance from edge (m)
Cut edge
B
Magnitude of edge influence (%)
0
1
2
3
0 5 10 20 40 40 20 10 5 0
Lake edge
Distance from edge (m)
Cut edge
C
Magnitude of edge influence (%)
0
1
2
3
0 20 40 60 100 60 40 20 0
Lake edge
Distance from edge (m)
Cut edge

Figure 4-9. Predicted trends in the magnitude of edge influence on canopy tree density (Model 1: Limitation, Model 2: Combination, Model 3: Resistance, Model 4: Combination modified by resistance) across 16 yr old buffers of three different widths: A. 25m, B. 100m, C. 200m. Magnitude of edge influence is the proportional increase or decrease compared to interior forest (see methods). Parallel lines (long dash) represent magnitude of edge influence corresponding to critical values of interior forest conditions, for comparison with the predicted trends. Values outside these critical values are significantly different from the range of variation in interior forest, and thus exhibit a significant edge influence.

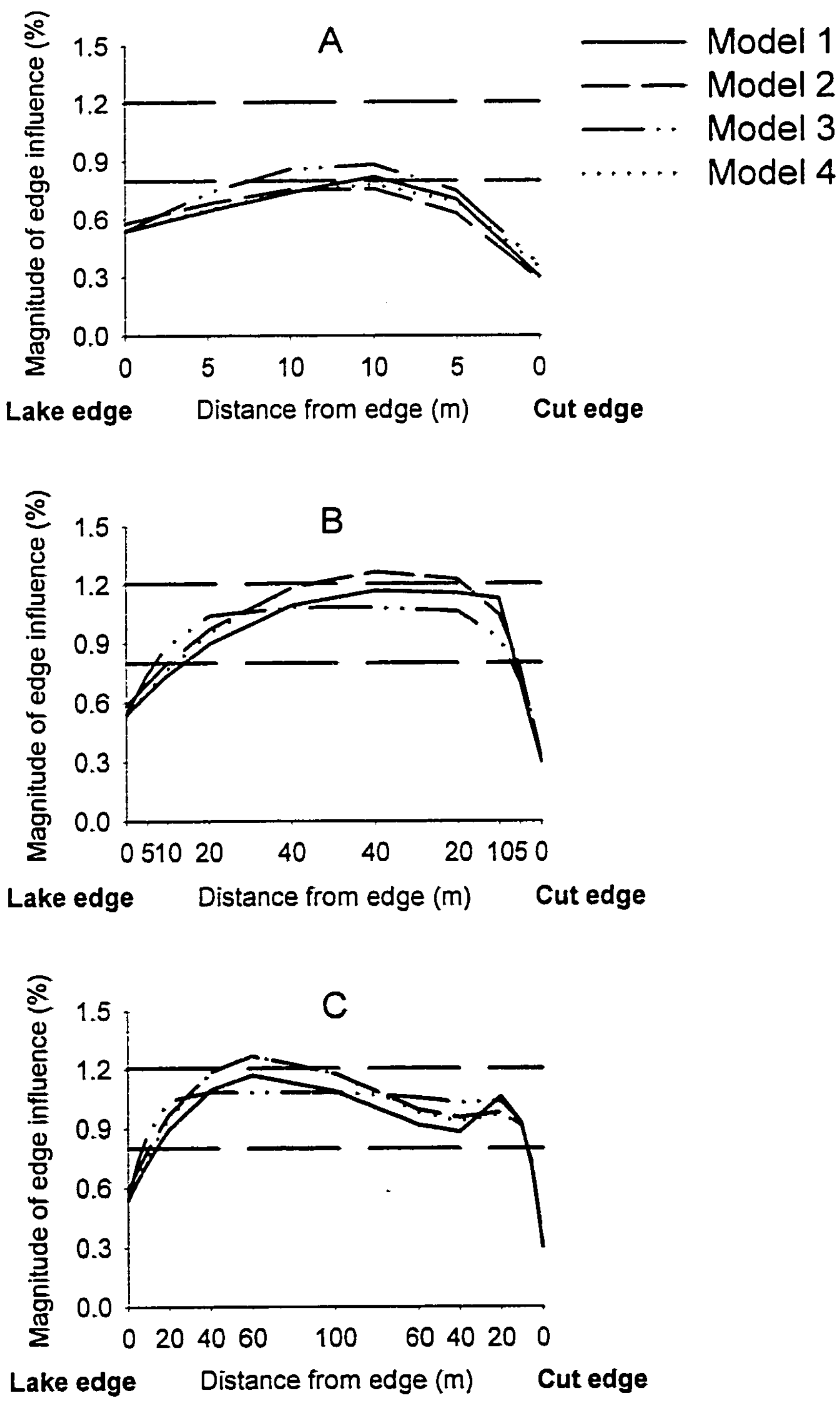
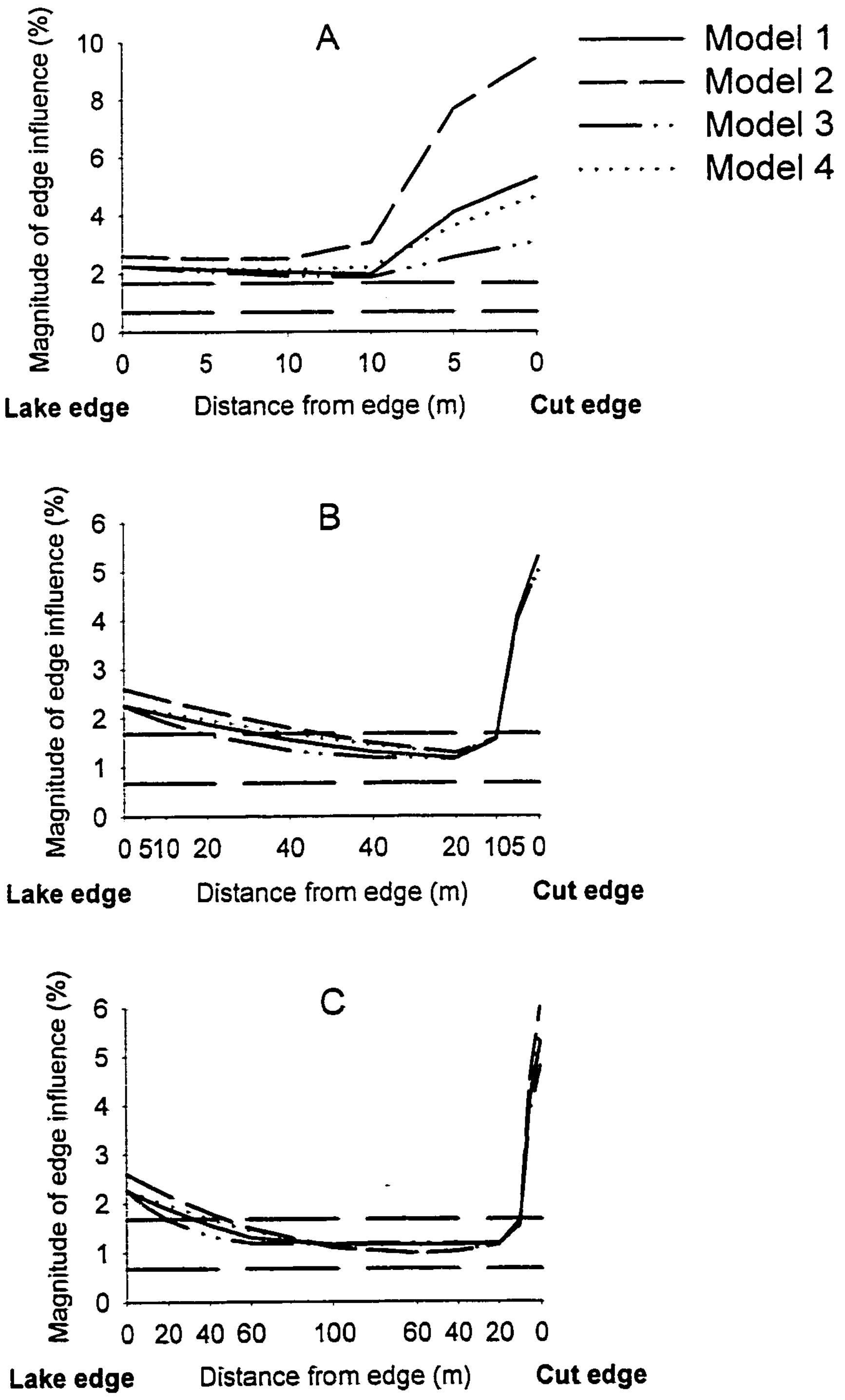

A
B
C
Model 1
Model 2
Model 3
Model 4
Magnitude of edge influence (%)
1.5
1.2
0.9
0.6
0.3
0.0
0 5 10 10 5 0
0 5 10 20 40 40 20 10 5 0
0 20 40 60 100 60 40 20 0
Lake edge
Distance from edge (m)
Cut edge

Figure 4-10. Predicted trends in the magnitude of edge influence on mid-canopy tree density (Model 1: Limitation, Model 2: Combination, Model 3: Resistance, Model 4: Combination modified by resistance) across 16 yr old buffers of three different widths: A. 25m, B. 100m, C. 200m. Magnitude of edge influence is the proportional increase or decrease compared to interior forest (see methods). Parallel lines (long dash) correspond to the critical values of interior forest conditions (using sample size of n=10), for comparison with the predicted trends. Values outside these critical values are significantly different from the range of variation in interior forest, and thus exhibit a significant edge influence.


A
Model 1
Model 2
Model 3
Model 4
Magnitude of edge influence (%)
0
2
4
6
8
10
0
5
10
10
5
0
Lake edge
Distance from edge (m)
Cut edge
B
Magnitude of edge influence (%)
0
1
2
3
4
5
6
0 5 10 20 40 40 20 10 5 0
Lake edge
Distance from edge (m)
Cut edge
C
Magnitude of edge influence (%)
0
1
2
3
4
5
6
0 20 40 60 100 60 40 20 0
Lake edge
Distance from edge (m)
Cut edge

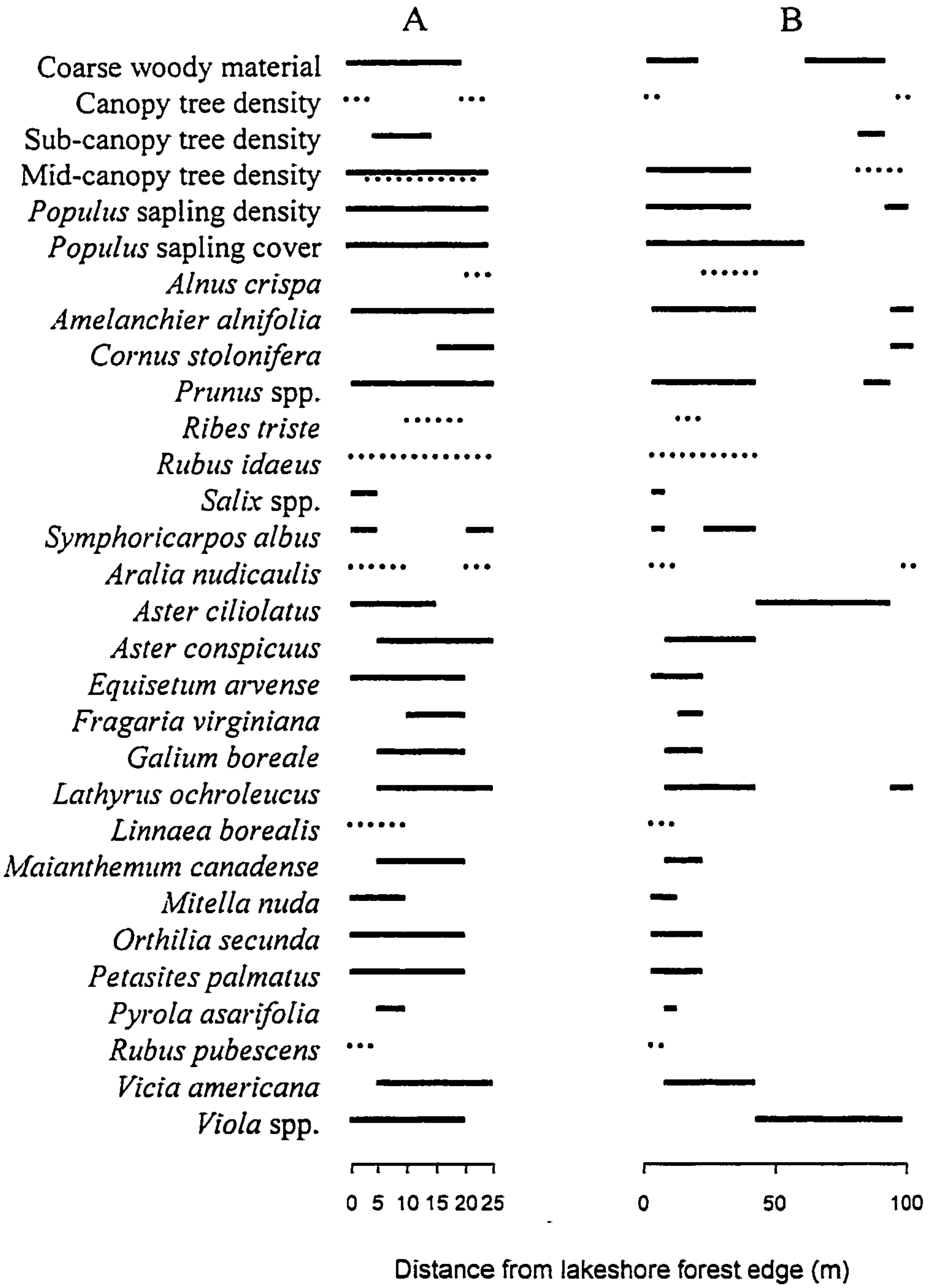
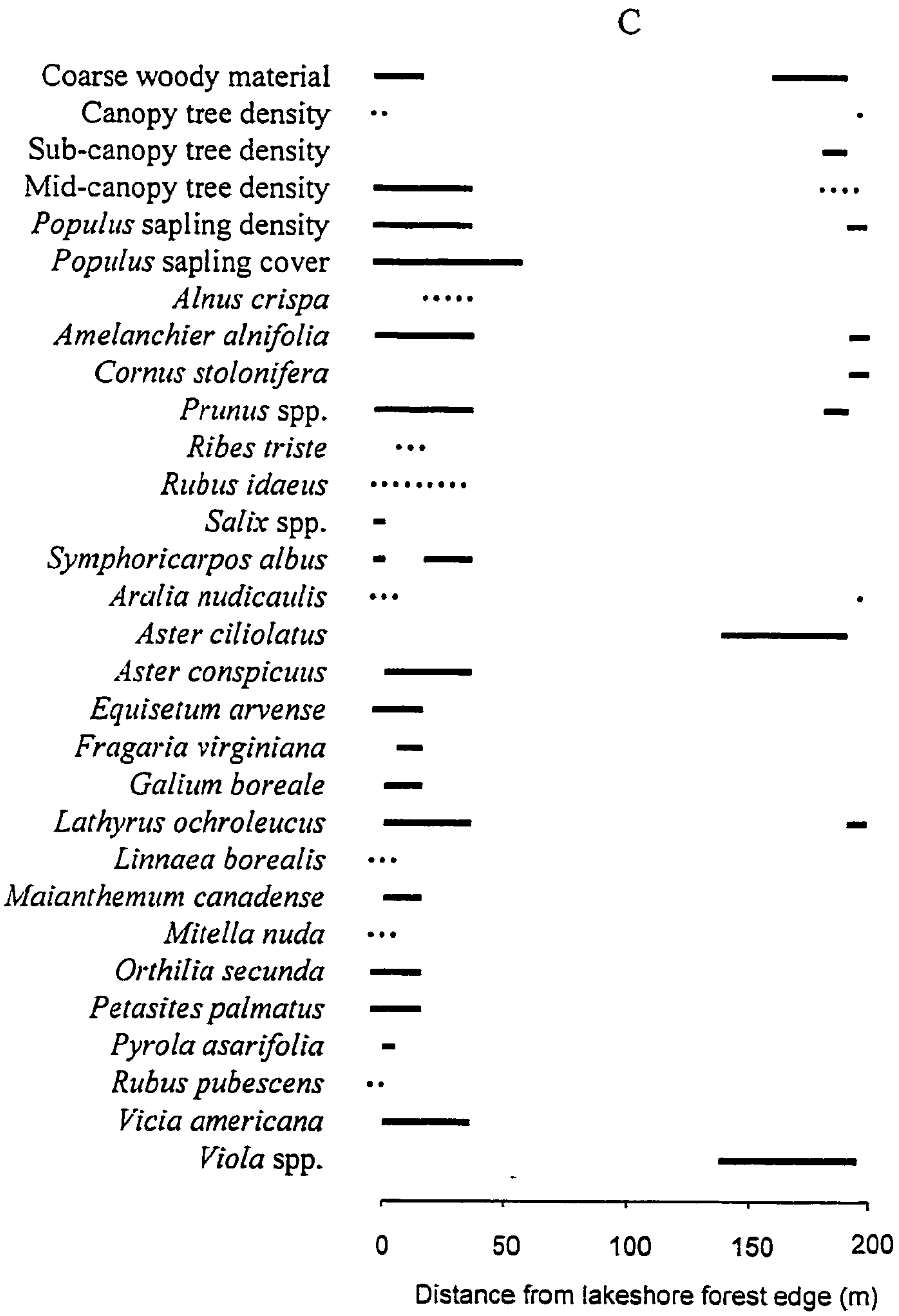


Figure 4-11. Predicted distance of edge influence in 1 yr old buffers of three different widths: A. 25m, B. 100m, C. 200m, based on the limitation model. Lines represent distances where average values are predicted to be significantly greater (solid lines) or less (dotted lines) than in interior forest. In A, note that the mid-canopy tree density was significantly greater at lakeshore edges, but significantly lower at 1 yr old clearcut edges.


C
Coarse woody material
Canopy tree density
Sub-canopy tree density
Mid-canopy tree density
Populus sapling density
Populus sapling cover
Alnus crispa
Amelanchier alnifolia
Cornus stolonifera
Prunus spp.
Ribes triste
Rubus idaeus
Salix spp.
Symphoricarpos albus
Aralia nudicaulis
Aster ciliolatus
Aster conspicuus
Equisetum arvense
Fragaria virginiana
Galium boreale
Lathyrus ochroleucus
Linnaea borealis
Maianthemum canadense
Mitella nuda
Orthilia secunda
Petasites palmatus
Pyrola asarifolia
Rubus pubescens
Vicia americana
Viola spp.
0
50
100
150
200
Distance from lakeshore forest edge (m)

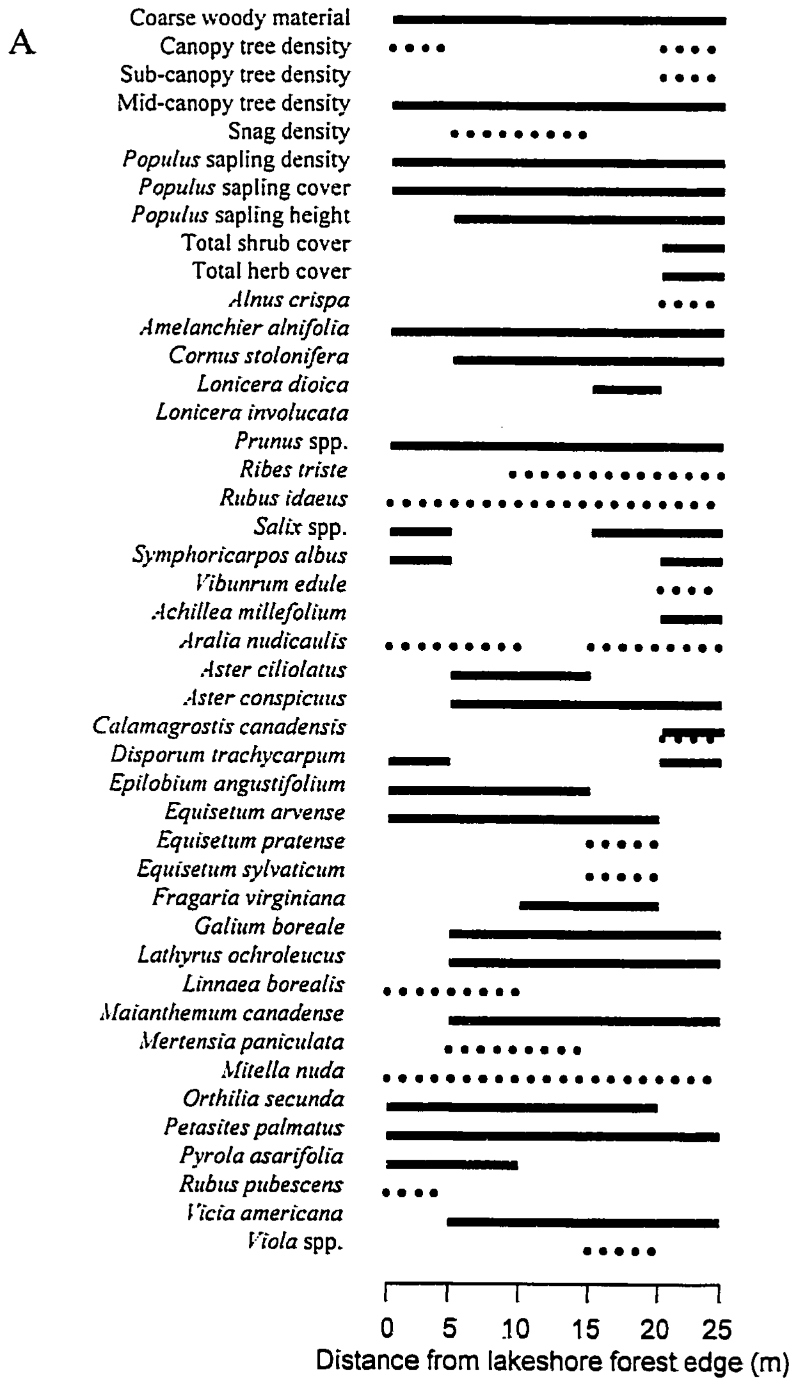
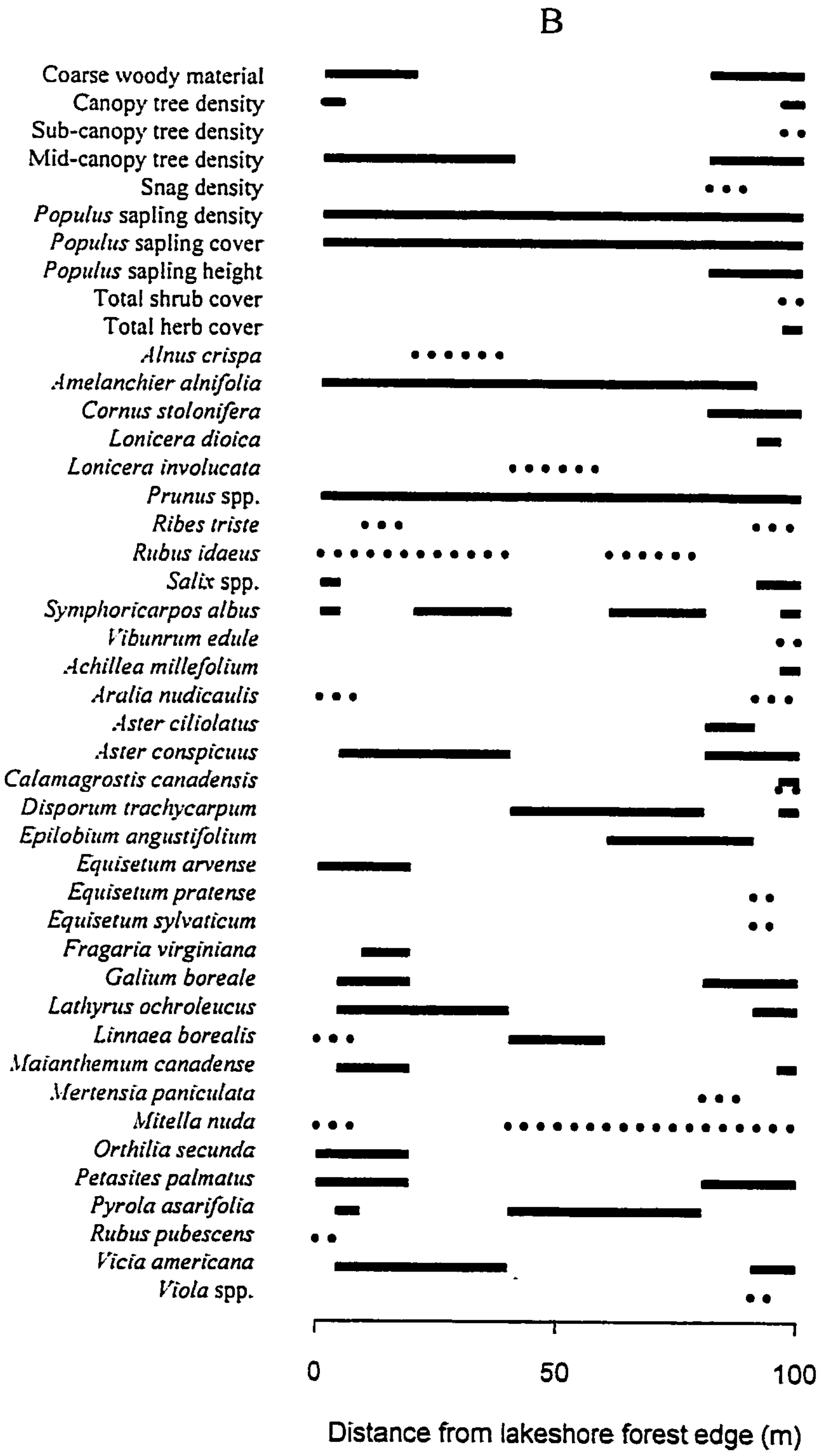
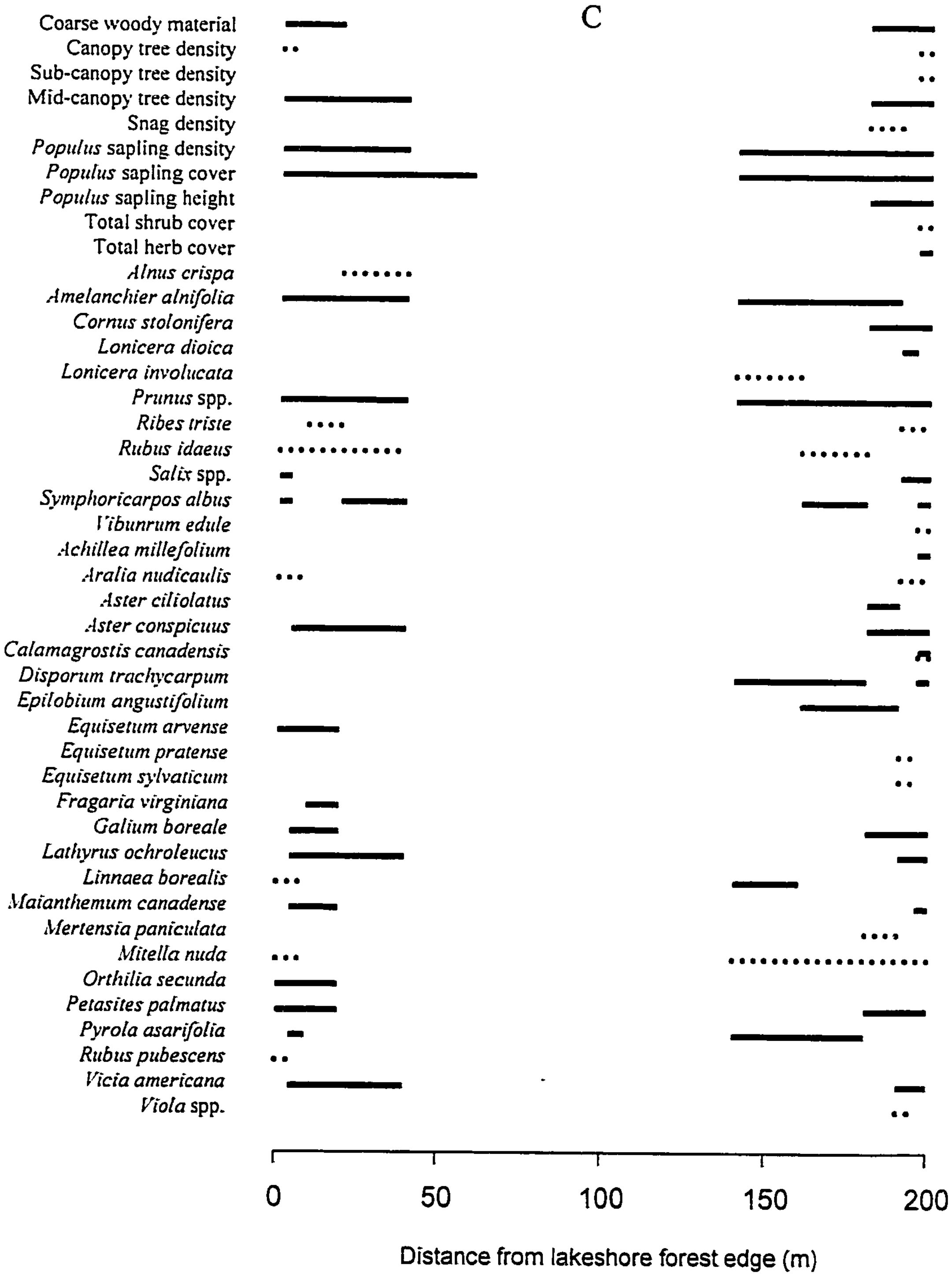


Figure 4-12. Predicted distance of edge influence in older buffers of three different widths: A. 25m, B. 100m, C. 200m. Lines represent distances where average values are predicted to be significantly greater (solid lines) or less (dotted lines) than in interior forest. Results for the older edges were combined by using the larger of the two DEI values from 5 or 16 yr old clearcut edges. Note that the cover of *Calamagrostis canadensis* was significantly greater at 5 yr old edges, but significantly lower at 16 yr old edges.


B
Coarse woody material
Canopy tree density
Sub-canopy tree density
Mid-canopy tree density
Snag density
Populus sapling density
Populus sapling cover
Populus sapling height
Total shrub cover
Total herb cover
Alnus crispa
Amelanchier alnifolia
Cornus stolonifera
Lonicera dioica
Lonicera involucata
Prunus spp.
Ribes triste
Rubus idaeus
Salix spp.
Symphoricarpos albus
Vibunrum edule
Achillea millefolium
Aralia nudicaulis
Aster ciliolatus
Aster conspicuus
Calamagrostis canadensis
Disporum trachycarpum
Epilobium angustifolium
Equisetum arvense
Equisetum pratense
Equisetum sylvaticum
Fragaria virginiana
Galium boreale
Lathyrus ochroleucus
Linnaea borealis
Maianthemum canadense
Mertensia paniculata
Mitella nuda
Orthilia secunda
Petasites palmatus
Pyrola asarifolia
Rubus pubescens
Vicia americana
Viola spp.
0
50
100
Distance from lakeshore forest edge (m)


C
Coarse woody material
Canopy tree density
Sub-canopy tree density
Mid-canopy tree density
Snag density
Populus sapling density
Populus sapling cover
Populus sapling height
Total shrub cover
Total herb cover
Alnus crispa
Amelanchier alnifolia
Cornus stolonifera
Lonicera dioica
Lonicera involucata
Prunus spp.
Ribes triste
Rubus idaeus
Salix spp.
Symphoricarpos albus
Vibunrum edule
Achillea millefolium
Aralia nudicaulis
Aster ciliolatus
Aster conspicuus
Calamagrostis canadensis
Disporum trachycarpum
Epilobium angustifolium
Equisetum arvense
Equisetum pratense
Equisetum sylvaticum
Fragaria virginiana
Galium boreale
Lathyrus ochroleucus
Linnaea borealis
Maianthemum canadense
Mertensia paniculata
Mitella nuda
Orthilia secunda
Petasites palmatus
Pyrola asarifolia
Rubus pubescens
Vicia americana
Viola spp.
0
50
100
150
200
Distance from lakeshore forest edge (m)

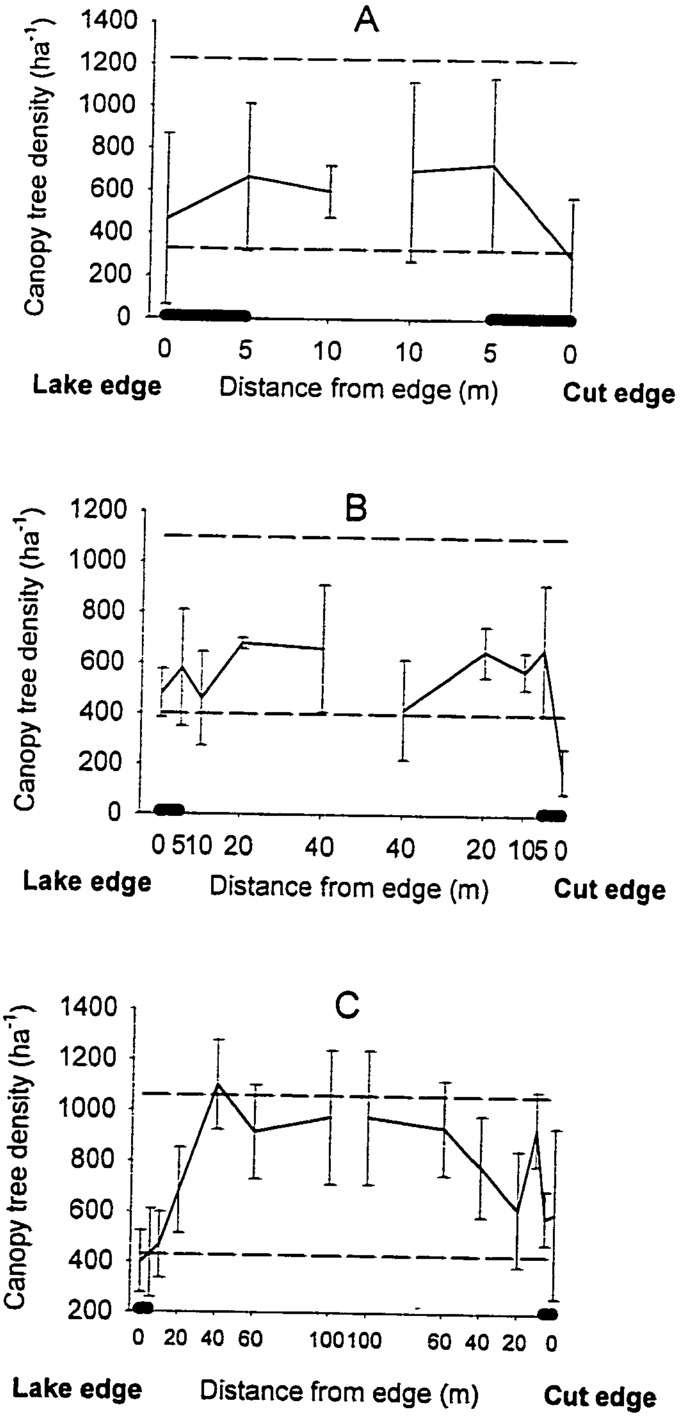


Figure 4-13. Average canopy tree density in the first year post-harvest across buffers of three different widths: A. 25m, B. 100m, C. 200m. Distances are from either the lakeshore or clearcut forest edge. Dashed lines represent critical values from the range of variation in interior riparian forest determined by randomization tests. The thick solid lines indicate the predicted distance of edge influence (from Figure 4-11). Bars represent ± 1 SE.

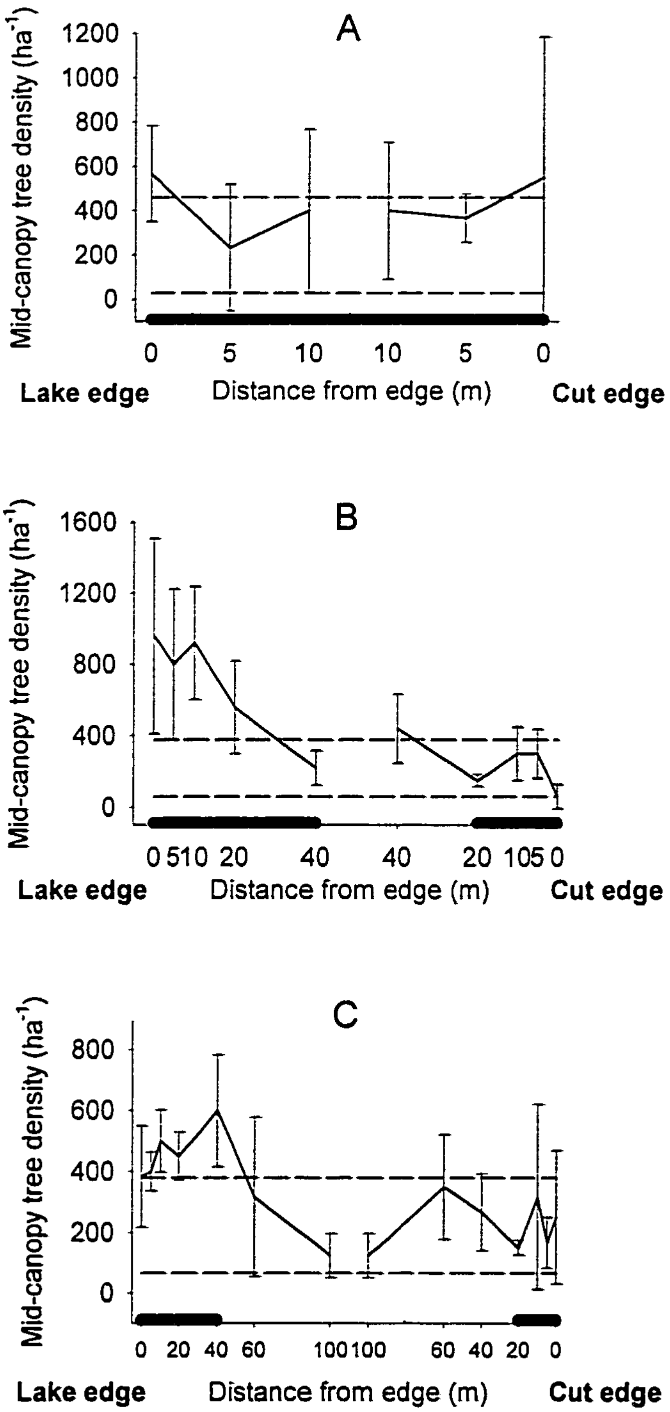


Figure 4-14. Average mid-canopy tree density in the first year post-harvest across buffers of three different widths: A. 25m, B. 100m, C. 200m. Distances are from either the lakeshore or clearcut forest edge. Dashed lines represent critical values from the range of variation in interior riparian forest determined by randomization tests. The thick solid lines indicate the predicted distance of edge influence (from Figure 4-11). Bars represent ± 1 SE.

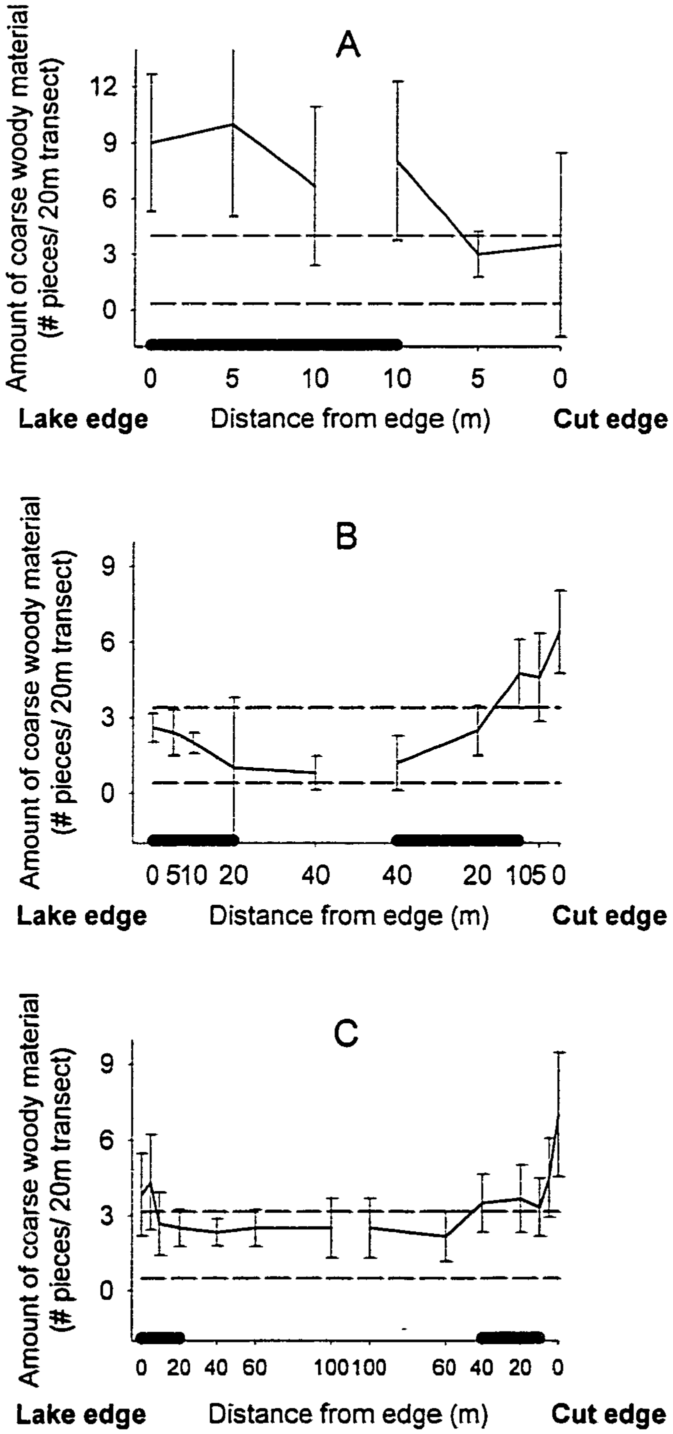


Figure 4-15. Average amount of coarse woody material in the first year post-harvest across buffers of three different widths: A. 25m, B. 100m, C. 200m. Distances are from either the lakeshore or clearcut forest edge. Dashed lines represent critical values from the range of variation in interior riparian forest determined by randomization tests. The thick solid lines indicate the predicted distance of edge influence (from Figure 4-11). Bars represent ± 1 SE.

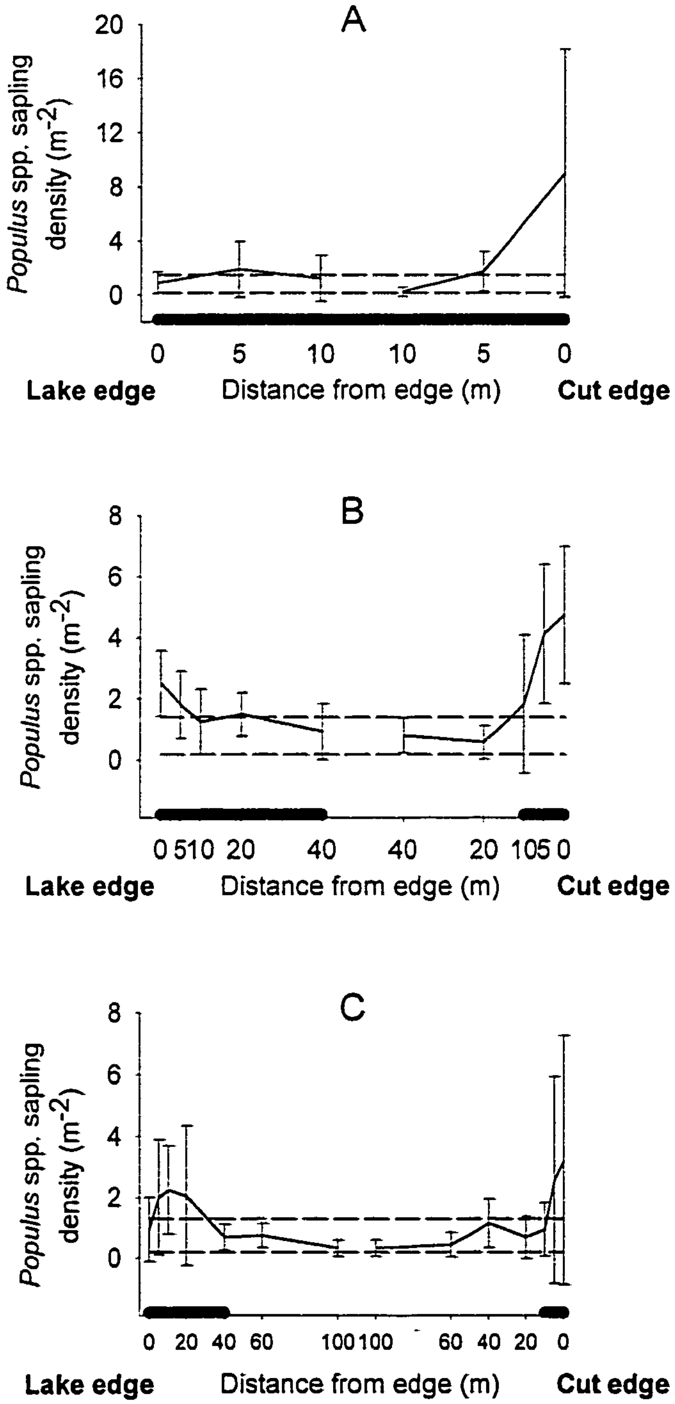


Figure 4-16. Average *Populus* spp. sapling density in the first year post-harvest across buffers of three different widths: A. 25m, B. 100m, C. 200m. Distances are from either the lakeshore or clearcut forest edge. Dashed lines represent critical values from the range of variation in interior riparian forest determined by randomization tests. The thick solid lines indicate the predicted distance of edge influence (from Figure 4-11). Bars represent ± 1 SE; error was calculated among subplots.

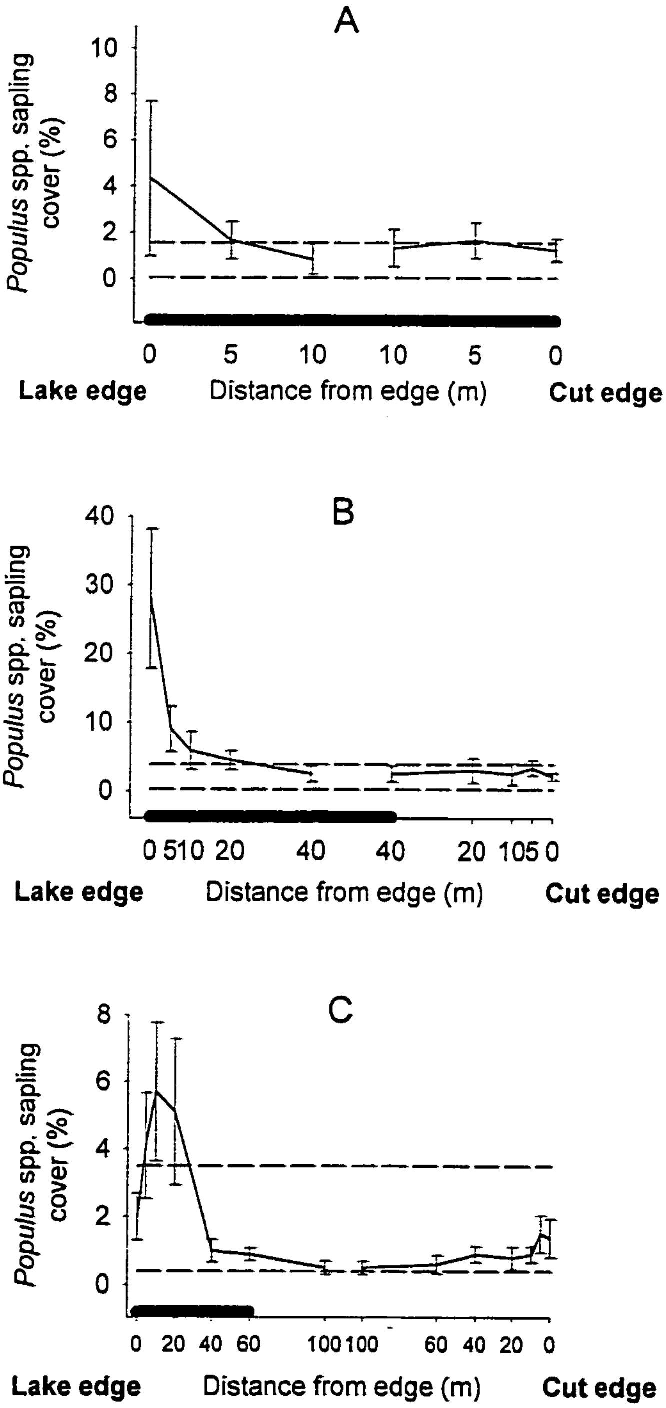


Figure 4-17. Average *Populus* spp. sapling cover in the first year post-harvest across buffers of three different widths: A. 25m, B. 100m, C. 200m. Distances are from either the lakeshore or clearcut forest edge. Dashed lines represent critical values from the range of variation in interior riparian forest determined by randomization tests. The thick solid lines indicate the predicted distance of edge influence (from Figure 4-11). Bars represent ± 1 SE; error was calculated among subplots.

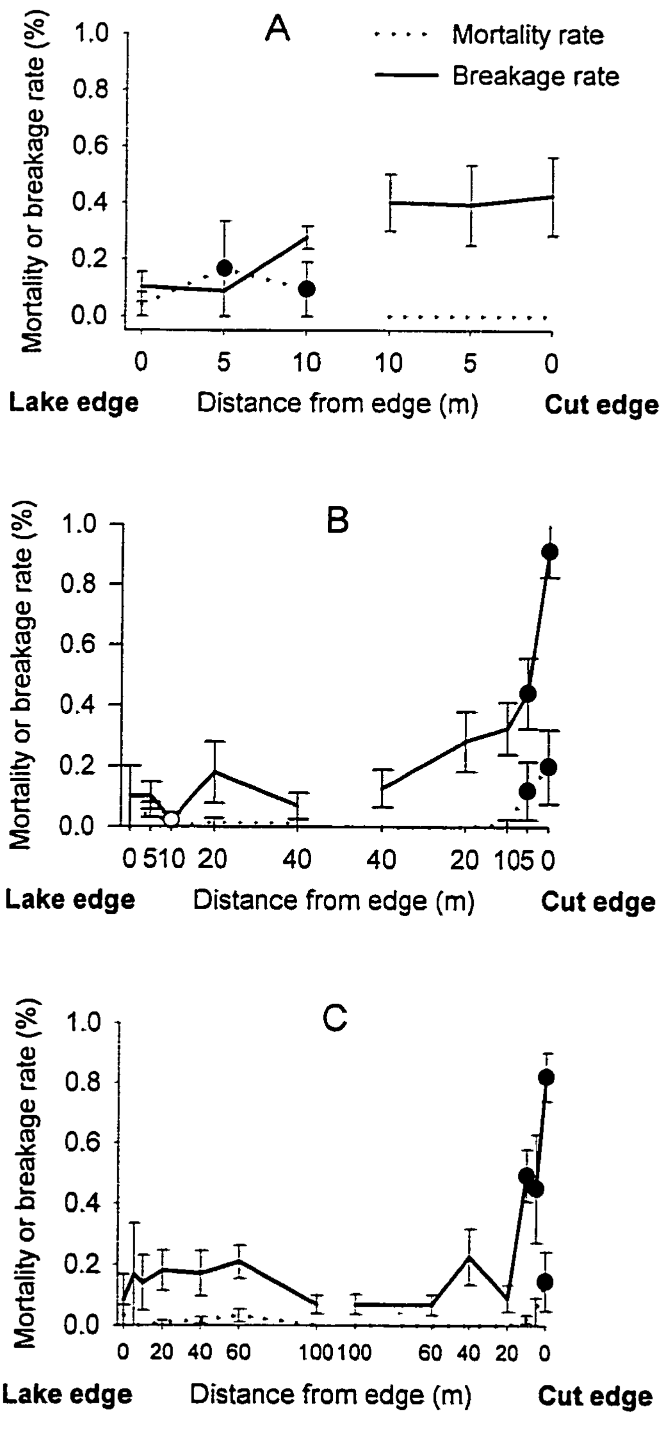


Figure 4-18. Mortality and snag breakage rates across buffers of three different widths: A. 25m, B. 100m, C. 200m. Distances are from either the lakeshore or clearcut forest edge. Symbols represent rates that were significantly greater (filled circles) or less (open circles) than rates in interior forest over the same time period. Bars represent ± 1 SE.

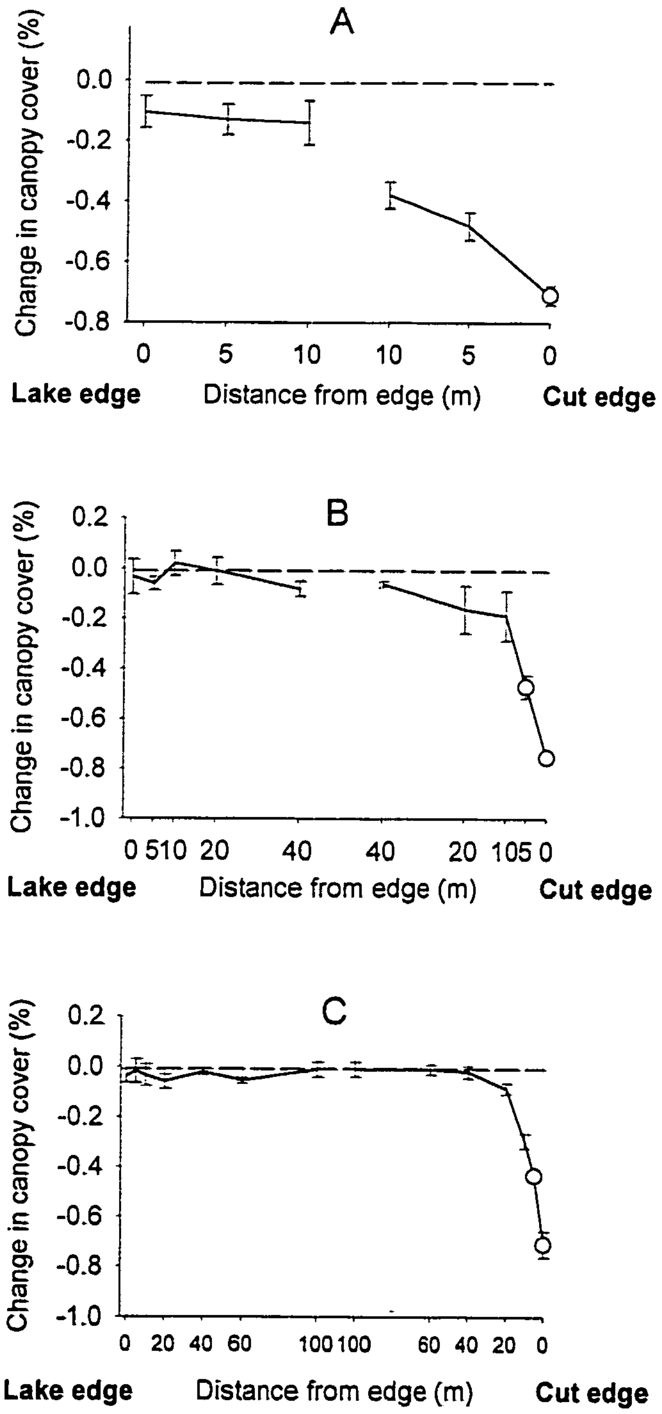


Figure 4-19. Change in canopy cover from the pre-harvest year to the first post-harvest year across buffers of three different widths: A. 25m, B. 100m, C. 200m. Distances are from either the lakeshore or clearcut forest edge. Symbols represent changes that were significantly less than in interior forest. Dashed lines represent the average change in interior forest. Bars represent ± 1 SE.

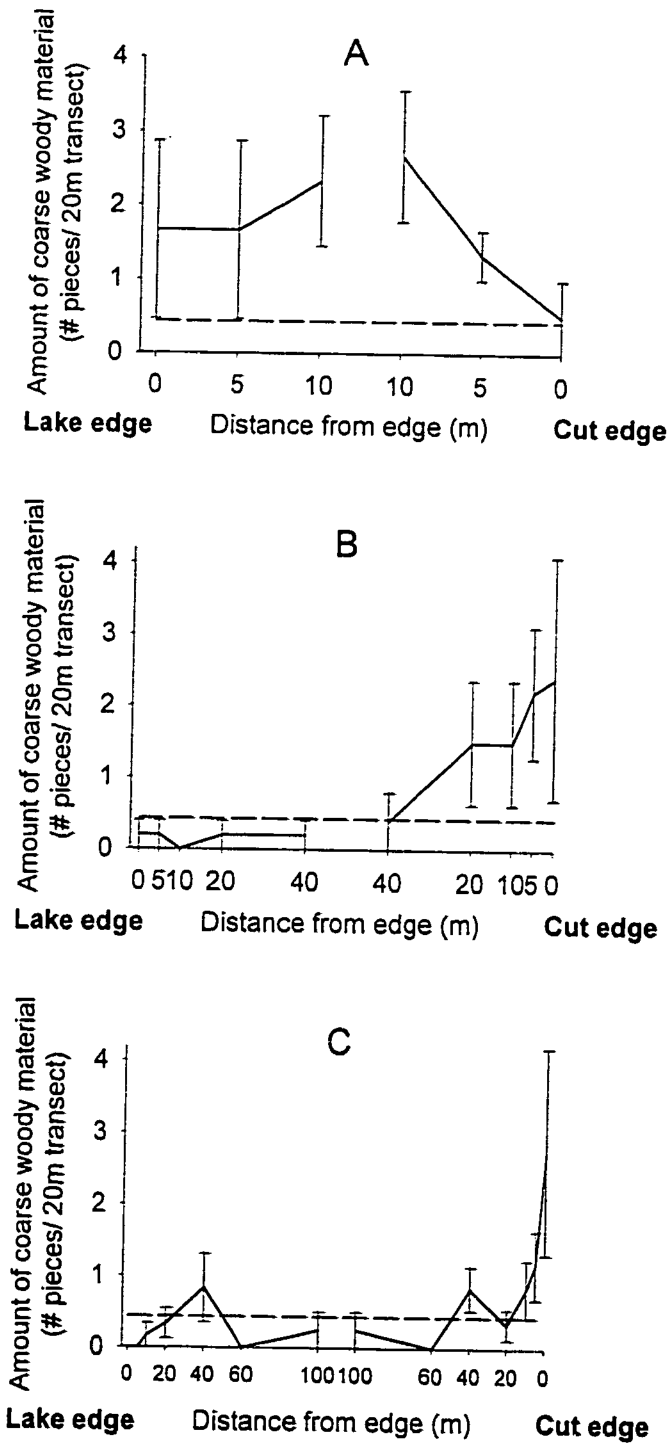


Figure 4-20. Accumulation of coarse woody material from the pre-harvest year to the first post-harvest year across buffers of three different widths: A. 25m, B. 100m, C. 200m. Distances are from either the lakeshore or clearcut forest edge. Dashed lines represent the average accumulation in interior forest. No values were significantly different than changes in interior forest. Bars represent ± 1 SE.

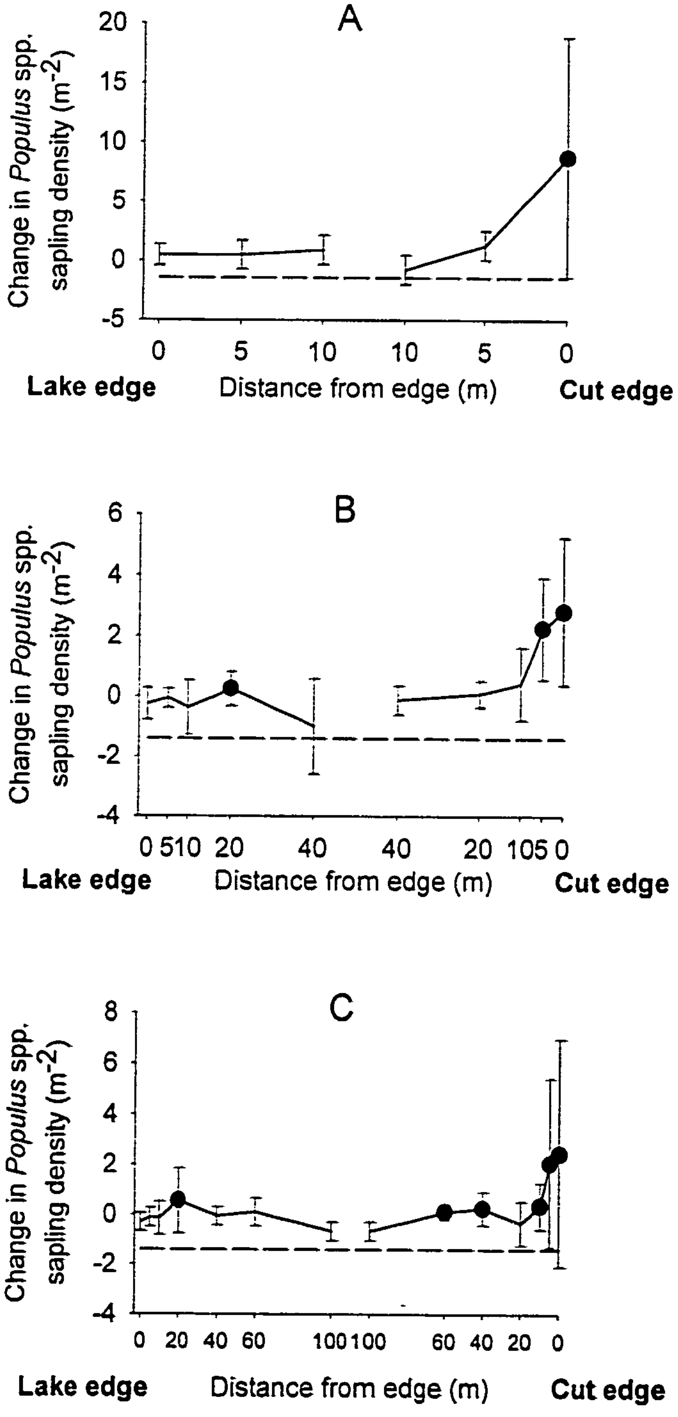


Figure 4-21. Change in *Populus* spp. sapling density from the pre-harvest year to the first post-harvest year across buffers of three different widths: A. 25m, B. 100m, C. 200m. Distances are from either the lakeshore or clearcut forest edge. Symbols represent changes that were significantly greater than in interior forest. Dashed lines represent the average change in interior forest. Bars represent ± 1 SE.

Plate 4-1. A portion of the 25m buffer surrounding a lake in the Lac La Biche study area. In this part of the buffer, most of the trees blew down following harvesting of the adjacent cutblock.

CHAPTER 5. CONCLUSIONS

Forest structure and composition were significantly different at both lakeshore and clearcut forest edges than in interior aspen-dominated boreal forest. Thus, these natural and artificial edges can be described as distinct elements in the heterogeneous mixedwood landscape mosaic. Specific conclusions from this research include (numbers and letters correspond to objectives listed in Chapter 1):

1. Lakeshore forest edges were characterized by greater structural diversity including higher amounts of downed coarse woody material, saplings and mid-canopy trees; but fewer canopy trees and snags. Some understory herb and shrub species were more abundant near the edge, while others were less abundant.
   A. The lakeshore distance of edge influence (DEI) was generally 40m, although estimates of DEI varied considerably for different response variables, and did not always start at 0m.
   B. In riparian forest, four selected species exhibited different patterns of abundance along the edge-to-interior gradient.
2. Following harvest, clearcut edges experienced damage to live trees and snags, increasing coarse woody material. Prolific suckering of *Populus* spp. was accompanied by a decrease in total shrub cover and some changes in the cover of individual herb and shrub species.
   A. The clearcut DEI extended about 20m into the forest for most response variables, although some significant effects were detected at greater distances.
   B. Edges of older cutblocks also had higher sapling density and cover, accompanied by lower overall shrub cover, as compared to the interior forest. Many herbs had greater cover at the older edges, while a few herbs had lower cover. Tree density was greater at 16 yr old edges since some of the saplings had developed into mid-canopy trees. Overall, DEI was not substantially different at edges of different age.
3. Four alternative models of magnitude of edge influence (MEI) in buffers were developed which incorporated different interactions of edge influence: 1) edge influence limited to the strongest influence from either the lakeshore or clearcut edge, 2) combined edge influence from both lakeshore and clearcut edges, 3) resistance of the riparian forest to clearcut edge influence and 4) combined edge influence modified by resistance. Predictions of the width of interior forest in buffers were made for 1 yr old and older buffers by subtracting the lakeshore and clearcut DEI from the actual buffer width for three different widths: 25, 100 and 200m. The models and predictions could only be tested for 1 yr old buffers.
   A. There was greater MEI with combination of edge influence and lower MEI with resistance, particularly in narrow buffers. The models predicted that there would be virtually no interior forest left in 25m buffers. In the 100m buffers, only a few variables were predicted to be significantly different from interior forest throughout most or all of the buffer width. A considerable width of interior forest habitat (approx. 100m) was predicted for the 200m

buffers.

B. Empirical results did not fit the models very well, but lower MEI and DEI for structural changes in narrow buffers provided some evidence for resistance of the riparian forest to additional edge influence. Predictions of the amount of interior forest left in 1 yr old buffer zones were generally validated by the empirical results for forest structure, but not understory composition, most likely due to inadequate sample sizes.

SYNTHESIS

Comparison of forest structure and composition of lakeshore and clearcut edges

In this section, I compare edge influence at lakeshore forest edges (using the adjacent riparian data set, Chapter 2) and at clearcut edges of different age (Chapter 3). The structure of natural, inherent lakeshore forest edges resembled that of older clearcut forest edges. At both lakeshore forest edges and 16 yr old clearcut edges, there was a greater amount of downed coarse woody material, fewer canopy trees and more mid-canopy trees, with similar distance of edge influence (DEI) for both types of edge. However, at lakeshore forest edges, the trends in canopy tree density and mid-canopy tree density along the edge-to-interior gradient were more gradual than at the older clearcut edges (Figure 5-1). Overall, after sixteen years of tree mortality, snag damage and sapling growth, forest structure at clearcut edges approximated the structure of more permanent lakeshore edges; however, this similarity may only be transient as clearcut edges continue to develop. Interior forest wildlife species that avoid lakeshore edges (e.g. Ovenbird, Lambert 1998), possibly due to forest structure, may be most affected by clearcut edge influence at this stage of development.

At lakeshore forest edges, average *Populus* spp. sapling density, cover and height were similar to the older clearcut edges where saplings were well established but had not yet become trees. Sapling densities resembled those at 16 yr old edges (Figure 5-2A), but at the lakeshore edge there was a greater DEI (0-40m). Sapling cover at the lakeshore forest edges was most similar to the 5 yr old edges (Figure 5-2B) with similar DEI (0-60m). Greater *Populus* spp. sapling height was evident further into the forest at the lakeshore forest edges (DEI=0-60m) than at the older clearcut edges (DEI=0-20m). Average maximum height was similar to the 5 yr old edges (Figure 5-2C).

Increased light and associated increased temperature could contribute to suckering at both types of edge. However, disturbance is likely a more important factor. Recruitment of *Populus* spp. saplings at clearcut edges consisted of a pulse of suckering during the summer following harvesting, with limited subsequent recruitment. At lakeshore forest edges, suckering could arise periodically from the roots of trees at the edge that die from blowdown and/or flooding.

Understory composition differed between lakeshore and clearcut forest edges, although some species exhibited similar responses to edge influence at both types of edges (Chapters 2 and 3). Four shrub species (*Amelanchier alnifolia, Lonicera dioica, Prunus* spp., *Salix* spp.) and seven herb species (*Aster conspicuus, Galium boreale,* *Lathyrus ochroleucus, Maianthemum canadense, Petasites palmatus, Pyrola asarifolia, Vicia americana*) were considered 'edge-positive' species (greater cover at the edge) at both lakeshore and clearcut forest edges. Three 'edge-negative' shrub species (*Alnus crispa, Ribes triste, Rubus idaeus*) and only one herb species (*Mitella nuda)* had lower cover at both types of edge. Although responses were sometimes similar, edge influence often extended further at lakeshore forest edges. Also, DEI started at 5 or 10m from the lakeshore forest edge for some shrub and herb species, but generally began right at the clearcut edge (0m).

Differences in responses of understory herbs and shrubs could be attributed to differences in environmental factors between lakeshore and clearcut edges. Although increased light and wind are characteristic of all forest edges (and associated changes in temperature and moisture), the riparian shrub zone often present between the lake and the forest edge could modify light conditions at the edge, accounting for some of the differences in understory composition between the two edge types. In addition, lakeshore forest edges form as the result of a complex gradient across the riparian ecotone and could be influenced by topographic and hydrologic factors (water table depth, disturbance from flooding and ice scour). Therefore, individual species at lakeshore forest edges could be responding to one or more of these abiotic factors which would not be present at clearcut edges. Another factor contributing to differences in species responses between edge types is the time lag; the vegetation at lakeshore forest edges has had longer to respond to edge-induced gradients than the vegetation at clearcut edges.

Natural forest edges, such as lakeshore edges, develop simultaneously with the adjacent forest stand, and yet are dynamic with continuous tree mortality and sapling recruitment. The edge along a lakeshore is more aptly described as an area of transition between riparian vegetation and forest. In contrast, clearcut edges are established almost instantaneously; after harvest, the structure of the edge changes as the adjacent cutblock regenerates. At different stages following edge creation, structural and compositional elements of clearcut edges may temporarily resemble the more permanent natural lakeshore edges. Overall, however, lakeshore forest edges are more different than the adjacent interior forest (the number of response variables with significant DEI is higher than at clearcut edges, Figures 2-4 and 3-8), and are wider (greater DEI) than clearcut edges. Despite many similarities, lakeshore and clearcut edges provide two distinctive landscape boundaries with different structure, composition and temporal dynamics.

Edge influence within the boreal forest landscape

Although similar in structure and composition, lakeshore and clearcut edges illustrate different types of boundaries on the landscape, due to the contrast between the edge and the adjacent forest and non-forested communities. Lakeshore forest edges form 40m wide distinct elements within forest communities with different structure and composition, and may function as natural boundaries in the boreal forest landscape. At these lakeshore forest edges, there is a mantel (Forman 1997) of increased sapling growth at and just outside the edge, which could function as habitat or as a barrier for fauna. The natural forest edge may also function as a gradient, or gradual transition between habitats. The results of spatial pattern analysis of different species across the lakeshore forest edge (Chapter 2) rcveal that different plant species may be responding to the edge in two different ways: as a boundary of a patch, or as a continual gradient. The mantel may also serve as an intermediate habitat between the forest and riparian vegetation.

Following harvesting, clearcut edges appear as prominent components of the fragmented boreal forest landscape (Plate 5-1). I do not think that clearcut edges provide barriers for wildlife, since very few variables (e.g. increased coarse woody material) were different at the edge than in either adjacent community. Rather, the harvested areas themselves are more likely to influence the movement of fauna. Van der Maarel (1990) also suggests that landscape elements rather than ecotones can form barriers. However, if the clearcut edge habitat is unsuitable for some wildlife species, it could function as an extension of the cutblocks on the landscape, resulting in an increase of the area of forest affected by timber harvest.

A new approach to the study of edge influence

Through my research on lakeshore and clearcut edges, I developed a new method, the critical values approach, which considers edges in the context of variability in interior forest (similar to Laurance et al. 1998a). The critical values approach and spatial pattern analysis of selected species along the edge-to-interior gradient begin to answer some of the calls for new methodology in research on boundaries. The critical values approach to quantifying DEI which incorporates pre/post-harvest data is one of the first methods that I know of that evaluates changes over time following forest harvesting; previous research has focused on the characteristics of edge-related patterns after edge creation. Using this approach, I investigated edge development within the context of change in interior forest which allowed me to infer mechanisms for changes at the edge in the first two years post-harvest, rather than simply investigating patterns after edge creation.

The critical values approach provides an objective criterion for determining DEI in the context of the range of variability within a reference forest, and does not assume random sampling. It can be an improvement over using confidence intervals to measure variation in interior forest (e.g. Laurance et al. 1998a) since it allows for any type of sampling design. It also differs substantially from curve-fitting techniques which have used models that assume the maximum or minimum value is at the edge (e.g. Chen et al. 1992, Laurance et al. 1998a).

My results and others (e.g. Murcia 1995) challenge previously held ideas about edge width. Non-monotonic responses to edge influence are more common than previously thought (Murcia 1995, Didham 1997, Laurance et al. 1997a) and may be especially prevalent at natural, inherent edges such as lakeshore forest edges in the boreal forest (Chapter 2). Rather than assuming that edge influence begins at the edge (0m), it may be more proper to consider a zone of edge influence which may actually begin some distance into the forest or in the adjacent non-forested area (Cadenasso et al. 1997).

Changes in vegetation response are gradual along the edge-to-interior gradient; the magnitude of edge influence is not constant throughout the area affected by edge influence. Thus, in any determination of DEI, as in most data analyses, an arbitrary but objective decision must be made. I chose to use the familiar 5% significance level rather than the 2/3 criterion provided by Chen et al. (1992) or 10% rule by Chen et al. (1996). My criterion also differs from Chen et al. (1992, 1996) since I use the criterion to compare to the variation in interior forest, rather than to the difference in values between the edge and interior.

Both the edge detection techniques and the critical values approach were developed in order to analyze nonnormal and spatially autocorrelated data that are common in boundary research. However, randomization tests do not overcome the problems of independence among samples (Legendre and Legendre 1998). This may not be much of a problem in the critical values approach since samples used in the randomization tests to assess the variation in interior forest were usually at least 50m apart (except using the upland interior forest data set, Chapter 2). Also, for each permutation, averages of one sample from each transect were calculated from data that were independent. This differs from ANOVA used to determine the existence of an edge effect (e.g. Wales 1972, Fox et al. 1997). ANOVA and other statistical tests assume that samples are independent; with positive spatially autocorrelated data, significant results are detected too often (Legendre and Legendre 1998). In the critical values approach, spatial autocorrelation would most likely affect the results when testing for significant differences from the range of variation in interior forest at neighbouring distances from the edge. With positive autocorrelation, distances close together would be more likely to be both significantly or not significantly different than interior forest. This effect could be partly alleviated by averaging across many transects. Complete randomization for each distance instead of grouping along transects may be preferable, but would be logistically very difficult and time-consuming. An advantage of sampling along transects is to control for variation among sites.

The critical values approach to quantifying distance of edge influence does not incorporate or recognize the spatial distribution of plots in the sampling design. Edge detection techniques which require contiguous quadrats are more appropriate for analyzing spatial pattern. These methods (e.g. split moving window analysis and wavelet analysis) assess the spatial structure of the data along each transect. Additional information can be gained such as the pattern of change along the edge-to-interior gradient, how this pattern differs at various scales (e.g. this study), as well as patch size (not assessed in this study). These techniques are appropriate for investigating the pattern of change along a gradient, but do not lend themselves to the determination of DEI. Although boundaries can be detected by such methods as the regions of highest change (Fortin 1994), DEI or edge width is best determined as the zone in which forest conditions are significantly different from interior forest, which may not coincide exactly with the width of boundaries determined by edge detection. Edge detection techniques and methods that quantify DEI are complementary analyses that provide information on the extent and pattern of edge influence.

A limitation of the critical values approach, and of randomization tests in general, is that statistical inferences apply to samples rather than the underlying population (Crowley 1992, Manly 1997). I can infer that samples are representative of the population; however, this would not be a statistical inference. Since I replicated transects at several sites in one to three study areas, I feel that I can safely infer that my results apply to the population of aspen-dominated mixedwood boreal forest in the general study region. One of the potential problems of studies that sample exclusively at one edge is that edge influence might be confounded by other gradients at the site. In my study, a shift in species composition along a single transect may be related to ecosite differences or edaphic variability. However, sampling transects from different sites would have undoubtedly dissipated such effects if they were inherent in the lakeshore edge-to-interior gradient.

The critical values approach for determining DEI can detect edge influence in variables with different response curves and zones of edge influence (e.g DEI does not have to start at 0m, Chapter 2), and should be flexible with regards to the type of response variable, size of plots, number of plots along transects and within reference data sets, and number of transects. My randomization test should be applicable to any ecosystem, any edge, any scale of sampling and various sampling designs. However, further testing on artificial and empirical data sets is needed to completely assess the capabilities of the critical values approach. Other methods (e.g. Chen et al. 1992, Laurance et al. 1998a) may be acceptable for relatively homogeneous systems with more closed canopy forest and very distinct edge effects (with responses that can be fitted to curves along the edge-to-interior gradient), but may not be as suited to more heterogeneous ecosystems such as the mixedwood boreal forest. A further advantage of the critical values approach is that different reference data sets can be used, providing information on edge influence in different contexts. Results can be incorporated into fragmentation models such as the Core Area Model (Laurance and Yensen 1991), and used for predicting the amount of interior forest in buffer zones of different widths, as I have done in Chapter 4. The critical values approach is simple to understand and easy to program using standard computer software. I hope that it will aid in comparing DEI among different ecosystems and types of edge, and thus provide the consistent methodology advocated by Murcia (1995).

Edge influence in forested ecosystems

Edge influence varies among ecosystems, types of edge, and edge ages. Estimates of distance of edge influence (DEI) for lakeshore and clearcut forest edges in the boreal forest fall within the range of DEI reported for temperate forest edges, but well below results from tropical forest edges and clearcut edges in Douglas-fir forests (Table 5-1). Distance of edge influence appears to be mostly related to the type of forest; almost all estimates of DEI greater than 50m were measured in more productive ecosystems with less frequent large-scale natural disturbance (tropical rainforest and Douglas-fir forest, Table 5-1). For created edges in the boreal forest, edge influence may not be as extensive or dramatic since these forests are generally disturbance-adapted with many inherent edges, and relatively open, shorter, deciduous canopies.

Given the diversity of situations, it is questionable whether generalizations of edge influence are useful (Crome 1997). However, there is some consensus among almost all studies of edge influence on forest vegetation. At all forest/ non-forest edges, structure and composition respond to edge-induced gradients of wind, light and related variables, generally without accompanying soil disturbance (except flooding disturbance and other changes in edaphic factors at some natural inherent edges) or destruction of vegetation (except perhaps increased browsing). Greater light and wind relative to interior forest are common to all edges. However, edges differ in: 1) the response of vegetation to microclimatic gradients at the edge, 2) the extent of that response (DEI), and 3) the timing of response. Greater light generally leads to greater productivity, a common response at all edges. That productivity is manifest in different ways: through growth of shrubs (Matlack 1993), development of a herbaceous understory (Ranney et al. 1981), invasion of non-native plants (Brothers and Spingarn 1992), germination and growth of tree seedlings (Chen et al. 1992), or, as in the boreal forest, suckering and growth of the dominant clonal trees. A more universal response at edges is structural damage to live and dead trees from increased wind (DeWalle 1983, Ferreira and Laurance 1997, Laurance et al. 1998a), and the subsequent production of coarse woody material (Chen et al. 1992, Esseen 1994).

This comparison of edge influence in the boreal forest and in other ecosystems illustrates some common trends that could form the basis of a universal theory of edge influence. In order to generalize beyond site-specific studies, such a theory could be developed by exploring causal and regulatory factors of edge influence (Murcia 1995). According to Murcia, understanding mechanisms for edge influence will enable us to predict the extent and magnitude of edge influence, and to reduce detrimental effects of forest fragmentation. As Murcia (1995) suggests, research on edge influence still has a long way to go before the development of a theory of edge influence that is not site-specific. Towards such a theory, I propose the following mechanisms for edge influence in general:

1. Increased wind at edges causes structural damage to live and dead trees, and greater coarse woody material.
2. Increased light at the edge from the adjacent unforested area, and from canopy openings caused by structural damage, leads to greater productivity in the understory and tree regeneration (modified from Murcia 1995).

However, within these general guidelines, responses in vegetation at different types of edges in different ecosystems appear to be site-specific. Several regulating factors could control the magnitude and distance of edge influence at different sites:

1. Edge type and edge age.
2. Disturbance type, frequency, intensity.
3. Canopy height and cover.
4. Resistance to edge influence (e.g. wind firmness of trees, development of the understory).
5. Extent of canopy structural damage (for understory responses).

In addition, individual species responses to edge influence could be related to their life form, mode of reproduction, growth rate, and other characteristics. These mechanisms and regulating factors could provide the basis for mechanistic hypotheses which Murcia (1995) would have us test. For example, the hypothesis I generated in Chapter 2, that primary responses to edge influence have narrower DEI than secondary responses (similar to regulating factor 5 above), also appeared to be true for clearcut edges (Chapter 3): DEI for sapling density and cover was usually considerably greater than DEI for structural damage. These mechanisms for edge influence and regulating factors for specific ecosystems provide the framework for the development of a universal theory of edge influence.

RECOMMENDATIONS

Future research on edge influence

This is the first study in the boreal forest to quantify distance of edge influence on forest structure and composition. As such, it provides information on the extent of edge influence from a natural, inherent edge and from different ages of created edges next to rapidly regenerating cutblocks, edges that are common in the boreal forest landscape. However, for a greater understanding of edge influence in the boreal forest and other ecosystems, more research is needed. Here I list potential research questions generated from this study:

1. For inherent and maintained created edges, is distance of edge influence greater for understory composition than for forest structure? This hypothesis, generated from my data, needs to be tested for other ecosystems and types of well established edges.
2. How is edge influence on forest structure and composition at lakeshore edges (and in buffer zones) related to abiotic factors? This question will be addressed in a collaboration with another researcher in TROLS who measured microclimate at the same plots as mine along the lakeshore and buffer transects.
3. What are the temporal dynamics of forest structure and composition at lakeshore edges? An interesting study would be to monitor vegetation in permanent plots at lakeshore edges, and correlate changes in vegetation to changes in water table depth.
4. How do natural forest edges, such as the lakeshore forest edge, function as boundaries on the landscape (as habitat, barriers, conduits, source or sink, Forman 1997)? This question would be best addressed through collaboration with an animal ecologist, by observing animal behaviour across and along edges, and relating that to vegetation, possibly using spatial pattern analysis.
5. At clearcut edges in the boreal forest, is *Populus* spp. suckering causing the decrease in shrub cover, or preventing the development of a dense understory? The best approach to answer this question would be a removal experiment to test the response of the understory with and without *Populus* spp. suckering. Unfortunately, this might be logistically difficult or impossible.
6. How do clearcut edges in the boreal forest change over time after the second year post-harvest? With my pre/post-harvest comparisons (an experimental approach to studying edges), I was able to isolate changes in forest structure and composition due to edge influence, at least in the initial stages. Ideally, monitoring permanent plots at clearcut edges from pre-harvest through and beyond canopy closure would be the best approach to understanding succession at clearcut edges.
7. Is there an interactive effect of edge influence or resistance in buffer zones? Unfortunately sample size was too low to properly answer this question in this study. In order to adequately address this question, I recommend: a sample size of at least 10

(since this seemed to be appropriate in Chapters 2 and 3) for each buffer width, buffers of different width (particularly between 25 and 100m where edge influence is most likely to interact), and using older buffers.

Implications for wildlife and management

Years after much of northern Alberta had been allocated for timber harvest, research by Cumming et al. (1994) suggested that with current plans, harvesting is probably only economically sustainable with losses of wildlife habitat and conversion to single-species stands. Loss of habitat for some interior forest species may be even greater than they predicted if edge influence is considered. In the current two pass system of forest harvesting using irregularly shaped 40 ha cutblocks, edge influence could affect up to one-third of the remaining forest (using distance of edge influence = 20m, Chapter 3), although this amount could be substantially less where remnant forested areas are not entirely surrounded by clearcut edges. Since distance of edge influence (DEI) does not change substantially through time, at least for the first 16 years following harvest (Chapter 3), the amount of edge habitat is expected to remain constant through time. However, the structure of the edge habitat will change, particularly as saplings grow.

Even though structure and composition at clearcut edges was significantly different from interior forest up to 20m from the edge, this change in habitat may not be detrimental to biodiversity. Only two species (*Viburnum edule* and *Mitella nuda*) were consistently lower in abundance at edges of cutblocks of all ages, although other less common species may also be adversely affected by edge influence. There is also some evidence that wildlife in this region may not avoid recent clearcut edges. In the same study area, edge influence on birds was not very strong at clearcut edges compared to aspen/spruce edges (Song 1998), and the overall effect of fragmentation on bird communities was relatively small (Schmiegelow et al. 1997). However, some interior forest wildlife species that avoid lakeshore edges (e.g. Ovenbird, Lambert 1998), may also avoid older clearcut edges that have similar structure. Overall, I do not expect that the change in habitat at edges created by harvesting will greatly affect biodiversity, yet edge influence may still be a concern for some interior forest species (*Viburnum edule*, *Mitella nuda*, Ovenbirds, and probably other uncommon species). This situation is very different from tropical rainforests in which many interior forest species are adversely affected by the edge, and where small fragments with high edge:interior ratios could lead to species disappearances within fragments (Laurance and Bierregaard 1997). In the boreal forest where natural forest edges are already common, wildlife has been accustomed to natural inherent edges adjacent to water bodies and natural created edges from fire. Some, perhaps early-successional, species may benefit from increased amount of edge habitat on the landscape.

Edge influence is one of many concerns for management in the boreal forest and may not be as important for wildlife as other consequences of harvesting and fragmentation such as reduction of the amount of mixed coniferous/deciduous forest (Song 1998), reduction of habitat, area effects and connectivity. Even when considering edge influence from created edges, there are still many unknown factors: edge influence on many other organisms (and uncommon plants), and the effect of changes in forest structure at the edge on wildlife beyond five years post-harvest. Still, based on the conclusions of my research, some recommendations can be made:

1. Since DEI is not that extensive, I do not advocate the use of large clearcuts and large remnant forested areas in order to reduce edge influence. The natural disturbance paradigm could potentially include very large clearcuts to mimic large fires, but the reduction in edge habitat should not be a reason to take this approach in the study area. Also, consideration of other factors including aesthetics and ethical reasons is needed before any change in policy (see Hunter 1993).
2. Incorporate a DEI of 20m at clearcut edges, and a DEI of 40m at lakeshore edges into harvest plans to delimit the area of effective interior forest. Distance of edge influence is an important consideration in determining the size and shape of cutblocks (and for choosing between clearcutting and partial harvesting). I consider these DEIs, which account for most variables, to be good estimates for the entire community. However, DEI differs among variables, and managers may decide to use different DEI, for example if managing for a particular wildlife species that may be sensitive to particular structural characteristics.
3. Given that edge influence may be detrimental to some aspects of biodiversity, it would be best not to completely eliminate interior forest in remnant forested areas. Increasing the size of remnant forested areas or using more regular shapes would decrease the amount of edge habitat; thus, small irregularly shaped remnant areas should be avoided. An alternative is to maintain a variety of sizes and shapes of remnant forested areas so that some interior forest is left on the landscape.
4. Edge influence is most important in narrow remnant forested areas such as riparian buffers left around lakes and streams following harvesting. In 100m buffer zones, up to 60% will be considered 'edge' (using clearcut and lakeshore DEI of 20m and 40m). Buffer management is a complex issue that involves protection of aquatic ecosystems and providing connectivity for wildlife species on the landscape. Riparian buffers are an important unharvested component of landscapes fragmented by timber extraction. These riparian corridors could preserve some degree of habitat connectivity on the landscape for wildlife, plants and gene flow. For buffer management, answers to the following questions could provide the start of a decision support system to determine the shape and extent of buffers on the landscape:
    - A. What aquatic and wetland ecosystems should be protected with buffers?
    - B. Which of these buffers should also provide interior forest habitat? (These buffers would provide linear corridors of interior forest habitat on the landscape.)
    - C. How wide should the corridor of interior forest be?

    The first question would be answered by aquatic ecologists, the next two by wildlife ecologists. The results of my research would then be used to determine the final buffer width by incorporating the DEI from both lakeshore and clearcut edges.

In 1953, Whittaker commented, 'Vegetation presents a field of phenomena notably lacking in fixed points of reference, lines of division, invariable rules, and easy definitions.' In many ways, edges embody this statement. The line of division between edge habitat and interior forest is not easy to define. Distance of edge influence is best determined using more than one fixed point of reference in interior forest. And any rules on edge influence are likely to vary in space and time. In the boreal forest, lakeshore and clearcut edges are important features of the heterogeneous landscapes, with their own distinct structure and composition, and should be considered in forest management.

LITERATURE CITED

Bierregaard, R. O., Jr., T. E. Lovejoy, V. Kapos, A. A. dos Santos, and R. W. Hutchings. 1992. The biological dynamics of tropical rainforest fragments. BioScience **42**:859-866.

Brothers, T. S., and A. Spingarn. 1992. Forest fragmentation and alien plant invasion of central Indiana old-growth forests. Conservation Biology **6**:91-100.

Cadenasso, M. L., M. M. Traynor, and S. T. A. Pickett. 1997. Functional location of forest edges: gradients of multiple physical factors. Canadian Journal of Forest Research **27**:774-782.

Camargo, J. L. C., and V. Kapos. 1995. Complex edge effects on soil moisture and microclimate in central Amazonian forest. Journal of Tropical Ecology **11**:205-221.

Chen, J., J. F. Franklin, and T. A. Spies. 1992. Vegetation responses to edge environments in old-growth Douglas-fir forests. Ecological Applications **2**:387-396.

Chen, J., J. F. Franklin, and J. S. Lowe. 1996. Comparison of abiotic and structurally defined patch patterns in a hypothetical forest landscape. Conservation Biology **10**:854-862.

Crome, F. H. J. 1997. Researching tropical forest fragmentation: shall we keep on doing what we're doing? Pages 485-501 *in* W. F. Laurance and R. O. Bierregaard Jr., editors. Tropical forest remnants: Ecology, management and conservation of fragmented communities. The University of Chicago Press, Chicago.

Crowley, P. H. 1992. Resampling methods for computation-intensive data analysis in ecology and evolution. Annual Review of Ecology and Systematics **23**:405-447.

DeWalle, D. R. 1983. Wind damage around clearcuts in the ridge and valley province of Pennsylvania. Journal of Forestry :158-159, 172.

Didham, R. K. 1997. The influence of edge effects and forest fragmentation on leaf litter invertebrates in central Amazonia. Pages 55-69 *in* W. F. Laurance and R. O. Bierregaard Jr., editors. Tropical forest remnants: Ecology, management and conservation of fragmented communities. The University of Chicago Press, Chicago.

Esseen, Per-A. 1994. The mortality patterns after experimental fragmentation of an old-growth conifer forest. Biological Conservation **68**:19-28.

Ferreira, L. V., and W. F. Laurance. 1997. Effects of forest fragmentation on mortality and damage of selected trees in central Amazonia. Conservation Biology **11**:797-801.

Forman, R. T. T. 1997. Land mosaics: The ecology of landscapes and regions. Cambridge University Press, Cambridge.

Fortin, M.-J. 1994. Edge detection algorithms for two-dimensional ecological data. Ecology **75**:956-965.

Fox, B. J., J. E. Taylor, M. D. Fox, and C. Williams. 1997. Vegetation changes across edges of rainforest remnants. Biological Conservation **82**:1-13.

Fraver, S. 1994. Vegetation responses along edge-to-interior gradients in the mixed hardwood forests of the Roanoke River basin, North Carolina. Conservation Biology **8**:822-832.

Gosz, J. R. 1991. Fundamental ecological characteristics of landscape boundaries. Pages 8-30 *in* M. M. Holland, P. G. Risser and R. J. Naiman, editors. Ecotones: the role of landscape boundaries in the management and restoration of changing environments. Chapman and Hall, New York.

Helle, P., and J. Muona. 1985. Invertebrate numbers in edges between clear-fellings and mature forests in northern Finland. Silva Fennica **19**:281-294.

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

Jose, S., A. R. Gillespie, S. J. George, and B. M. Kumar. 1996. Vegetation responses along edge-to-interior gradients in a high altitude tropical forest in peninsular India. Forest Ecology and Management **87**:51-62.

Lambert, J. D. 1998. Ovenbirds (*Seiurus aurocapillus*) in riparian buffer strips: short-term response to upland timber harvest in Alberta's boreal mixed-wood forest. M.Sc. thesis, University of Alberta, Edmonton, Canada.

Laurance, W. F. 1991. Edge effects in tropical forest fragments: application of a model for the design of nature reserves. Biological Conservation **57**:205-219.

Laurance, W. F., and E. Yensen. 1991. Predicting the impacts of edge effects in fragmented habitats. Biological Conservation **55**:77-92.

Laurance, W. F., and R. O. Bierregaard Jr., editors. 1997. Tropical forest remnants: ecology, management, and conservation of fragmented communities. The University of Chicago Press, Chicago.

Laurance, W. F., R. O. Bierregaard Jr., C. Gascon, R. K. Didham, A. P. Smith, A. J. Lynam, V. M. Viana, T. E. Lovejoy, K. E. Sieving, J. W. Sites Jr., M. Andersen, M. D. Tocher, E. A. Kramer, C. Restrepo, and C. Moritz. 1997a. Tropical forest fragmentation: synthesis of a diverse and dynamic discipline. Pages 502-514 *in* W. F. Laurance and R. O. Bierregaard Jr., editors. Tropical forest remnants: Ecology, management and conservation of fragmented communities. The University of Chicago Press, Chicago.

Laurance, W. F., S. G. Laurance, L. V. Ferreira, J. M. Rankin-de Merona, C. Gascon, and T. E. Lovejoy. 1997b. Biomass collapse in Amazonian forest fragments. Science **278**:1117-1118.

Laurance, W. F., L. V. Ferreira, J. M. Rankin-de Merona, and S. G. Laurance. 1998a. Rain forest fragmentation and the dynamics of Amazonian tree communities. Ecology **79**:2032-2040.

Laurance, W. F., L. V. Ferreira, J. M. Rankin-de Merona, S. G. Laurance, R. W. Hutchings, and T. E. Lovejoy. 1998b. Effects of forest fragmentation on recruitment patterns in Amazonian tree communities. Conservation Biology **12**:460-464.

Legendre, P. and L. Legendre. 1998. Numerical Ecology. Second English edition. Elsevier Science, Amsterdam, The Netherlands.

Machtans, C. S., Marc-A. Villard, and S. J. Hannon. 1996. Use of riparian buffer strips as movement corridors by forest birds. Conservation Biology **10**:1366-1379.

Malcolm, J. R. 1994. Edge effects in central Amazonian forest fragments. Ecology **75**:2438-2445.

Manly, B. F. J. 1997. Randomization, bootstrap and Monte Carlo methods in Biology. Chapman and Hall, London, U.K.

Matlack, G. R. 1993. Microenvironment variation within and among forest edge sites in the eastern United States. Biological Conservation **66**:185-194.

Matlack, G. R. 1994. Vegetation dynamics of the forest edge - trends in space and successional time. Journal of Ecology **82**:113-123.

Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. Trends in Ecology and Evolution **10**:58-62.

Noss, R. F. 1987. Corridors in real landscapes: a reply to Simberloff and Cox. Conservation Biology **1**:159-164.

Palik, B. J., and P. G. Murphy. 1990. Disturbance versus edge effects in sugar-maple/beech forest fragments. Forest Ecology and Management **32**:187-202.

Ranney, J. W., M. C. Bruner, and J. B. Levenson. 1981. The importance of edge in the structure and dynamics of forest islands. Pages 67-95 *in* R. L. Burgess and D. M. Sharpe, editors. Forest Island Dynamics in Man-Dominated Landscapes. Springer-Verlag, New York.

Schmiegelow, F. K. A., C. S. Machtans, and S. J. Hannon. 1997. Are boreal birds resilient to forest fragmentation? An experimental study of short-term community responses. Ecology **78**:1914-1932.

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. dissertation, University of Alberta, Edmonton, Canada.

Turton, S. M., and H. J. Freiburger. 1997. Edge and aspect effects on the microclimate of a small tropical forest remnant on the Atherton Tableland, northeastern Australia. Pages 45-54 *in* W. F. Laurance and R. O. Bierregaard Jr., editors. Tropical forest remnants: Ecology, management and conservation of fragmented communities. The University of Chicago Press, Chicago.

Wales, B. A. 1972. Vegetation analysis of north and south edges in a mature oak-hickory forest. Ecological Monographs **42**:451-471.

Whittaker, R. H. 1953. A consideration of climax theory: the climax as a population and pattern. Ecological Monographs **23**:41-78.

Williams-Linera, G. 1990. Vegetation structure and environmental conditions of forest edges in Panama. Journal of Ecology **78**:356-373.

TABLE 5-1. Summary of distance of edge influence (DEI) on forest structure and composition from different studies, in order of increasing DEI. In some studies, DEI was quantified; in others, it was summarized in the text of the article. Information is also provided on the location, type of ecosystem, type of edge, response variables and maximum distance (in m) sampled. Maintained edges are usually next to agricultural land and are older edges unless otherwise reported. S and N refer to south-facing and north-facing where results were substantially different.

Study	Location	Ecosystem	Type of edge	Response variables	DEI (m)	Max. dist.
Brothers and Spingarn 1992	Indiana, USA	Deciduous	Maintained	Non-native plants	2	50
Palik and Murphy 1990	Michigan, USA	Deciduous	Maintained	Canopy tree density and composition, ground layer composition	5-10(N)	50
Matlack 1994	Pennsylvania, USA	Deciduous forest	Recent, < 5 yr old	Understory species composition	8-10*	40
Williams-Linera 1990	Panama	Tropical premontane wet forest	Maintained, up to 12 yr old	Canopy cover, density and basal area of woody plants, density of dead trees	5-15	60
Ranney et al. 1981	Wisconsin, USA	Deciduous	Maintained	Tree and sapling basal area, stem density, species richness	15	30
Fox et al. 1997	Australia	Temperate rainforest	Maintained	Plant species composition	4-16	20
Palik and Murphy 1990	Michigan, USA	Deciduous	Maintained	Canopy tree density and composition	15-20(S)	50
Matlack 1994	Pennsylvania, USA	Deciduous forest	Maintained	Understory species composition	18-20*	40
This study	**Alberta, Canada**	***Populus* spp. forest**	**Clearcut, up to 16 yr old**	**Structure and composition**	**20**	**100-200**
Wales 1972	New Jersey, USA	Deciduous	Maintained	Revegetation	20	30

Bierregaard et al. 1992	Amazon, Brazil	Tropical rainforest	New clearcut	Seedling recruitment and growth	25	?
Fraver 1994	North Carolina, USA	Deciduous	Maintained	Species cover, richness and composition	10-30(N)	100
Jose et al. 1996	India	High-altitude tropical forest	Natural, grassland/ forest edge	Plant species composition	15-30	45
Turton and Freiburger 1997	Australia	Tropical rainforest	Maintained	Dicot seedlings	30	70
Matlack 1994	Pennsylvania, USA	Deciduous forest	Embedded (continuous canopy across edge)	Understory species composition	22-32*	40
Malcolm 1994	Amazon, Brazil	Tropical rainforest	Clearcut, 4-9 yr old, some regeneration	Understory foliage thickness	35	>100
This study	**Alberta, Canada**	***Populus* spp. forest**	**Lakeshore**	**Structure and composition**	**20-40**	**100-200**
Chen et al. 1992	Oregon, USA	Old-growth Douglas fir	10-15 yr old clearcut	Canopy cover	44	240
Palik and Murphy 1990	Michigan, USA	Deciduous	Maintained	Ground layer composition	45(S)	50
Matlack 1993	Pennsylvania, USA	Deciduous forest	Recent, < 5 yr old	Shrub cover	50	50
Chen et al. 1992	Oregon, USA	Old-growth Douglas fir	10-15 yr old clearcut	Logs	56	240
Chen et al. 1992	Oregon, USA	Old-growth Douglas fir	10-15 yr old clearcut	Tree density	59	240
Fraver 1994	North Carolina, USA	Deciduous	Maintained	Species cover, richness and composition	50-60(S)	100
Malcolm 1994	Amazon, Brazil	Tropical rainforest	Clearcut, 4-9 yr old, some regeneration	Overstory foliage thickness	60	>100

Chen et al. 1996	Oregon, USA	Old-growth Douglas fir	15-20 yr old clearcut	Edge species: *Gaultheria shallon*	75	?
Laurance et al. 1998a	Amazon, Brazil	Tropical rainforest	Clearcut, up to 14 yr old, some regeneration	Tree damage	85	>500
Camargo and Kapos 1995	Amazon, Brazil	Tropical rainforest	Maintained, 4 yr old edge	Height of greatest foliage density	80-100	>500
Ferreira and Laurance 1997	Amazon, Brazil	Tropical rainforest	Maintained, 3-7 yr old	Tree mortality and damage in the family Myrtaceae	100	>500
Laurance et al. 1997b	Amazon, Brazil	Tropical rainforest	Clearcut, up to 17 yr old, some regeneration	Loss in biomass	100	>1000
Laurance et al. 1998b	Amazon, Brazil	Tropical rainforest	Clearcut, up to 12 yr old, some regeneration	Tree recruitment	100	>500
Chen et al. 1992	Oregon, USA	Old-growth Douglas fir	10-15 yr old clearcut	Snags	125	240
Chen et al. 1992	Oregon, USA	Old-growth Douglas fir	10-15 yr old clearcut	Seedling regeneration	16-137	240
Laurance 1991	Australia	Tropical rainforest	Maintained	Canopy and subcanopy damage	150	>1000
Chen et al. 1996	Oregon, USA	Old-growth Douglas fir	15-20 yr old clearcut	Interior species: *Goodyera oblongifolia*	225	?
Laurance et al. 1998a	Amazon, Brazil	Tropical rainforest	Clearcut, up to 14 yr old, some regeneration	Tree turnover	280	>500
Laurance et al. 1998a	Amazon, Brazil	Tropical rainforest	Clearcut, up to 14 yr old, some regeneration	Tree mortality	335	>500
Laurance 1991	Australia	Tropical rainforest	Maintained	Non-native genus (*Solanum*)	up to 500	>1000

*Overall species composition data was unclear, these values are from two species (*Phryma leptostachya, Viola* spp.) reported in the text as examples.

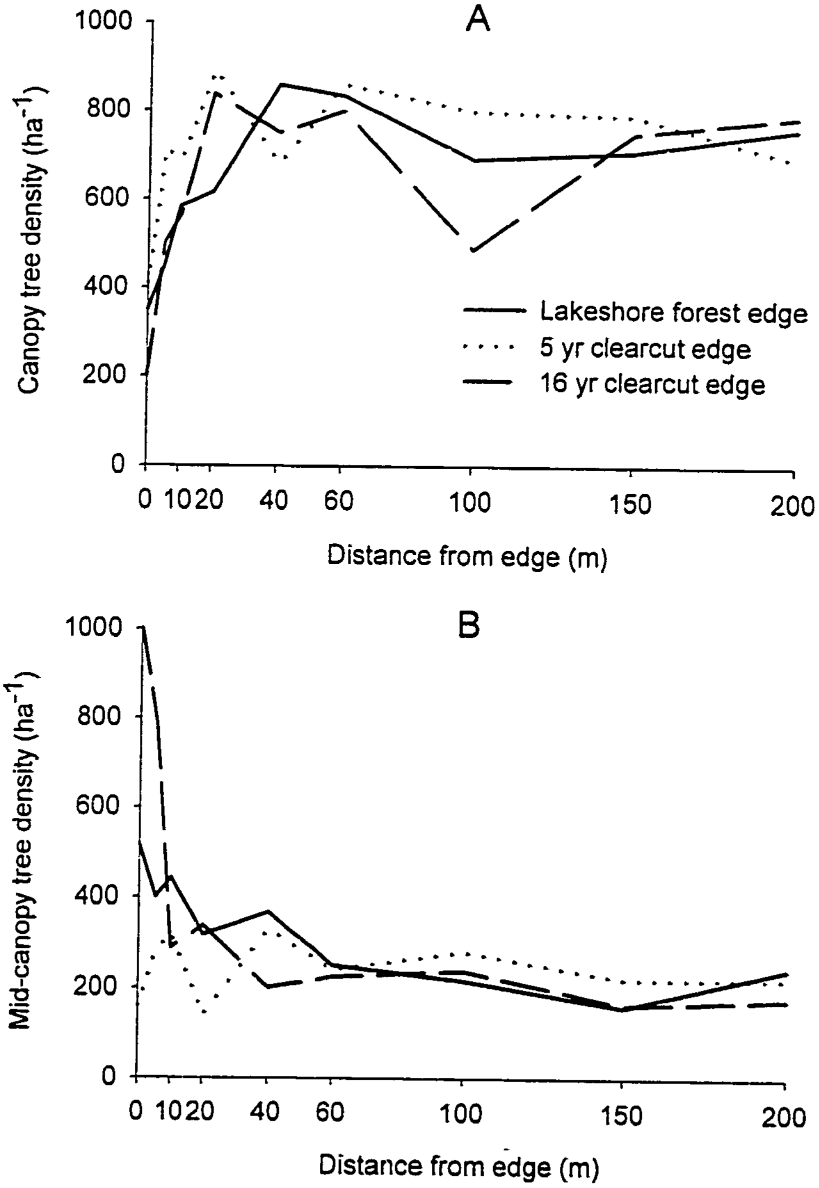


Figure 5-1. Tree density along the edge-to-interior gradient for lakeshore forest edges, 5 yr and 16 yr old clearcut forest edges. A. Canopy tree density. B. Mid-canopy tree density.

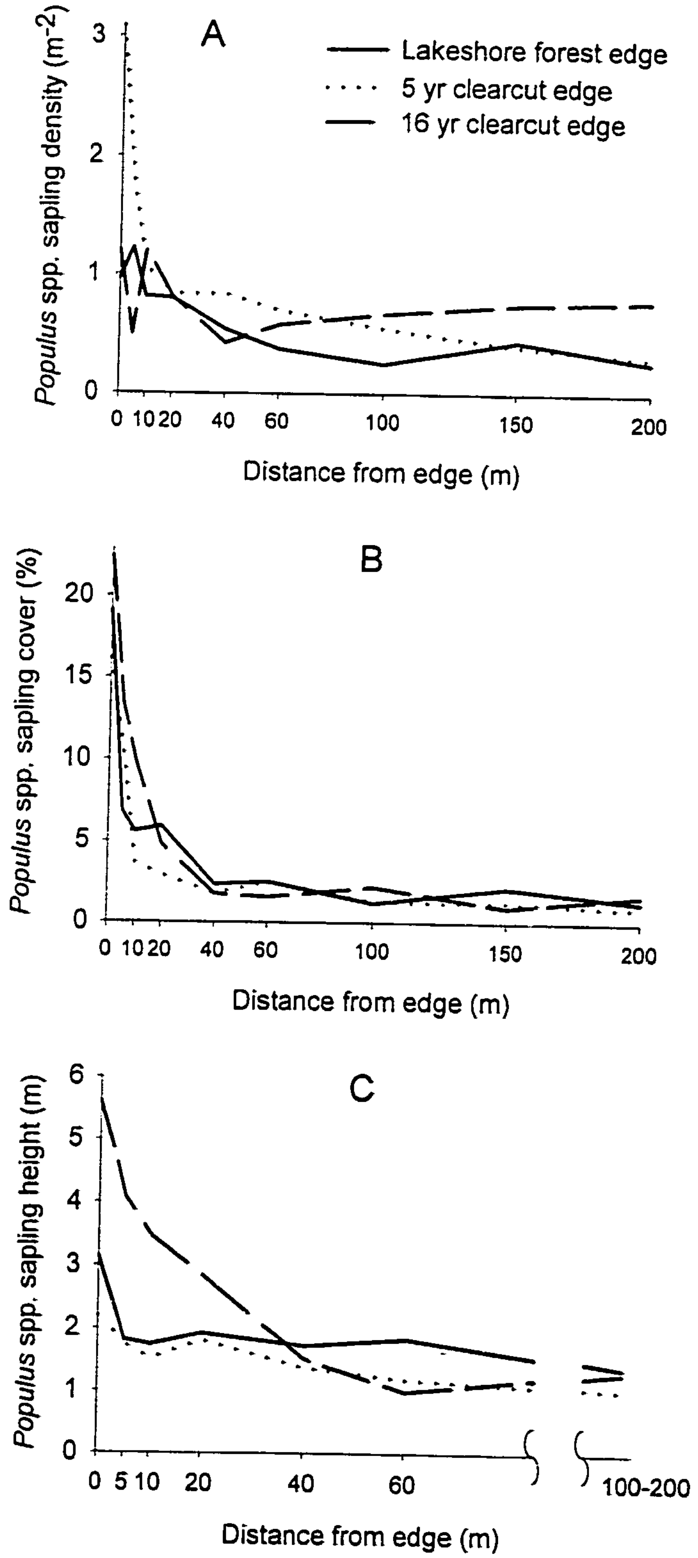


Figure 5-2. Sapling characteristics along the edge-to-interior gradient for lakeshore forest edges, 5 yr and 16 yr old clearcut forest edges. A. Density. B. Cover. C. Maximum height.

Plate 5-1. Aerial photograph of one of the TROLS study lakes following harvest. Clearcut edges have become a prominent feature of the fragmented boreal forest landscape. (Aerial photograph provided courtesy of the TROLS research project.)

APPENDICES

APPENDIX 2-1. Average values of the understory species at different distances from the lakeshore forest edge, in the non-forested riparian zone (-10m) and in the upland interior forest. The superscripts 'a' and 'b' designate values that are significantly different from the adjacent riparian and upland interior reference data sets respectively. Values at two consecutive distances that are significantly different from either reference data set are shaded; values significantly different from both reference data sets are highlighted by a box. For individual shrub and herb covers, species are subdivided into 'edge-positive', 'edge-negative' and other species (greater cover, lower cover, and no significant trend near the edge respectively); only common species with > 10% frequency were included. Fifty-one of the 268 significant results in this table were expected due to random chance.

	Distance from lakeshore forest edge (m)										
Response variable	**-10**	**0**	**5**	**10**	**20**	**40**	**60**	**100**	**150**	**200**	**interior**
Shrubs											
Edge-positive species											
Amelanchier alnifolia	6.8^{ab} ± 4.0	9.8^{ab} ± 3.3	10.0^{ab} ± 3.0	6.2^{ab} ± 1.8	7.8^{ab} ± 2.9	8.2^{ab} ± 2.9	4.0^{b} ± 1.0	2.6 ± 0.8	2.1 ± 0.9	2.9 ± 1.2	1.6 ± 0.3
Lonicera dioica	0.4^{a} ± 0.3	1.2 ± 0.4	1.6^{b} ± 0.7	2.2^{ab} ± 0.6	1.6^{b} ± 0.7	0.8 ± 0.3	1.6^{b} ± 0.4	1.6^{b} ± 0.6	0.7 ± 0.2	1.6^{b} ± 0.6	0.7 ± 0.1
Prunus spp. (*P. pensylvanica* and *P. virginiana*)	1.4^{a} ± 0.7	1.0^{a} ± 0.6	3.5^{ab} ± 2.2	2.8^{a} ± 1.4	4.8^{ab} ± 3.6	4.0^{ab} ± 2.7	0.6 ± 0.5	0.3 ± 0.3	0.0 ± 0.0	0.6 ± 0.3	1.0 ± 0.3
Salix spp.	18.4^{ab} ± 6.5	5.6^{ab} ± 3.1	1.3^{ab} ± 0.6	0.4 ± 0.3	1.0^{a} ± 0.6	0.1 ± 0.1	4.0^{ab} ± 3.0	0.3 ± 0.3	0.3 ± 0.2	0.0 ± 0.0	0.3 ± 0.1
Symphoricarpos albus (could include *S. occidentalis*)	1.3 ± 0.6	2.2^{a} ± 0.7	3.8^{ab} ± 1.7	1.6 ± 0.4	2.7^{ab} ± 1.0	2.2^{ab} ± 1.5	1.6 ± 0.5	1.8 ± 0.6	1.2 ± 0.4	1.0 ± 0.3	1.3 ± 0.2
Vaccinium myrtilloides	5.2^{ab} ± 4.1	8.0^{ab} ± 5.6	2.5^{ab} ± 2.0	8.0^{ab} ± 4.4	0.5 ± 0.5	0.4 ± 0.3	0.1 ± 0.1	0.2 ± 0.2	0.8^{b} ± 0.5	1.6^{b} ± 1.5	0.2 ± 0.1

Edge-negative species											
Alnus crispa	5,5 ± 3,2	5,0 ± 2,2	10,0 ± 5,9	7,5 ± 4,9	0,0^{ab} ± 0,0	2,3^{ab} ± 1,5	4,6^{b} ± 4,5	12,0 ± 6,1	6,8 ± 4,1	5,2 ± 4,0	10,7 ± 1,6
Ribes triste	0,8^{b} ± 0,3	2,2 ± 0.8	2,0 ± 0,8	1,3^{a} ± 0,6	1,1^{ab} ± 0,6	2,9 ± 1,2	1,9 ± 1,1	3,0 ± 1,5	4,4 ± 1,6	3,2 ± 1,5	3,5 ± 0,5
Rubus idaeus	7,2^{b} ± 3,9	2,4^{a} ± 1,1	2,0^{a} ± 1,0	1,8^{a} ± 0,6	2,6^{a} ± 0,7	1,6^{a} ± 0,6	6,0^{b} ± 2,3	6,1^{b} ± 2,4	8,2^{b} ± 3,5	7,2^{b} ± 2,9	2,3 ± 0,3
Other species											
Cornus stolonifera	0,4 ± 0,2	0,2 ± 0,2	0,8 ± 0,5	1,2 ± 0,6	1,2 ± 1,0	1,0 ± 0,6	1,6 ± 0,8	1,5 ± 1,0	1,2 ± 1,0	0,5 ± 0,5	0,5 ± 0,3
Corylus cornuta	5,2 ± 4,5	4,8 ± 4,5	10,8 ± 6,0	9,2 ± 6,2	10,8 ± 5,9	10,8 ± 5,6	25,0^{ab} ± 8,4	7.6 ± 5.0	9,2 ± 5,1	6,0 ± 3.6	10,7 ± 1,8
Lonicera involucrata	2,2 ± 1,6	4,3 ± 2,7	5,5 ± 3,6	1,9 ± 1,1	1,7 ± 0,8	4,0 ± 2,1	2,1 ± 1,1	5,6 ± 3,2	3,4 ± 1,7	2,7 ± 1,5	2,8 ± 0,6
Ribes oxyacanthoides[1]	1,2 ± 0,6	1,5 ± 0,8	0,4^{a} ± 0,2	1,3 ± 1,0	0,5^{a} ± 0,3	1,8 ± 0,8	0,8 ± 0,4	1,4 ± 0,6	2,2 ± 1,0	0,8 ± 0.5	1,1 ± 0,2
Rosa acicularis	4,9^{ab} ± 1,8	8,2 ± 2,1	6,0^{b} ± 1,6	11,4 ± 2,7	12,9 ± 2,3	12,5 ± 2,5	14,7 ± 3,2	9,2 ± 2,5	12,2 ± 2,3	12,0 ± 2,9	11,4 ± 1,1
Viburnum edule	1,0^{ab} ± 0,5	6,2 ± 2,7	7,4 ± 2,8	7,2 ± 2.5	7,2 ± 1,6	13,8^{a} ± 2,8	11,0 ± 2,3	7,4 ± 1,6	8.9 ± 2,8	11,0 ± 2,5	9,5 ± 0,9

[1] *Ribes oxyacanthoides* includes *R. lacustre*.

Response variable	0	5	10	20	40	60	100	150	200	interior
Herbs										
Edge positive species										
Apocynum androsaemifolium	0.8^{a} ± 0,7	2,9^{ab} ± 1,9	2,3^{a} ± 2,3	0,5^{a} ± 0,4	1,3^{a} ± 1,3	1,7^{a} ± 1,1	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,6 ± 0,3
Aster conspicuus	2,3 ± 0,8	3,2^{a} ± 1,5	4,8^{ab} ± 1,6	3,1^{a} ± 1,8	5,2^{ab} ± 1,6	2,4 ± 1,2	1,4 ± 1,0	1.9 ± 1,0	0,4 ± 0,2	2,0 ± 0,4
Carex spp.	1,0^{b} ± 0,7	0,2^{b} ± 0,1	0,1 ± 0,05	0,2^{b} ± 0,1	0,2^{b} ± 0,1	0,2^{b} ± 0,1	0,1 ± 0,1	0,1 ± 0.05	0,2^{b} ± 0,1	0,04±0,01
Equisetum arvense	0,6^{ab} ± 0,1	0,7^{ab} ± 0,2	0,5^{ab} ± 0,1	0,3^{ab} ± 0,1	0,2^{b} ± 0,1	0,2^{b} ± 0,1	0,2^{b} ± 0,1	0,1^{b} ± 0,1	0,1 ± 0,05	0,03±0,01
Fragaria virginiana	2,2 ± 0,6	2,7 ± 0,8	4,0^{a} ± 1,0	4,2^{ab} ± 1,1	2,1 ± 1,0	1,8 ± 0,6	1,1^{b} ± 0,4	2,3 ± 0,7	2,5 ± 1,0	2,5 ± 0,3
Galium boreale	0,7 ± 0,2	1,1^{ab} ± 0,2	0,8^{ab} ± 0,1	1,0^{ab} ± 0,2	0,5 ± 0,1	0,7^{b} ± 0,1	0,6 ± 0,1	0,6 ± 0,1	0,6 ± 0,1	0,5 ± 0,03
Lathyrus ochroleucus	2,5 ± 0,5	6,0^{a} ± 1,2	6,7^{ab} ± 1,4	7,3^{ab} ± 1,5	6,7^{ab} ± 1,6	3,3 ± 1,1	4,8 ± 1,3	3.8 ± 1,1	3,2 ± 0,9	4,1 ± 0,4
Maianthemum canadense	3,3 ± 0,8	5,9^{ab} ± 1,6	8,8^{ab} ± 2,4	5,6^{ab} ± 1,1	4,5^{b} ± 0,9	3,5 ± 0,7	4,6^{ab} ± 1,3	3,3 ± 0,8	1,7^{ab} ± 0,4	2,7 ± 0,2
Orthilia secunda	0,3^{a} ± 0,2	0,4^{a} ± 0,3	0,8^{ab} ± 0,7	0,3^{a} ± 0,2	0,03±0,03	0,2^{a} ± 0,1	0,1 ± 0,1	0,0 ± 0,0	0,0 ± 0,0	0,2 ± 0,04
Petasites palmatus	4,9^{ab} ± 1,5	3,8^{ab} ± 1,2	3,9^{ab} ± 1,7	4,4^{ab} ± 1,0	3,0 ± 0,8	3,4^{b} ± 1,1	2,9 ± 0,9	2,4 ± 0,6	1,9 ± 0,5	1,7 ± 0,2
Pyrola asarifolia	0,6 ± 0,2	1,4^{ab} ± 0,3	1,6^{ab} ± 0,3	1,0 ± 0,3	0,4 ± 0,1	0,3 ± 0,1	0.9 ± 0,3	0,6 ± 0,3	0,4 ± 0,3	0,6 ± 0,1
Thalictrum venulosum	0,2^{b} ± 0,2	0,2^{b} ± 0,2	0,2^{b} ± 0,1	1,2^{ab} ± 0,7	0,1^{b} ± 0,1	0,4^{b} ± 0,2	0,2^{b} ± 0,2	0,2^{b} ± 0,1	0,3^{b} ± 0,2	0,0 ± 0,0
Vicia americana	0,9^{b} ± 0,3	1,4^{ab} ± 0,5	2,3^{ab} ± 0,6	1,2^{ab} ± 0,3	1,5^{ab} ± 0,4	0,7^{b} ± 0,4	1,2^{ab} ± 0,4	0.5 ± 0.2	0,1^{a} ± 0,1	0,3 ± 0,1
grass spp.[1]	0,7^{ab} ± 0,2	0,5^{ab} ± 0,2	0,5^{ab} ± 0,2	0,4^{ab} ± 0,1	0,4^{ab} ± 0,1	0,4^{ab} ± 0,1	0,2 ± 0,1	0,2 ± 0,1	0,1 ± 0,1	0,2 ± 0.03

Edge negative species										
Aralia nudicaulis	13^{ab} ± 3	19^{a} ± 4	23^{a} ± 5	33^{b} ± 5	22^{a} ± 4	28 ± 5	27 ± 5	32 ± 5	31 ± 5	24 ± 1
Cornus canadensis	2,2^{ab} ± 1,0	3,6^{b} ± 1,7	2,3^{ab} ± 0,8	5,6 ± 2,6	7,8^{a} ± 2,3	3,3^{ab} ± 1,1	4,2^{b} ± 1,2	7,3 ± 1,7	4,5^{b} ± 1,5	8,5 ± 0,7
Linnaea borealis	0^{ab} ± 0	0,3^{ab} ± 0,2	0,8^{ab} ± 0,3	1,4 ± 0,7	1,0^{ab} ± 0,4	1,4 ± 1,0	2,1 ± 1,0	2,1 ± 0,9	4,8 ± 2,4	2,9 ± 0,4
Mitella nuda	0,1^{ab} ± 0,1	0,3^{ab} ± 0,1	0,3^{ab} ± 0,1	0,9 ± 0,5	1,0 ± 0,4	0,7^{b} ± 0,3	0,7 ± 0,3	0,9 ± 0,3	1,3 ± 0,5	1,4 ± 0,2
Rubus pubescens	3,1^{a} ± 0,9	3,0^{a} ± 1,1	5,7 ± 1,4	7,0 ± 1,7	8,2 ± 2,0	4,8 ± 1,3	7,8 ± 2,5	6,5 ± 2,3	7,0 ± 2,0	5,4 ± 0,6
Other species										
Achillea millefolium	0,0 ± 0,0	0,1^{a} ± 0,1	0,0 ± 0,0	0,1^{a} ± 0,1	0,03±0,03	0,1 ± 0,1	0,03±0,03	0,03±0,03	0,1 ± 0,05	0,04±0,02
Actaea rubra	0,3 ± 0,2	0,0 ± 0,0	0,2 ± 0,2	0,1 ± 0,1	0,7^{a} ± 0,7	0,2 ± 0,2	0,2 ± 0,2	0,1 ± 0,1	0,3 ± 0,2	0,5 ± 0,1
Aster ciliolatus	1,5 ± 0,6	3,4 ± 1,1	4,9^{ab} ± 1,8	1,5 ± 0,7	2,1 ± 0,9	2,8 ± 1,0	3,2 ± 1,4	2,4 ± 1,0	2,0 ± 0,8	2,2 ± 0,3
Calamagrostis canadensis	0,9 ± 0,1	0,7^{ab} ± 0,1	0,8 ± 0,1	0,9 ± 0,1	1,2 ± 0,2	0,9 ± 0,1	1,0 ± 0,2	0,9 ± 0,1	1,2 ± 0,1	1,0 ± 0,1
Disporum trachycarpum	0,4 ± 0,3	1,4^{a} ± 0,9	0,0^{ab} ± 0,0	0,5 ± 0,2	0,1^{ab} ± 0,05	1,7^{a} ± 1,3	0,4 ± 0,2	0,6 ± 0,4	1,0 ± 0,5	1,2 ± 0,2
Epilobium angustifolium	1,0 ± 0,3	1,3 ± 0,4	1,6 ± 0,7	1,2 ± 0,4	1,7^{b} ± 0,4	1,1 ± 0,4	1,1 ± 0,4	1,4 ± 0,5	2,2^{b} ± 0,8	0,8 ± 0,1
Equisetum pratense	0,03 ± 0,03	0,1 ± 0,05	0,03 ± 0,03	0,2 ± 0,1	0,1 ± 0,1	0,0 ± 0,0	0,0 ± 0,0	0,1 ± 0,1	0,1 ± 0,05	0,1 ± 0,02
Equisetum sylvaticum	0,03±0,03	0,03±0,03	0,1 ± 0,05	0,0 ± 0,0	0,03±0,03	0,03±0,03	0,1 ± 0,05	0,1 ± 0,1	0,1 ± 0,05	0,1 ± 0,02
Galium triflorum	0,0^{b} ± 0,0	0,1 ± 0,05	0,0^{b} ± 0,0	0,1 ± 0,05	0,2^{a} ± 0,1	0,1 ± 0,05	0,0^{b} ± 0,0	0,1 ± 0,1	0,1 ± 0,1	0,1 ± 0,02
Mertensia paniculata	0,9 ± 0,4	1,9 ± 1,0	0,7 ± 0,4	0,8 ± 0,4	2,2^{b} ± 1,2	1,4 ± 0,6	1,9 ± 1,4	1,5 ± 1,0	0,6 ± 0,2	0,8 ± 0,2
Trientalis borealis	0,1 ± 0,1	0,3 ± 0,2	0,1 ± 0,1	0,2 ± 0,1	0,03±0,03	0,0 ± 0,0	0,1 ± 0,1	0,2 ± 0,1	0,2 ± 0,2	0,1 ± 0,03

Viola spp. (mostly *V. canadensis*)	0,5 ± 0,4	0,3 ± 0,2	0,4 ± 0,3	0,3 ± 0,1	$2,1^{a}$ ± 1,1	0.4 ± 0.2	0.9 ± 0.7	0.7 ± 0.3	0.1 ± 0.1	0.9 ± 0.2
Flowering (% plants in flower or fruit)										
Cornus canadensis	1,4 ± 1,4	2,3 ± 2,3	3,5 ± 2,5	1,8 ± 1,0	2,4 ± 1,1	0,8 ± 0,8	7,1 ± 3,7	5,6 ± 2,2	10,5 ± 4,8	6,1 ± 0,9
Galium boreale	$3,5^{ab}$ ± 3,0	$0,5^{ab}$ ± 0,5	$1,0^{ab}$ ± 1,0	$3,4^{ab}$ ± 2,5	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0
Maianthemum canadense	1,1 ± 1,1	3,3 ± 1,4	3,3 ± 1,4	3,3 ± 1,3	7,7 ± 4,6	4,0 ± 1,7	3,3 ± 1,7	4,3 ± 3,7	3,8 ± 2,5	4,6 ± 0,9
Leaf characteristics (cm)										
Aralia nudicaulis - length of longest leaflet	$9,0^{ab}$ ± 0,5	10,3 ± 1,0	9,9 ± 0,9	$9,2^{b}$ ± 0,8	$9,5^{b}$ ± 0,6	9,9 ± 0,8	10.3 ± 1.0	$9,5^{b}$ ± 1,1	9,7 ± 0,8	10,6 ± 0,2
Fragaria virginiana - length of middle leaflet	5,7 ± 0,3	6,1 ± 0,4	5,7 ± 0,4	$5,2^{ab}$ ± 0,4	5,7 ± 0,4	6,0 ± 0,3	5,4 ± 0,4	6,2 ± 0,3	5,6 ± 0,3	6,0 ± 0,1
Petasites palmatus - length of petiole	$21,0^{ab}$ ± 1,8	$20,7^{ab}$ ± 2,4	17,1 ± 1,8	$19,2^{b}$ ± 1,8	18,1 ± 1,1	17,3 ± 1,2	18,0 ± 1,5	18,5 ± 1,7	16,4 ± 1,4	17 ± 0,4
Petasites palmatus - width	10,5 ± 1,1	$11,4^{b}$ ± 1,2	10,6 ± 1,1	10,2 ± 0,7	10,0 ± 0,9	9,2 ± 0,5	$11,8^{b}$ ± 1,1	9,9 ± 1,1	8,9 ± 0,9	9,4 ± 0,3

[a] = significantly different from the adjacent riparian forest.

[b] = significantly different from the upland interior forest.

[1] All grass species except *Calamagrostis canadensis*, includes *Elymus innovatus*.

Appendix 3-1. Average values for all common shrub and herb species (frequency > 10% along at least one set of transects), as well as shrub and herb species richness, flowering and leaf characteristics, at different distances from the edges of clearcuts of different ages (pre=pre-harvest). Shaded values for 1 and 2 yr represent changes from the previous year that were significantly different ($p<0.05$) relative to changes in interior forest (100-200m), and for 5 and 16 yr represent average values that were significantly different from average values in interior forest. Fifty-nine of the 318 significant results in this table were expected due to random chance. Data are means ± 1 SE; standard error was calculated among all subplots.

	Age (yr)	0m	5m	10m	20m	40m	60m	100-200m
Shrub richness	pre	6.0 ± 0.5	5.9 ± 0.3	5.4 ± 0.3	5.8 ± 0.3	5.4 ± 0.3	5.2 ± 0.4	5.1 ± 0.2
(# species per subplot)	1	5.6 ± 0.4	6.2 ± 0.4	5.5 ± 0.3	5.8 ± 0.4	5.4 ± 0.4	5.2 ± 0.4	5.4 ± 0.2
	2	5.8 ± 0.3	6.1± 0.4	5.5 ± 0.3	6.0 ± 0.4	5.6 ± 0.4	4.8 ± 0.4	5.6 ± 0.2
	5	5.1 ± 0.4	5.0 ± 0.5	5.2 ± 0.5	5.5 ± 0.3	5.2 ± 0.4	5.8 ± 0.5	5.8 ± 0.2
	16	5.3 ± 0.3	5.2 ± 0.4	5.2 ± 0.4	5.6 ± 0.4	5.0 ± 0.3	5.1 ± 0.3	5.1 ± 0.2
Shrubs								
Alnus crispa	pre	8.3 ± 4.8	7.8 ± 3.0	12.2 ± 5.0	9.5 ± 3.3	8.3 ± 4.9	16.2 ± 6.9	11.4 ± 2.9
	1	7.8 ± 3.8	8.1 ± 4.1	16.2 ± 6.4	9.0 ± 3.0	6.7 ± 4.4	15.6 ± 6.8	12.6 ± 3.1
	2	6.8 ± 3.6	8.0 ± 3.8	10.8 ± 5.1	11.9 ± 4.6	3.8 ± 1.9	13.6 ± 5.9	12.1 ± 3.0
	5	4.8 ± 4.5	3.0 ± 2.0	5.0 ± 4.5	7.7 ± 5.2	6.0 ± 3.4	7.2 ± 4.2	6.3 ± 2.1
	16	6.5 ± 4.6	12.5 ± 7.0	5.2 ± 5.0	18.2 ± 6.9	5.5 ± 3.0	6.3 ± 4.0	6.6 ± 2.5
Alnus rugosa	pre	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 ± 0.0
	1	0.0 ± 0.0	0.0 ± 0.0	1.5 ± 1.5	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
	2	0.0 ± 0.0	0.0 ± 0.0	2.0 ± 2.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.02 ± 0.02
	5	3.2 ± 3.0	2.0 ± 2.0	2.5 ± 2.5	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	1.9 ± 1.0
	16	4.4 ± 3.8	0.3 ± 0.3	10.0 ± 6.8	0.3 ± 0.3	2.3 ± 1.9	5.0 ± 5.0	5.6 ± 2.8
Amelanchier alnifolia	pre	2.3 ± 0.7	1.8 ± 0.7	2.2 ± 1.1	0.6 ± 0.3	2.0 ± 1.1	2.0 ± 0.8	1.2 ± 0.4
	1	2.1 ± 0.7	2.0 ± 1.0	1.9 ± 1.0	0.5 ± 0.3	1.6 ± 1.0	1.8 ± 0.7	0.9 ± 0.3
	2	1.6 ± 0.6	1.8 ± 0.7	1.5 ± 0.7	0.4 ± 0.2	1.5 ± 1.0	1.3 ± 0.6	0.7 ± 0.2
	5	0.8 ± 0.3	0.9 ± 0.3	1.3 ± 0.4	1.5 ± 0.7	1.9 ± 1.1	2.6 ± 1.1	0.6 ± 0.2
	16	0.7 ± 0.6	1.3 ± 1.3	0.1 ± 0.1	0.3 ± 0.3	0.4 ± 0.3	0.0 ± 0.0	0.4 ± 0.2
Cornus stolonifera	pre	2.0 ± 1.4	0.5 ± 0.5	0.3 ± 0.3	2.0 ± 2.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
	1	1.0 ± 0.7	0.3 ± 0.3	0.2 ± 0.2	0.2 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1
	2	2.0 ± 1.4	0.5 ± 0.5	0.5 ± 0.5	0.2 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1
	5	0.0 ± 0.0	0.0 ± 0.0	0.3 ± 0.3	0.3 ± 0.3	0.1 ± 0.1	0.5 ± 0.3	0.4 ± 0.2
	16	0.2 ± 0.2	1.3 ± 1.3	1.6 ± 1.3	2.5 ± 1.1	0.0 ± 0.0	0.6 ± 0.6	0.1 ± 0.05
Corylus cornuta	pre	13.8 ± 6.1	18.0 ± 6.6	7.9 ± 3.9	9.3 ± 4.8	2.3 ± 1.6	6.4 ± 4.4	12.8 ± 3.5
	1	6.1 ± 3.1	14.4 ± 5.2	7.3 ± 3.6	8.5 ± 4.6	2.7 ± 1.8	5.4 ± 4.1	11.1 ± 3.3
	2	4.6 ± 2.4	9.5 ± 3.9	5.0 ± 2.8	7.0 ± 4.2	2.7 ± 1.8	5.3 ± 4.1	10.5 ± 3.3
	5	0.2 ± 0.2	4.6 ± 2.8	2.3 ± 2.0	0.3 ± 0.3	0.0 ± 0.0	2.3 ± 2.0	2.7 ± 1.9
	16	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 ± 0.0
Lonicera dioica	pre	0.4 ± 0.2	0.9 ± 0.5	1.1 ± 0.5	1.2 ± 0.5	0.5 ± 0.3	0.4 ± 0.2	0.7 ± 0.2
	1	0.1 ± 0.1	0.7 ± 0.2	0.7 ± 0.3	1.0 ± 0.3	0.7 ± 0.3	0.6 ± 0.2	0.7 ± 0.2
	2	0.3 ± 0.1	0.5 ± 0.2	0.5 ± 0.2	0.5 ± 0.1	0.6 ± 0.3	0.3 ± 0.1	0.6 ± 0.1
	5	1.3 ± 0.5	0.6 ± 0.2	1.8 ± 1.0	0.8 ± 0.2	0.7 ± 0.2	1.0 ± 0.2	1.3 ± 0.3
	16	0.3 ± 0.2	0.8 ± 0.4	1.1 ± 0.5	0.4 ± 0.2	0.2 ± 0.1	0.0 ± 0.0	0.4 ± 0.1

Lonicera involucrata	pre	7.0 ± 2.9	1.3 ± 0.6	1.9 ± 1.1	3.1 ± 1.7	2.2 ± 1.5	1.5 ± 0.7	2.8 ± 1.0
	1	6.9 ± 3.1	1.7 ± 1.0	2.6 ± 1.4	5.4 ± 2.8	1.7 ± 1.0	1.6 ± 0.7	3.3 ± 1.2
	2	5.6 ± 2.9	1.4 ± 1.0	2.3 ± 1.2	5.6 ± 2.9	2.4 ± 1.6	2.0 ± 1.1	4.0 ± 1.5
	5	0.8 ± 0.5	0.3 ± 0.2	1.3 ± 1.0	0.5 ± 0.5	3.5 ± 3.5	0.5 ± 0.2	2.5 ± 0.8
	16	0.5 ± 0.3	5.0 ± 3.0	0.9 ± 0.6	3.4 ± 1.8	0.9 ± 0.6	0.8 ± 0.6	5.3 ± 2.0
Prunus pensylvanica	pre	0.5 ± 0.5	0.3 ± 0.3	2.5 ± 2.0	1.0 ± 0.7	0.3 ± 0.3	0.2 ± 0.2	0.2 ± 0.1
	1	0.6 ± 0.5	0.1 ± 0.1	0.6 ± 0.5	1.3 ± 1.0	0.3 ± 0.3	0.2 ± 0.2	0.2 ± 0.1
	2	0.2 ± 0.1	1.7 ± 1.5	1.1 ± 1.0	1.7 ± 1.5	0.2 ± 0.2	0.1 ± 0.1	0.2 ± 0.1
	5	0.1 ± 0.1	1.1 ± 1.0	1.5 ± 1.1	0.3 ± 0.3	0.5 ± 0.5	0.3 ± 0.2	0.0 ± 0.0
	16	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Ribes oxyacanthoides[1]	pre	1.8 ± 1.0	0.7 ± 0.3	0.9 ± 0.5	1.6 ± 0.7	1.4 ± 0.6	1.4 ± 0.7	0.8 ± 0.2
	1	1.0 ± 0.5	0.6 ± 0.3	0.8 ± 0.3	1.1 ± 0.4	1.7 ± 0.6	1.4 ± 1.0	1.3 ± 0.4
	2	0.6 ± 0.3	0.3 ± 0.1	0.8 ± 0.5	0.9 ± 0.5	1.0 ± 0.3	0.9 ± 0.5	0.7 ± 0.2
	5	0.8 ± 0.5	1.0 ± 0.5	1.6 ± 1.0	1.1 ± 0.4	0.4 ± 0.3	0.5 ± 0.3	1.7 ± 0.5
	16	2.9 ± 1.9	5.2 ± 2.1	4.4 ± 2.2	2.5 ± 0.9	4.4 ± 3.1	5.2 ± 2.5	5.3 ± 1.3
Ribes triste	pre	4.0 ± 1.8	4.3 ± 1.8	4.0 ± 1.5	2.0 ± 0.7	5.0 ± 1.2	4.7 ± 1.7	2.7 ± 1.0
	1	3.8 ± 1.6	5.9 ± 2.7	5.6 ± 2.4	4.3 ± 2.1	5.8 ± 1.3	4.5 ± 1.5	3.3 ± 1.1
	2	3.4 ± 2.0	3.1 ± 1.1	4.2 ± 1.4	3.7 ± 1.7	4.7 ± 1.1	6.7 ± 2.0	3.2 ± 0.7
	5	1.5 ± 1.0	1.6 ± 0.7	2.1 ± 1.1	5.3 ± 2.4	7.5 ± 2.4	8.5 ± 3.2	5.1 ± 0.9
	16	4.2 ± 1.9	6.0 ± 2.4	10.4 ± 3.1	6.0 ± 1.6	7.4 ± 2.7	7.9 ± 2.3	7.9 ± 1.5
Rosa acicularis	pre	14.8 ± 3.9	14.6 ± 3.9	11.4 ± 3.2	9.4 ± 2.3	13.6 ± 3.3	11.5 ± 4.4	9.2 ± 1.5
	1	12.6 ± 3.1	9.1 ± 2.3	8.7 ± 2.2	7.6 ± 1.8	10.4 ± 2.6	13.9 ± 4.3	8.5 ± 1.3
	2	9.2 ± 3.1	5.3 ± 1.5	7.8 ± 1.9	6.6 ± 1.7	8.1 ± 2.6	10.8 ± 3.5	8.4 ± 1.2
	5	6.1 ± 1.1	7.2 ± 1.4	6.5 ± 1.1	6.9 ± 1.0	13.4 ± 3.5	5.9 ± 1.5	8.2 ± 1.0
	16	11.2 ± 1.9	9.1 ± 1.7	8.4 ± 1.8	12.1 ± 2.5	10.3 ± 2.7	15.8 ± 4.3	10.1 ± 1.7
Rubus idaeus	pre	2.6 ± 0.8	1.9 ± 0.4	1.4 ± 0.4	2.8 ± 0.7	2.2 ± 0.7	1.4 ± 0.4	2.8 ± 0.8
	1	3.9 ± 1.6	3.6 ± 1.4	1.8 ± 0.7	4.4 ± 1.4	2.1 ± 0.6	2.0 ± 0.7	3.2 ± 1.1
	2	3.6 ± 1.4	2.0 ± 0.6	1.1 ± 0.4	3.0 ± 0.8	2.2 ± 0.7	1.5 ± 0.6	3.2 ± 1.2
	5	1.1 ± 0.5	0.6 ± 0.2	0.8 ± 0.2	0.9 ± 0.3	1.4 ± 0.3	1.9 ± 0.7	2.0 ± 0.6
	16	2.6 ± 1.2	1.8 ± 0.9	3.4 ± 1.9	1.6 ± 0.5	1.9 ± 0.7	5.2 ± 1.4	4.6 ± 1.1
Salix spp.	pre	0.7 ± 0.5	0.6 ± 0.5	0.2 ± 0.2	0.1 ± 0.1	0.6 ± 0.5	0.1 ± 0.1	0.3 ± 0.1
	1	0.3 ± 0.3	0.3 ± 0.3	0.1 ± 0.1	0.3 ± 0.2	0.2 ± 0.2	0.1 ± 0.1	0.8 ± 0.5
	2	0.2 ± 0.2	0.1 ± 0.1	0.1 ± 0.1	0.3 ± 0.2	0.1 ± 0.1	0.1 ± 0.1	0.5 ± 0.3
	5	0.3 ± 0.2	0.4 ± 0.2	0.3 ± 0.2	0.8 ± 0.5	0.5 ± 0.2	0.2 ± 0.1	0.2 ± 0.1
	16	5.8 ± 3.2	8.8 ± 5.5	4.4 ± 3.0	1.7 ± 1.2	0.5 ± 0.3	0.4 ± 0.3	0.8 ± 0.5
Symphoricarpos albus (could include *S. occidentalis*)	pre	1.6 ± 0.4	1.6 ± 0.5	1.6 ± 0.6	1.5 ± 0.6	1.5 ± 0.5	1.2 ± 0.5	0.9 ± 0.2
	1	1.0 ± 0.2	1.1 ± 0.2	1.3 ± 0.4	1.7 ± 0.6	1.4 ± 0.4	1.4 ± 0.5	0.9 ± 0.2
	2	1.3 ± 0.2	0.9 ± 0.2	1.1 ± 0.3	1.3 ± 0.5	1.5 ± 0.6	1.2 ± 0.5	0.7 ± 0.1
	5	0.8 ± 0.3	0.6 ± 0.1	0.8 ± 0.5	2.4 ± 1.5	3.9 ± 2.4	0.8 ± 0.3	0.8 ± 0.2
	16	0.4 ± 0.3	0.6 ± 0.4	0.1 ± 0.1	0.1 ± 0.1	0.2 ± 0.2	0.4 ± 0.3	0.2 ± 0.1
Viburnum edule	pre	11.4 ± 3.7	12.2 ± 2.3	10.9 ± 3.5	9.3 ± 2.2	9.9 ± 2.7	8.7 ± 2.6	7.8 ± 1.4
	1	6.4 ± 1.7	7.2 ± 1.5	9.1 ± 2.4	8.2 ± 1.8	6.1 ± 1.2	7.3 ± 1.7	9.0 ± 1.4
	2	4.4 ± 1.2	5.3 ± 1.2	5.5 ± 1.7	5.4 ± 1.3	7.9 ± 2.6	7.9 ± 1.9	6.6 ± 1.2
	5	3.5 ± 0.7	5.9 ± 2.2	7.7 ± 2.6	10.5 ± 2.9	11.1 ± 2.1	8.2 ± 2.2	10.4 ± 1.6
	16	10.0 ± 2.9	9.7 ± 2.0	14.1 ± 3.0	13.8 ± 3.4	14.9 ± 3.3	11.1 ± 2.1	16.5 ± 2.3

Herb richness (# species per subplot)	pre	9.5 ± 0.5	9.8 ± 0.6	9.4 ± 0.5	9.2 ± 0.5	9.7 ± 0.5	9.2 ± 0.5	8.7 ± 0.3
	1	9.2 ± 0.4	9.9 ± 0.6	9.9 ± 0.5	9.5 ± 0.4	9.4 ± 0.5	9.3 ± 0.5	8.6 ± 0.3
	2	9.6 ± 0.4	9.7 ± 0.5	9.7 ± 0.6	9.1 ± 0.5	9.2 ± 0.5	9.1 ± 0.5	8.3 ± 0.3
	5	9.9 ± 0.7	9.6 ± 0.7	10.0 ± 0.5	9.9 ± 0.7	10.1 ± 0.6	8.9 ± 0.6	9.3 ± 0.3
	16	9.6 ± 0.8	8.8 ± 0.7	8.6 ± 0.6	8.3 ± 0.7	8.1 ± 0.5	8.6 ± 0.5	7.8 ± 0.3
Herbs								
Total	pre	65 ± 7	60 ± 6	70 ± 7	80 ± 6	65 ± 6	68 ± 5	63 ± 4
	1	63 ± 5	71 ± 7	79 ± 7	82 ± 5	72 ± 6	72 ± 6	70 ± 4
	2	45 ± 5	37 ± 5	34 ± 3	46 ± 5	36 ± 4	38 ± 3	36 ± 3
	5	36 ± 3	37 ± 4	39 ± 5	36 ± 4	41 ± 4	34 ± 4	40 ± 3
	16	51 ± 7	48 ± 6	42 ± 4	48 ± 6	41 ± 5	44 ± 5	39 ± 3
Achillea millefolium	pre	0.0 ± 0.0	0.0 ± 0.0	0.03 ± 0.03	0.1 ± 0.1	0.1 ± 0.05	0.0 ± 0.0	0.1 ± 0.05
	1	0.0 ± 0.0	0.0 ± 0.0	0.03 ± 0.03	0.03 ± 0.03	0.03 ± 0.03	0.03 ± 0.03	0.03 ± 0.02
	2	0.0 ± 0.0	0.0 ± 0.0	0.03 ± 0.03	0.03 ± 0.03	0.01 ± 0.05	0.03 ± 0.03	0.1± 0.04
	5	0.2 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.03 ± 0.03	0.03 ± 0.03	0.03 ± 0.03	0.1 ± 0.02
	16	0.04 ± 0.04	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Actaea rubra	pre	0.4 ± 0.3	0.2 ± 0.1	1.1 ± 0.7	0.7 ± 0.7	0.2 ± 0.1	1.3 ± 0.6	0.2 ± 0.1
	1	0.1 ± 0.05	0.4 ± 0.3	1.9 ± 1.1	1.0 ± 0.7	0.3 ± 0.2	2.1 ± 1.0	0.4 ± 0.2
	2	0.1 ± 0.1	0.1 ± 0.1	1.1 ± 0.7	0.9 ± 0.7	0.3 ± 0.2	1.1 ± 0.4	0.4 ± 0.2
	5	0.4 ± 0.3	0.4 ± 0.3	0.1 ± 0.1	0.2 ± 0.1	0.4 ± 0.2	0.4 ± 0.3	0.3 ± 0.2
	16	0.4 ± 0.3	1.3 ± 0.9	0.04 ± 0.04	0.5 ± 0.3	0.2 ± 0.2	0.5 ± 0.3	0.3 ± 0.2
Aralia nudicaulis	pre	21.1 ± 3.5	15.9 ± 3.2	24.3 ± 4.6	29.6 ± 4.6	25.1 ± 4.3	31.5 ± 3.9	23.9 ± 2.4
	1	16.3 ± 2.9	16.0 ± 3.3	22.5 ± 3.5	24.7 ± 4.2	21.4 ± 3.2	25.9 ± 3.0	21.9 ± 2.1
	2	9.2 ± 2.0	7.7 ± 2.0	7.5 ± 1.4	14.8 ± 3.0	10.4 ± 2.0	12.4 ± 2.2	9.5 ± 1.4
	5	5.7 ± 1.7	5.8 ± 2.1	5.4 ± 1.5	8.7 ± 2.2	10.8 ± 3.0	10.8 ± 3.4	10.1 ± 1.7
	16	13.5 ± 2.9	14.0 ± 3.5	14.7 ± 2.6	20.4 ± 4.0	21.0 ± 4.0	14.7 ± 3.2	12.2 ± 1.6
Aster ciliolatus	pre	2.5 ± 1.1	1.5 ± 0.7	2.5 ± 1.2	1.9 ± 0.5	3.9 ± 1.4	3.8 ± 1.4	1.3 ± 0.3
	1	2.7 ± 1.1	2.5 ± 1.0	3.6 ± 1.3	3.0 ± 0.9	5.1 ± 1.7	5.1 ± 2.0	1.8 ± 0.4
	2	2.7 ± 1.1	0.6 ± 0.2	2.2 ± 0.9	1.3 ± 0.4	1.9 ± 0.7	3.0 ± 1.5	1.1 ± 0.3
	5	1.6 ± 0.4	1.9 ± 0.7	2.9 ± 1.0	2.5 ± 1.1	1.8 ± 0.3	1.0 ± 0.4	1.3 ± 0.2
	16	5.3 ± 2.7	1.1 ± 0.3	0.6 ± 0.3	0.9 ± 0.3	0.8 ± 0.4	0.1 ± 0.1	1.5 ± 0.6
Aster conspicuus	pre	2.5 ± 1.0	4.0 ± 1.6	2.8 ± 1.3	1.5 ± 1.0	0.9 ± 0.5	1.0 ± 0.7	1.7 ± 0.6
	1	2.0 ± 0.8	2.8 ± 1.2	3.8 ± 1.5	2.1 ± 1.4	1.2 ± 0.7	0.5 ± 0.4	1.7 ± 0.6
	2	1.8 ± 0.6	1.9 ± 1.0	1.5 ± 0.5	1.7 ± 0.8	1.2 ± 1.0	1.4 ± 0.9	1.1 ± 0.4
	5	0.4 ± 0.2	0.8 ± 0.7	0.1 ± 0.1	0.4 ± 0.3	0.2 ± 0.1	0.0 ± 0.0	0.8 ± 0.3
	16	1.3 ± 0.9	1.3 ± 0.9	1.3 ± 1.9	2.5 ± 1.4	0.3 ± 0.2	0.8 ± 0.6	0.1 ± 0.1
Calamagrostis canadensis	pre	1.0 ± 0.2	1.4 ± 0.2	1.0 ± 0.2	0.9 ± 0.2	1.1 ± 0.2	0.9 ± 0.2	1.0 ± 0.1
	1	2.4 ± 0.8	3.5 ± 1.0	2.0 ± 1.0	3.1 ± 1.4	3.3 ± 2.0	1.8 ± 0.7	2.6 ± 0.6
	2	2.3 ± 0.9	1.2 ± 0.2	0.8 ± 0.1	1.1 ± 0.3	1.0 ± 0.2	0.9 ± 0.1	1.3 ± 0.2
	5	5.5 ± 3.0	2.4 ± 1.3	1.1 ± 0.1	1.2 ± 0.2	0.9 ± 0.1	1.5 ± 0.3	1.2 ± 0.1
	16	1.0 ± 0.1	1.0 ± 0.04	1.3 ± 0.1	1.3 ± 0.2	1.1 ± 0.1	1.1 ± 0.1	1.6 ± 0.3
Carex spp.	pre	0.03 ± 0.03	0.03 ± 0.03	0.0 ± 0.0	0.03 ± 0.03	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.03
	1	0.03 ± 0.03	0.03 ± 0.03	0.1 ± 0.05	0.03 ± 0.03	0.1 ± 0.05	0.0 ± 0.0	0.1 ± 0.02
	2	0.03 ± 0.03	0.03 ± 0.03	0.1 ± 0.05	0.1 ± 0.1	0.03 ± 0.03	0.0 ± 0.0	0.1 ± 0.04
	5	0.03 ± 0.03	0.03 ± 0.03	0.1 ± 0.05	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.02 ± 0.02
	16	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0	0.03 ± 0.02

Cornus canadensis	pre	9.2 ± 2.4	9.1 ± 2.3	8.6 ± 1.7	11.6 ± 2.1	8.8 ± 2.2	5.0 ± 1.3	8.1 ± 1.4
	1	7.3 ± 1.5	9.2 ± 2.0	12.2 ± 2.8	11.5 ± 1.9	9.3 ± 2.3	5.5 ± 1.4	10.5 ± 1.6
	2	5.5 ± 1.5	5.7 ± 1.7	5.4 ± 1.2	6.7 ± 1.7	5.6 ± 1.7	2.6 ± 0.6	5.9 ± 1.2
	5	3.0 ± 0.9	3.4 ± 1.0	5.9 ± 1.4	4.1 ± 1.0	4.1 ± 1.0	1.8 ± 0.5	4.3 ± 0.7
	16	2.5 ± 0.9	2.0 ± 0.7	2.7 ± 1.3	3.0 ± 0.8	2.0 ± 0.5	4.3 ± 1.5	3.4 ± 0.7
Disporum trachycarpum	pre	0.7 ± 0.3	1.9 ± 1.0	1.7 ± 0.8	1.6 ± 0.7	1.5 ± 0.7	0.3 ± 0.2	1.1 ± 0.5
	1	0.9 ± 0.4	0.9 ± 0.5	2.3 ± 1.2	1.5 ± 0.7	2.2 ± 1.0	0.6 ± 0.4	1.2 ± 0.4
	2	0.5 ± 0.1	0.3 ± 0.1	0.6 ± 0.2	1.4 ± 0.7	0.9 ± 0.4	0.5 ± 0.2	0.6 ± 0.2
	5	0.4 ± 0.2	0.4 ± 0.3	0.3 ± 0.2	0.4 ± 0.2	0.9 ± 0.4	0.4 ± 0.2	0.1 ± 0.1
	16	0.04 ± 0.04	0.8 ± 0.5	0.3 ± 0.1	0.2 ± 0.1	1.2 ± 0.9	0.3 ± 0.2	0.4 ± 0.3
Epilobium angustifolium	pre	0.3 ± 0.1	0.7 ± 0.3	0.9 ± 0.4	1.2 ± 0.7	1.2 ± 0.4	0.5 ± 0.2	0.8 ± 0.2
	1	0.5 ± 0.3	0.4 ± 0.2	0.5 ± 0.2	0.3 ± 0.1	0.9 ± 0.4	0.9 ± 0.7	0.6 ± 0.2
	2	0.4 ± 0.1	0.7 ± 0.4	0.6 ± 0.4	0.8 ± 0.5	0.5 ± 0.2	0.3 ± 0.2	0.6 ± 0.3
	5	1.8 ± 0.7	0.6 ± 0.1	1.7 ± 0.5	0.9 ± 0.4	0.9 ± 0.7	0.7 ± 0.2	0.5 ± 0.1
	16	2.8 ± 0.6	6.5 ± 1.6	4.8 ± 1.5	4.3 ± 2.2	2.5 ± 1.1	2.4 ± 1.0	2.3 ± 0.8
Equisetum arvense	pre	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.03
	1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.03
	2	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.05	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.03
	5	0.03 ± 0.03	0.03 ± 0.03	0.1 ± 0.05	0.1 ± 0.05	0.03 ± 0.03	0.0 ± 0.0	0.1 ± 0.03
	16	0.04 ± 0.04	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1	0.04 ± 0.04	0.03 ± 0.02
Equisetum pratense	pre	0.0 ± 0.0	0.03 ± 0.03	0.03 ± 0.03	0.1 ± 0.1	0.1 ± 0.05	0.03 ± 0.03	0.1 ± 0.03
	1	0.1 ± 0.1	0.03 ± 0.03	0.03 ± 0.03	0.2 ± 0.1	0.1 ± 0.1	0.1 ± 0.05	0.1 ± 0.03
	2	0.1 ± 0.1	0.03 ± 0.03	0.1 ± 0.05	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.05	0.1 ± 0.03
	5	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.03 ± 0.03	0.04 ± 0.02
	16	0.04 ± 0.04	0.0 ± 0.0	0.0 ± 0.0	0.04 ± 0.04	0.1 ± 0.1	0.04 ± 0.04	0.1 ± 0.04
Equisetum sylvaticum	pre	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.03 ± 0.03	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.04
	1	0.0 ± 0.0	0.03 ± 0.03	0.1 ± 0.05	0.1 ± 0.05	0.1 ± 0.05	0.1 ± 0.1	0.1 ± 0.04
	2	0.03 ± 0.03	0.1 ± 0.05	0.03 ± 0.03	0.2 ± 0.1	0.1 ± 0.1	0.2 ± 0.1	0.2 ± 0.04
	5	0.1 ± 0.1	0.03 ± 0.03	0.1 ± 0.1	0.1 ± 0.05	0.1 ± 0.1	0.03 ± 0.03	0.3 ± 0.1
	16	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.04 ± 0.04	0.2 ± 0.1	0.04 ± 0.04	0.1 ± 0.04
Fragaria virginiana	pre	2.9 ± 0.8	2.3 ± 0.6	2.3 ± 0.9	2.4 ± 0.6	2.6 ± 0.8	2.4 ± 0.8	2.6 ± 0.5
	1	4.0 ± 1.1	3.1 ± 0.9	2.1 ± 0.8	3.5 ± 1.1	2.4 ± 0.8	2.7 ± 0.9	3.5 ± 0.7
	2	3.9 ± 1.2	1.4 ± 0.3	0.7 ± 0.2	1.0 ± 0.3	1.5 ± 0.7	0.9 ± 0.2	1.3 ± 0.3
	5	1.6 ± 0.4	1.1 ± 0.2	1.4 ± 0.5	1.8 ± 0.5	1.2 ± 0.3	1.1 ± 0.4	1.0 ± 0.2
	16	1.2 ± 0.8	0.5 ± 0.2	0.5 ± 0.2	1.8 ± 1.3	0.5 ± 0.4	0.3 ± 0.2	0.3 ± 0.2
Galium boreale	pre	0.6 ± 0.1	0.5 ± 0.1	0.4 ± 0.1	0.6 ± 0.1	0.5 ± 0.1	0.5 ± 0.1	0.5 ± 0.1
	1	0.5 ± 0.1	0.5 ± 0.1	0.5 ± 0.1	0.6 ± 0.1	0.3 ± 0.1	0.5 ± 0.1	0.4 ± 0.1
	2	0.6 ± 0.1	0.6 ± 0.1	0.4 ± 0.1	0.6 ± 0.1	0.4 ± 0.1	0.4 ± 0.1	0.4 ± 0.1
	5	0.8 ± 0.1	0.6 ± 0.1	0.6 ± 0.1	0.5 ± 0.1	0.7 ± 0.1	0.5 ± 0.1	0.5 ± 0.1
	16	0.5 ± 0.1	0.5 ± 0.1	0.6 ± 0.1	0.8 ± 0.2	0.3 ± 0.1	0.5 ± 0.1	0.3 ± 0.1
Galium triflorum	pre	0.1 ± 0.1	0.3 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.2 ± 0.1	0.2 ± 0.1	0.1 ± 0.03
	1	0.3 ± 0.2	0.6 ± 0.2	0.2 ± 0.1	0.3 ± 0.1	0.3 ± 0.1	0.6 ± 0.3	0.1 ± 0.1
	2	0.4 ± 0.2	0.4 ± 0.1	0.1 ± 0.1	0.2 ± 0.1	0.4 ± 0.1	0.2 ± 0.1	0.1 ± 0.03
	5	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.05	0.2 ± 0.1	0.2 ± 0.1	0.2 ± 0.1	0.5 ± 0.2
	16	0.04 ± 0.04	0.1 ± 0.1	0.2 ± 0.1	0.04 ± 0.04	0.2 ± 0.1	0.3 ± 0.2	0.3 ± 0.1

Lathyrus ochroleucus	pre	5.6 ± 1.6	4.0 ± 1.2	4.9 ± 1.6	4.5 ± 1.1	4.0 ± 1.5	2.8 ± 0.6	3.7 ± 0.6
	1	6.4 ± 1.6	4.9 ± 1.4	6.3 ± 1.9	3.5 ± 1.4	4.1 ± 1.3	2.9 ± 1.1	2.4 ± 0.5
	2	3.3 ± 0.7	3.9 ± 1.3	2.1 ± 0.7	1.0 ± 0.4	1.4 ± 0.7	1.3 ± 0.7	1.3 ± 0.4
	5	4.7 ± 0.9	8.2 ± 1.9	6.3 ± 1.6	2.2 ± 0.7	2.6 ± 0.7	2.6 ± 1.2	2.3 ± 0.5
	16	2.5 ± 0.6	3.8 ± 1.2	3.7 ± 1.0	1.2 ± 0.4	0.8 ± 0.4	1.4 ± 0.6	1.0 ± 0.3
Linnaea borealis	pre	1.8 ± 0.6	2.7 ± 0.7	3.2 ± 1.1	3.9 ± 1.4	1.0 ± 0.3	2.4 ± 1.1	3.8 ± 0.9
	1	1.7 ± 0.5	3.3 ± 1.2	2.4 ± 0.8	5.5 ± 2.6	1.5 ± 0.4	4.0 ± 2.1	4.9 ± 1.1
	2	1.4 ± 0.7	1.3 ± 0.7	1.4 ± 0.7	1.1 ± 0.4	1.0 ± 0.4	1.7 ± 1.0	1.1 ± 0.3
	5	0.6 ± 0.3	1.1 ± 0.7	0.4 ± 0.1	0.4 ± 0.2	2.1 ± 1.2	0.8 ± 0.4	1.0 ± 0.3
	16	2.3 ± 1.3	0.8 ± 0.3	1.5 ± 1.3	0.3 ± 0.1	0.9 ± 0.5	3.5 ± 1.5	0.4 ± 0.2
Maianthemum canadense	pre	3.6 ± 0.7	3.0 ± 0.8	2.7 ± 0.5	2.5 ± 0.5	2.4 ± 0.5	2.0 ± 0.4	2.8 ± 0.4
	1	2.1 ± 0.4	3.8 ± 1.0	3.6 ± 0.9	2.3 ± 0.4	2.9 ± 0.8	2.4 ± 0.7	3.5 ± 0.5
	2	1.4 ± 0.2	2.4 ± 1.0	2.0 ± 0.5	1.3 ± 0.2	1.5 ± 0.3	2.0 ± 0.7	2.3 ± 0.3
	5	1.5 ± 0.4	1.4 ± 0.3	2.5 ± 0.7	2.0 ± 0.4	1.6 ± 0.3	1.7 ± 0.4	1.6 ± 0.3
	16	3.3 ± 1.1	1.9 ± 0.5	1.0 ± 0.3	2.6 ± 0.7	1.2 ± 0.3	2.4 ± 0.6	1.1 ± 0.3
Mertensia paniculata	pre	0.3 ± 0.2	0.9 ± 0.5	1.6 ± 0.9	0.4 ± 0.2	1.0 ± 0.7	1.2 ± 0.7	0.7 ± 0.3
	1	0.2 ± 0.2	1.6 ± 0.9	1.3 ± 0.7	0.6 ± 0.4	1.6 ± 0.9	1.3 ± 1.0	0.9 ± 0.3
	2	0.4 ± 0.3	1.2 ± 0.7	0.5 ± 0.3	0.7 ± 0.4	0.6 ± 0.3	0.5 ± 0.2	1.0 ± 0.4
	5	0.2 ± 0.1	1.4 ± 0.7	0.5 ± 0.3	1.2 ± 0.6	3.0 ± 1.0	1.6 ± 0.7	3.2 ± 0.8
	16	1.3 ± 0.6	3.3 ± 1.8	0.3 ± 0.1	0.5 ± 0.2	1.5 ± 1.3	1.1 ± 0.6	1.6 ± 0.5
Mitella nuda	pre	2.3 ± 1.0	1.8 ± 0.5	1.8 ± 0.4	1.6 ± 0.3	1.5 ± 0.3	0.7 ± 0.2	1.0 ± 0.3
	1	2.2 ± 0.8	3.4 ± 1.2	2.7 ± 0.6	3.6 ± 1.1	2.6 ± 0.8	1.2 ± 0.3	2.3 ± 0.7
	2	1.2 ± 0.4	0.7 ± 0.2	1.2 ± 0.4	1.0 ± 0.2	1.4 ± 0.7	0.7 ± 0.2	1.2 ± 0.4
	5	0.4 ± 0.1	0.3 ± 0.1	0.6 ± 0.2	0.8 ± 0.2	1.8 ± 1.0	1.5 ± 0.3	4.3 ± 1.0
	16	0.1 ± 0.1	0.04 ± 0.04	0.2 ± 0.1	0.4 ± 0.2	1.4 ± 0.5	2.5 ± 0.8	3.3 ± 0.7
Orthilia secunda	pre	0.3 ± 0.2	0.1 ± 0.1	0.1 ± 0.1	0.4 ± 0.2	0.0 ± 0.0	0.1 ± 0.05	0.1 ± 0.1
	1	0.1 ± 0.1	0.3 ± 0.1	0.03 ± 0.03	0.4 ± 0.2	0.0 ± 0.0	0.1 ± 0.1	0.1 ± 0.1
	2	0.03 ± 0.03	0.1 ± 0.1	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0	0.2 ± 0.1	0.1 ± 0.03
	5	0.0 ± 0.0	0.03 ± 0.03	0.03 ± 0.03	0.2 ± 0.1	0.03 ± 0.03	0.03 ± 0.03	0.04 ± 0.02
	16	0.0 ± 0.0	0.04 ± 0.04	0.04 ± 0.04	0.2 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.02 ± 0.02
Petasites palmatus	pre	1.2 ± 0.5	1.6 ± 0.4	1.2 ± 0.4	1.6 ± 0.6	1.3 ± 0.4	2.1 ± 0.7	2.0 ± 0.5
	1	1.9 ± 0.8	1.8 ± 0.6	1.0 ± 0.3	1.8 ± 1.0	1.8 ± 0.8	2.1 ± 0.6	2.1 ± 0.5
	2	0.8 ± 0.4	1.3 ± 0.5	0.9 ± 0.4	0.5 ± 0.2	0.9 ± 0.4	1.0 ± 0.3	0.8 ± 0.2
	5	2.2 ± 0.8	2.5 ± 0.8	1.6 ± 0.4	2.8 ± 0.9	0.8 ± 0.2	1.3 ± 0.5	0.7 ± 0.1
	16	4.7 ± 1.5	3.2 ± 1.2	2.8 ± 1.0	1.8 ± 0.9	0.5 ± 0.2	2.5 ± 0.8	1.6 ± 0.4
Pyrola asarifolia	pre	0.7 ± 0.2	0.8 ± 0.2	0.4 ± 0.2	0.5 ± 0.2	0.4 ± 0.1	0.5 ± 0.3	0.7 ± 0.2
	1	0.5 ± 0.2	0.8 ± 0.2	0.4 ± 0.1	0.9 ± 0.7	0.5 ± 0.2	0.3 ± 0.2	0.9 ± 0.2
	2	0.5 ± 0.2	0.4 ± 0.1	0.3 ± 0.1	0.3 ± 0.2	0.4 ± 0.1	0.5 ± 0.3	0.5 ± 0.1
	5	0.4 ± 0.2	0.6 ± 0.2	0.5 ± 0.2	0.6 ± 0.1	0.9 ± 0.4	0.4 ± 0.1	0.9 ± 0.4
	16	1.2 ± 0.5	0.2 ± 0.1	0.5 ± 0.1	1.0 ± 0.4	0.8 ± 0.4	0.8 ± 0.5	0.3 ± 0.1
Rubus pubescens	pre	4.9 ± 0.9	5.4 ± 1.5	5.2 ± 1.4	10.9 ± 3.4	4.8 ± 1.6	5.2 ± 1.4	4.0 ± 0.6
	1	8.6 ± 1.8	7.7 ± 2.3	6.2 ± 2.1	10.2 ± 3.6	6.5 ± 2.0	7.4 ± 2.0	5.8 ± 0.8
	2	6.8 ± 1.6	3.5 ± 1.1	3.7 ± 1.0	8.6 ± 3.1	3.4 ± 1.3	4.8 ± 1.5	4.1 ± 0.7
	5	3.0 ± 0.8	2.6 ± 0.8	3.4 ± 1.5	2.8 ± 0.7	5.0 ± 1.2	4.0 ± 0.7	3.8 ± 0.7
	16	4.8 ± 1.7	5.3 ± 1.9	3.7 ± 1.4	3.7 ± 1.5	3.0 ± 0.9	3.6 ± 1.2	6.0 ± 1.1

Thalictrum venulosum	pre	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 ± 0.0
	1	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 ± 0.0
	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	0.0 ± 0.0
	5	0.2 ± 0.2	0.2 ± 0.1	0.1 ± 0.05	0.2 ± 0.1	0.1 ± 0.1	0.4 ± 0.2	0.1 ± 0.1
	16	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 ± 0.0
Vicia americana	pre	0.3 ± 0.1	0.5 ± 0.2	0.3 ± 0.2	0.2 ± 0.1	0.3 ± 0.1	0.2 ± 0.1	0.4 ± 0.1
	1	0.3 ± 0.1	0.3 ± 0.1	0.1 ± 0.05	0.3 ± 0.2	0.2 ± 0.1	0.03 ± 0.03	0.1 ± 0.1
	2	0.4 ± 0.1	0.2 ± 0.1	0.2 ± 0.1	0.2 ± 0.1	0.1 ± 0.1	0.03 ± 0.03	0.1 ± 0.04
	5	0.6 ± 0.1	0.3 ± 0.2	0.5 ± 0.2	0.4 ± 0.1	0.3 ± 0.1	0.2 ± 0.1	0.3 ± 0.1
	16	0.5 ± 0.1	0.2 ± 0.1	0.5 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.03
Viola spp. (mostly *V. canadensis*)	pre	0.3 ± 0.2	1.1 ± 0.7	1.0 ± 0.7	1.1 ± 1.0	1.3 ± 0.7	2.3 ± 1.0	0.3 ± 0.1
	1	0.5 ± 0.3	1.0 ± 0.7	1.1 ± 0.7	1.2 ± 1.0	1.6 ± 0.7	2.9 ± 1.2	0.4 ± 0.1
	2	0.2 ± 0.2	0.3 ± 0.1	0.4 ± 0.2	0.5 ± 0.3	0.4 ± 0.1	0.9 ± 0.3	0.2 ± 0.05
	5	0.3 ± 0.2	0.2 ± 0.1	0.1 ± 0.1	0.4 ± 0.2	0.2 ± 0.1	0.5 ± 0.2	0.4 ± 0.1
	16	1.2 ± 0.6	0.3 ± 0.2	0.5 ± 0.2	0.1 ± 0.1	0.2 ± 0.1	0.3 ± 0.1	0.5 ± 0.2
grass[2] spp.	pre	0.1 ± 0.1	0.1 ± 0.1	0.2 ± 0.1	0.2 ± 0.1	0.3 ± 0.1	0.4 ± 0.2	0.2 ± 0.04
	1	0.2 ± 0.1	0.2 ± 0.1	0.2 ± 0.1	0.1 ± 0.1	0.3 ± 0.1	0.3 ± 0.1	0.3 ± 0.1
	2	0.1 ± 0.1	0.2 ± 0.1	0.2 ± 0.1	0.03 ± 0.03	0.2 ± 0.1	0.2 ± 0.1	0.2 ± 0.04
	5	0.4 ± 0.1	0.4 ± 0.1	0.4 ± 0.1	0.4 ± 0.1	0.4 ± 0.2	0.2 ± 0.1	0.2 ± 0.05
	16	0.3 ± 0.1	0.2 ± 0.1	0.04 ± 0.04	0.04 ± 0.04	0.0 ± 0.0	0.04 ± 0.04	0.0 ± 0.0
Flowering (% plants in flower or fruit)								
Cornus canadensis	pre	2.2 ± 1.2	5.8 ± 2.4	4.0 ± 2.3	6.2 ± 2.1	7.0 ± 2.8	9.8 ± 3.7	7.3 ± 1.9
	1	0.7 ± 0.5	4.7 ± 1.9	5.9 ± 2.7	3.4 ± 1.7	6.9 ± 2.7	8.2 ± 4.6	3.9 ± 1.0
	2	11.7 ± 3.2	13.5 ± 3.5	17.2 ± 3.7	12.2 ± 2.7	9.1 ± 2.6	6.2 ± 2.9	8.9 ± 1.9
	5	7.4 ± 2.3	10.7 ± 4.4	13.1 ± 3.3	7.8 ± 2.6	18.8 ± 5.4	14.1 ± 4.0	11.6 ± 2.0
	16	10.1 ± 4.3	18.2 ± 8.5	9.0 ± 4.0	10.4 ± 4.3	0.0 ± 0.0	10.6 ± 6.1	5.5 ± 1.4
Galium boreale	pre	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 ± 0.0
	1	0.0 ± 0.0	0.3 ± 0.3	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.3 ± 0.3	0.8 ± 0.8
	2	9.5 ± 6.8	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	3.0 ± 3.0
	5	0.0 ± 0.0	7.2 ± 4.0	1.9 ± 1.9	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
	16	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 ± 0.0
Maianthemum canadense	pre	2.1 ± 1.2	9.2 ± 3.7	2.1 ± 1.2	2.0 ± 1.5	2.4 ± 1.5	7.1 ± 4.6	5.7 ± 1.5
	1	0.8 ± 0.8	2.8 ± 1.2	3.7 ± 1.7	0.9 ± 0.9	1.6 ± 0.9	3.8 ± 3.1	5.5 ± 1.5
	2	2.1 ± 1.0	14.9 ± 4.3	3.5 ± 1.2	5.1 ± 2.3	7.1 ± 4.6	2.0 ± 1.1	6.3 ± 1.7
	5	1.8 ± 1.4	0.0 ± 0.0	0.7 ± 0.5	5.8 ± 3.6	2.9 ± 1.7	1.7 ± 1.2	3.3 ± 1.0
	16	1.0 ± 1.0	0.7 ± 0.7	3.2 ± 3.2	7.0 ± 3.6	2.3 ± 1.6	3.5 ± 3.1	2.6 ± 1.3
Leaf characteristics (cm)								
Aralia nudicaulis - length of longest leaflet	pre	11.1 ± 0.4	10.4 ± 0.7	10.2 ± 0.6	10.6 ± 0.6	10.9 ± 0.5	10.3 ± 0.7	10.6 ± 0.3
	1	7.8 ± 0.5	7.1 ± 0.4	7.8 ± 0.5	9.0 ± 0.5	8.2 ± 0.7	9.0 ± 0.3	8.5 ± 0.3
	2	7.9 ± 0.7	7.5 ± 0.5	7.8 ± 1.2	8.4 ± 0.8	8.1 ± 0.6	7.7 ± 0.4	8.3 ± 0.4
Fragaria virginiana - length of middle leaflet	pre	6.4 ± 0.5	5.9 ± 0.4	6.1 ± 0.3	6.1 ± 0.2	6.0 ± 0.2	6.2 ± 0.2	5.9 ± 0.2
	1	5.3 ± 0.3	5.1 ± 0.4	4.4 ± 0.4	5.9 ± 0.4	5.1 ± 0.3	5.1 ± 0.4	5.4 ± 0.2
	2	5.6 ± 0.6	5.5 ± 0.8	5.6 ± 0.7	6.2 ± 0.8	5.6 ± 0.6	6.3 ± 1.0	5.6 ± 0.4
Petasites palmatus - length of petiole	pre	18.8 ± 1.1	14.8 ± 1.7	18.8 ± 0.7	17.9 ± 1.5	16.6 ± 1.4	15.7 ± 0.8	17.1 ± 0.8
	1	12.8 ± 0.7	11.0 ± 1.1	14.4 ± 1.1	13.9 ± 1.4	16.4 ± 1.2	14.8 ± 0.8	15.0 ± 0.7
	2	16.6 ± 0.9	14.9 ± 1.5	14.2 ± 1.1	12.4 ± 1.1	15.7 ± 1.6	13.0 ± 1.2	15.9 ± 0.7
Petasites palmatus - width	pre	9.6 ± 0.9	9.1 ± 1.0	10.3 ± 0.7	9.8 ± 1.0	9.2 ± 1.0	8.5 ± 1.1	9.4 ± 0.6
	1	7.1 ± 0.5	6.9 ± 0.7	9.5 ± 0.6	8.5 ± 0.8	10.0 ± 1.0	8.5 ± 0.7	8.8 ± 0.4
	2	10.8 ± 0.9	8.8 ± 0.8	9.6 ± 0.8	9.1 ± 1.0	10.4 ± 0.9	9.6 ± 1.0	9.8 ± 0.4

---

[1] *Ribes oxyacanthoides* includes *R. lacustre*.

[2] All grass species except *Calamagrostis canadensis*, includes *Elymus innovatus*.

Appendix 4-1. Average pre- and post-harvest cover for common shrub and herb species (frequency > 10% in the 100m or 200m buffers) at different distances (in m) from the edges of buffers of three different widths. Shaded values were significantly different (p<0.05) from interior forest. Significant changes between pre- and post-harvest values compared to changes in interior forest are indicated with an asterix beside the post-harvest values. One hundred and thirty-nine of the 347 average values, and 70 of the 146 changes that were significantly different from interior forest were expected due to random chance. Data are means ± 1 SE; error was calculated among subplots.

25m Buffer		Lake edge					Cut edge
		0	5	10	10	5	0
Shrubs Total	Pre	42 ± 16	49 ± 12	69 ± 20	82 ± 19	95 ± 8	75 ± 9
	Post	32 ± 15	42 ± 11	56 ± 16	52 ± 17	79 ± 6	62 ± 6
Alnus crispa	Pre	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
	Post	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Amelanchier alnifolia	Pre	12.7 ± 5.0	10.5 ± 3.4	3.8 ± 1.4	9.0 ± 3.5	4.5 ± 1.8	3.8 ± 2.1
	Post	6.0* ± 3.2	7.8 ± 4.5	2.3* ± 0.9	4.0 ± 3.2	1.8* ± 0.8	1.3 ± 0.2
Cornus stolonifera	Pre	0.2 ± 0.2	0.2 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.2
	Post	0.0* ± 0.0	0.0* ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.2
Corylus cornuta	Pre	8.3 ± 8.3	26.0 ± 9.4	47.0 ±13.8	51.8 ±15.9	73.3 ±9.9	60.0 ±10.8
	Post	10.0 ±10.0	25.5 ±11.0	43.5 ±14.4	35.2 ±13.3	66.7 ± 8.4	55.0 ± 6.5
Lonicera dioica	Pre	0.0 ± 0.0	1.2 ± 0.5	1.8 ± 0.7	1.5 ± 0.8	1.2 ± 0.7	0.0 ± 0.0
	Post	0.0 ± 0.0	1.3 ± 0.8	1.3 ± 0.4	1.0 ± 0.5	1.0 ± 0.4	0.3 ± 0.3
Lonicera involucrata	Pre	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
	Post	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Prunus spp.(*P. pensylvanica* and *P. virginiana*)	Pre	1.7 ± 1.1	1.0 ± 1.0	1.2 ± 0.7	4.2 ± 1.4	1.3 ± 0.4	0.0 ± 0.0
	Post	0.3 ± 0.2	0.7 ± 0.5	0.8 ± 0.5	1.0* ± 0.3	1.2 ± 0.4	0.0 ± 0.0
Ribes oxyacanthoides[1]	Pre	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
	Post	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Ribes triste	Pre	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
	Post	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Rosa acicularis	Pre	11.7 ± 4.6	4.3 ± 1.4	5.0 ± 1.6	4.5 ± 1.3	9.5 ± 5.1	3.3 ± 1.2
	Post	12.5 ± 5.1	3.0 ± 0.4	3.7 ± 1.4	2.8 ± 0.6	5.8 ± 3.2	1.8 ± 0.8
Rubus idaeus	Pre	2.7 ± 1.7	1.8 ± 1.6	0.5 ± 0.3	1.8 ± 1.6	0.3 ± 0.2	0.3 ± 0.3
	Post	1.5 ± 1.0	2.0 ± 1.6	0.3 ± 0.2	1.0 ± 0.8	0.2 ± 0.2	0.3 ± 0.3
Salix spp.	Pre	1.7 ± 1.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
	Post	0.2* ± 0.2	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Symphoricarpos albus (could include *S. occidentalis*)	Pre	3.0 ± 1.6	3.2 ± 1.4	1.7 ± 0.4	1.2 ± 0.5	0.8 ± 0.3	5.5 ± 2.6
	Post	1.2* ± 0.8	1.7* ± 0.7	1.2 ± 0.4	0.8 ± 0.2	0.7 ± 0.2	1.8* ± 0.5
Vaccinium myrtilloides	Pre	0.0 ± 0.0	0.8 ± 0.8	6.7 ± 6.7	3.3 ± 3.3	1.7 ± 1.7	0.0 ± 0.0
	Post	0.0 ± 0.0	0.5 ± 0.5	1.7 ± 1.7	5.0* ± 5.0	0.8 ± 0.8	0.0 ± 0.0
Viburnum edule	Pre	0.0 ± 0.0	0.0 ± 0.0	0.8 ± 0.8	5.2 ± 5.0	2.2 ± 1.6	2.0 ± 1.2
	Post	0.0 ± 0.0	0.0 ± 0.0	0.7 ± 0.7	1.7 ± 0.9	1.2 ± 0.7	1.5 ± 0.5

Herbs	Total	Pre	33 ± 11	40 ± 8	25 ± 8	36 ± 13	43 ± 14	35 ± 11
		Post	21* ± 10	52 ± 14	34 ± 11	40 ± 14	49 ± 18	51* ± 14
	Achillea millefolium	Pre	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
		Post	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
	Actaea rubra	Pre	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
		Post	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
	Apocynum androsaemifolium	Pre	0.3 ± 0.3	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	4.3 ± 3.2
		Post	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	1.1 ± 1.1	4.2 ± 3.2
	Aralia nudicaulis	Pre	16.9 ± 9.2	15.3 ± 5.0	6.2 ± 2.7	12.4 ± 7.5	22.7 ± 9.9	1.7 ± 0.9
		Post	12.8 ± 7.9	14.3 ± 5.3	12.6 ± 4.8	16.0 ± 8.7	16.8 ± 7.6	1.2 ± 0.8
	Aster ciliolatus	Pre	0.0 ± 0.0	0.6 ± 0.6	0.2 ± 0.1	1.1 ± 0.5	0.3 ± 0.2	0.7 ± 0.7
		Post	0.0 ± 0.0	1.2 ± 1.1	0.7 ± 0.5	1.0 ± 0.6	0.6 ± 0.4	0.5* ± 0.5
	Calamagrostis canadensis	Pre	0.7 ± 0.3	0.3 ± 0.2	0.4 ± 0.2	0.2 ± 0.2	0.2 ± 0.1	0.3 ± 0.2
		Post	1.6 ± 1.1	0.7 ± 0.6	0.3 ± 0.2	0.3 ± 0.2	0.1 ± 0.1	0.0* ± 0.0
	Carex spp.	Pre	0.4 ± 0.2	0.2 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.0 ± 0.0
		Post	0.1* ± 0.1	0.2 ± 0.1	0.1 ± 0.1	0.2 ± 0.1	0.1 ± 0.1	0.2* ± 0.2
	Cornus canadensis	Pre	0.0 ± 0.0	6.4 ± 5.5	2.1 ± 1.1	0.6 ± 0.4	1.9 ± 0.7	9.3 ± 4.4
		Post	0.0 ± 0.0	8.8 ± 7.7	2.1 ± 1.1	1.7 ± 1.1	3.4 ± 1.4	8.3 ± 2.7
	Disporum trachycarpum	Pre	0.1 ± 0.1	0.1 ± 0.1	1.1 ± 1.1	0.2 ± 0.1	0.1 ± 0.1	0.7 ± 0.7
		Post	0.1 ± 0.1	0.1 ± 0.1	0.8 ± 0.5	0.4* ± 0.2	0.2 ± 0.1	0.7 ± 0.5
	Epilobium angustifolium	Pre	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0
		Post	0.3 ± 0.3	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.3 ± 0.3	0.0 ± 0.0
	Equisetum arvense	Pre	0.2 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
		Post	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
	Equisetum pratense	Pre	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
		Post	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.2* ± 0.2
	Fragaria virginiana	Pre	0.0 ± 0.0	0.9 ± 0.6	1.1 ± 0.6	0.2 ± 0.1	0.7 ± 0.2	0.0 ± 0.0
		Post	0.0 ± 0.0	1.2 ± 1.1	0.4 ± 0.3	0.6 ± 0.4	1.0 ± 0.4	0.0 ± 0.0
	Galium boreale	Pre	0.2 ± 0.1	1.6 ± 1.1	0.2 ± 0.1	0.2 ± 0.1	0.3 ± 0.2	0.5 ± 0.2
		Post	0.4 ± 0.2	1.4 ± 1.1	0.4 ± 0.3	0.1 ± 0.1	0.3 ± 0.2	0.3 ± 0.2
	Galium triflorum	Pre	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
		Post	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
	Lathyrus ochroleucus	Pre	1.3 ± 0.4	1.9 ± 0.5	1.6 ± 0.6	2.4 ± 1.1	2.1 ± 0.8	1.7 ± 0.9
		Post	1.3 ± 1.1	4.2 ± 2.2	4.4* ± 2.2	4.0 ± 2.3	3.4 ± 2.1	8.8* ± 5.2
	Linnaea borealis	Pre	0.0 ± 0.0	0.0 ± 0.0	0.8 ± 0.5	0.6 ± 0.4	2.2 ± 1.1	6.7 ± 6.7
		Post	0.0 ± 0.0	0.0 ± 0.0	1.1 ± 0.7	0.8 ± 0.5	1.2 ± 0.6	6.7 ± 6.7
	Lycopodium annotinum	Pre	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
		Post	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
	Maianthemum canadense	Pre	3.8 ± 2.3	1.9 ± 1.0	6.6 ± 4.3	7.2 ± 4.6	2.1 ± 1.1	1.2 ± 0.7
		Post	1.4 ± 1.1	8.6 ± 7.7	8.4 ± 4.2	6.7 ± 3.6	7.4 ± 4.6	2.2* ± 0.9
	Mertensia paniculata	Pre	0.0 ± 0.0	1.1 ± 1.1	0.0 ± 0.0	6.7 ± 6.7	5.6 ± 5.6	0.0 ± 0.0
		Post	0.0 ± 0.0	2.2 ± 2.2	0.0 ± 0.0	0.0* ± 0.0	5.6 ± 5.6	0.0 ± 0.0
	Mitella nuda	Pre	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1	0.1 ± 0.1	0.0 ± 0.0
		Post	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0

Orthilia secunda	Pre	0.0 ± 0.0	0.0 ± 0.0	0.4 ± 0.4	0.7 ± 0.3	0.4 ± 0.4	0.0 ± 0.0
	Post	0.0 ± 0.0	0.1 ± 0.1	0.3 ± 0.3	1.0 ± 0.6	1.2* ± 1.1	0.0 ± 0.0
Petasites palmatus	Pre	0.0 ± 0.0	0.9 ± 0.6	1.0 ± 0.7	0.3 ± 0.3	0.0 ± 0.0	1.0 ± 0.7
	Post	0.0 ± 0.0	1.2 ± 1.1	0.6 ± 0.6	1.7 ± 1.1	0.1 ± 0.0	2.3* ± 1.1
Pyrola asarifolia	Pre	0.2 ± 0.2	0.1 ± 0.1	0.7 ± 0.3	0.8 ± 0.4	1.9 ± 0.4	0.3 ± 0.2
	Post	0.0 ± 0.0	0.1 ± 0.1	0.3 ± 0.2	0.8 ± 0.5	2.6* ± 0.6	0.0* ± 0.0
Rubus pubescens	Pre	1.3 ± 1.1	0.0 ± 0.0	0.7 ± 0.4	0.9 ± 0.5	1.9 ± 1.1	2.8 ± 1.6
	Post	0.1 ± 0.1	0.0 ± 0.0	0.1 ± 0.1	2.8 ± 2.2	1.6 ± 1.1	8.3* ± 4.0
Thalictrum venulosum	Pre	0.0 ± 0.0	0.0 ± 0.0	0.8 ± 0.4	0.6 ± 0.6	0.3 ± 0.3	0.2 ± 0.2
	Post	0.0 ± 0.0	0.0 ± 0.0	0.9* ± 0.6	1.1* ± 1.1	1.1* ± 1.1	0.2 ± 0.2
Trientalis borealis	Pre	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
	Post	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Vaccinium vitis-idaea	Pre	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
	Post	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Vicia americana	Pre	1.1 ± 0.5	0.7 ± 0.5	0.3 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
	Post	0.0* ± 0.0	0.7 ± 0.4	0.0 ± 0.0	0.0 ± 0.0	0.3* ± 0.2	0.0 ± 0.0
Viola spp. (mostly *V. canadensis*)	Pre	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1	0.6 ± 0.4	0.3 ± 0.2	3.0 ± 1.6
	Post	0.0 ± 0.0	0.3 ± 0.2	0.0 ± 0.0	0.6 ± 0.4	0.2 ± 0.2	3.0 ± 1.6
Grass spp.[2]	Pre	0.6 ± 0.2	0.9 ± 0.3	0.8 ± 0.4	0.6 ± 0.2	0.2 ± 0.1	0.3 ± 0.2
	Post	0.1* ± 0.1	0.4* ± 0.2	0.6 ± 0.2	0.7 ± 0.2	0.3 ± 0.2	0.5 ± 0.2

[1] *Ribes oxyacanthoides* included *R. lacustre*.

[2] Grass spp. included all grass species (including *Elymus innovatus*) except for *Calamagrostis canadensis*.

100m Buffer		Lake edge 0	5	10	20	40	40	20	10	5	Cut edge 0
Shrubs Total	Pre	74 ± 23	62 ± 16	64 ± 19	75 ± 20	70 ± 16	76 ± 16	105 ± 23	67 ± 27	68 ± 16	52 ± 14
	Post	62 ± 14	74 ± 18	74 ± 20	68 ± 15	66 ± 16	80 ± 16	100 ± 8	75 ± 16	52 ± 10	28 ± 7
Alnus crispa	Pre	15.0 ± 10.0	15.0 ± 10.0	11.3 ± 11.3	8.8 ± 8.8	7.5 ± 5.3	5.0 ± 5.0	16.7 ± 13.1	36.7 ± 18.0	14.0 ± 6.5	14.0 ± 11.1
	Post	5.6* ± 3.7	13.9 ± 9.4	8.8 ± 8.8	7.5 ± 7.5	7.5 ± 4.9	5.0 ± 5.0	15.0*±11.5	38.3 ± 17.6	7.0* ± 4.9	1.9* ± 1.3
Amelanchier alnifolia	Pre	1.4 ± 0.7	11.9 ± 4.6	6.4 ± 3.2	10.6 ± 6.7	12.5 ± 6.7	10.0 ± 5.0	3.7 ± 2.0	0.5 ± 0.5	0.0 ± 0.0	0.5 ± 0.3
	Post	0.9 ± 0.5	7.4 ± 3.6	7.0 ± 3.1	6.3 ± 3.2	7.5 ± 3.7	7.5 ± 3.7	2.3 ± 1.1	0.2 ± 0.2	0.0 ± 0.0	0.4 ± 0.3
Cornus stolonifera	Pre	0.4 ± 0.4	0.5 ± 0.5	1.9 ± 1.3	0.2 ± 0.2	0.6 ± 0.6	0.6 ± 0.6	0.3 ± 0.3	0.0 ± 0.0	0.2 ± 0.2	0.0 ± 0.0
	Post	2.5 ± 2.5	1.2 ± 1.2	3.8* ± 2.6	1.2* ± 0.8	2.5 ± 2.5	2.5 ± 2.5	1.7* ± 1.7	0.0 ± 0.0	0.6 ± 0.6	0.0 ± 0.0
Corylus cornuta	Pre	0.0 ± 0.0	0.8 ± 0.6	0.0 ± 0.0	11.9 ± 9.8	4.1 ± 3.7	21.5 ± 11.8	35.8 ± 15.5	2.5 ± 1.7	3.9 ± 2.6	0.4 ± 0.2
	Post	0.1 ± 0.1	1.0 ± 0.4	0.1 ± 0.1	11.0 ± 9.9	7.8 ± 7.5	24.0 ± 12.5	30.0 ± 15.5	0.5 ± 0.5	1.9 ± 1.3	1.4 ± 1.2
Lonicera dioica	Pre	1.9 ± 1.3	0.3 ± 0.3	1.4 ± 0.6	0.9 ± 0.6	0.9 ± 0.6	0.3 ± 0.3	0.7 ± 0.7	0.2 ± 0.2	0.9 ± 0.4	1.8 ± 1.3
	Post	3.1 ± 2.5	0.4 ± 0.3	1.1 ± 0.6	0.9 ± 0.6	0.9 ± 0.5	0.3 ± 0.3	0.8 ± 0.8	0.2 ± 0.2	1.6 ± 0.8	2.8 ± 2.5
Lonicera involucrata	Pre	1.0 ± 0.7	1.2 ± 0.8	0.5 ± 0.3	1.5 ± 0.2	0.6 ± 0.5	0.6 ± 0.5	3.3 ± 3.3	0.3 ± 0.3	3.0 ± 2.5	1.2 ± 1.2
	Post	2.0 ± 1.2	5.0 ± 3.8	1.8 ± 1.2	2.9 ± 2.5	1.9 ± 1.3	2.0 ± 1.3	5.0 ± 5.0	1.7 ± 1.7	3.1 ± 2.5	2.5 ± 2.5
Prunus spp. (*P. pensylvanica* and *P. virginiana*)	Pre	1.4 ± 1.2	8.1 ± 5.2	6.5 ± 3.2	11.3 ± 8.8	7.5 ± 6.2	1.9 ± 1.3	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1
	Post	1.4 ± 0.7	10.2* ± 6.8	6.9* ± 3.9	7.6 ± 6.2	2.5 ± 1.6	1.4 ± 1.2	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1
Ribes oxyacanthoides[1]	Pre	0.6 ± 0.4	0.2 ± 0.2	2.6 ± 2.5	0.8 ± 0.5	1.8 ± 1.3	1.8 ± 1.3	0.8 ± 0.8	0.7 ± 0.7	1.2 ± 1.2	0.4 ± 0.3
	Post	1.9 ± 1.3	0.6 ± 0.6	2.9 ± 2.5	1.2 ± 0.8	2.5 ± 1.6	2.5 ± 1.6	3.5 ± 3.3	1.7 ± 1.7	2.5 ± 2.5	0.9 ± 0.6
Ribes triste	Pre	0.8 ± 0.4	1.4 ± 0.7	1.0 ± 0.6	2.4 ± 1.3	1.9 ± 1.3	1.3 ±1.3	0.7 ± 0.4	1.5 ± 1.0	0.4 ± 0.3	2.3 ± 1.3
	Post	1.5 ± 1.2	2.1 ± 1.2	2.0 ± 1.2	5.4 ± 3.7	3.1 ± 2.5	2.5 ± 2.5	2.2 ± 1.6	1.5 ± 1.0	0.9 ± 0.4	2.1 ± 1.3
Rosa acicularis	Pre	12.1 ± 3.7	6.8 ± 2.3	10.9 ± 4.4	14.6 ± 3.8	13.6 ± 4.8	18.9 ± 8.6	23.7 ± 10.1	8.8 ± 2.5	17.9 ± 6.6	10.6 ± 3.9
	Post	8.1 ± 1.3	8.4 ± 2.2	13.3 ± 3.8	13.0 ± 2.9	14.4 ± 5.1	19.5 ± 8.5	19.8 ± 8.5	11.7 ± 2.8	15.6 ± 4.8	4.3 ± 0.9

	Rubus idaeus	Pre	0.6 ± 0.4	0.4 ± 0.3	1.8 ± 1.2	2.3 ± 1.3	0.8 ± 0.4	1.1 ± 0.4	5.7 ± 3.2	2.2 ± 0.8	4.1 ± 2.4	1.4 ± 0.6
		Post	1.1 ± 0.6	0.8 ± 0.6	2.3 ± 1.2	3.6 ± 2.4	1.1 ± 0.6	1.1 ± 0.6	6.2 ± 3.1	6.3 ± 3.1	6.0 ± 2.5	4.1 ± 2.6
	Salix spp.	Pre	15.4 ± 11.0	2.8 ± 1.3	1.0 ± 0.7	3.4 ± 1.6	0.1 ± 0.1	0.3 ± 0.3	0.7 ± 0.5	0.0 ± 0.0	0.0 ± 0.0	0.5 ± 0.3
		Post	12.9 ± 8.5	4.9 ± 2.5	3.9 ± 2.6	4.4 ± 1.8	0.1 ± 0.1	0.3 ± 0.3	2.3 ± 1.6	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1
	Symphoricarpos albus (could include *S. occidentalis*)	Pre	0.6 ± 0.3	4.6 ± 3.7	2.0 ± 0.8	1.0 ± 0.4	4.3 ± 3.7	4.1 ± 3.7	3.0 ± 1.5	0.7 ± 0.3	3.0 ± 1.2	1.8 ± 0.8
		Post	1.8 ± 1.2	10.3 ± 7.5	4.0 ± 2.4	1.1 ± 0.6	1.9 ± 1.3	1.6 ± 1.2	2.8 ± 1.5	2.0 ± 1.6	2.9 ± 1.3	2.1 ± 1.2
	Vaccinium myrtilloides	Pre	20.0 ± 13.2	6.2 ± 4.9	15.0 ± 9.8	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 ± 0.0
		Post	17.5 ± 12.1	5.9 ± 4.9	13.8 ± 9.4	0.2* ± 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
	Viburnum edule	Pre	2.5 ± 1.6	1.6 ± 1.2	2.5 ± 1.3	2.8 ± 1.6	13.5 ± 3.7	8.9 ± 3.7	10.3 ± 5.0	13.2 ± 7.5	19.8 ± 5.7	17.0 ± 4.7
		Post	1.5 ± 0.8	2.0 ± 1.2	2.5 ± 1.3	1.4 ± 1.2	12.4 ± 4.5	9.8 ± 4.5	8.8 ± 5.3	11.0 ± 4.8	10.4 ± 2.3	4.9 ± 2.3
Herbs	Total	Pre	49 ± 9	74 ± 11	66 ± 17	81 ± 12	81 ± 11	75 ± 10	49 ± 9	70 ± 11	72 ± 10	79 ± 12
		Post	68 ± 12	68 ± 11	60 ± 11	78 ± 11	79 ± 9	83 ± 11	56 ± 11	91* ± 14	86 ± 14	79 ± 12
	Achillea millefolium	Pre	0.0 ± 0.0	0.3 ± 0.2	0.0 ± 0.0	0.2 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.2
		Post	0.0 ± 0.0	0.2 ± 0.1	0.0 ± 0.0	0.2 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0* ± 0.0	0.1* ± 0.1	0.0 ± 0.0	0.8 ± 0.8
	Actaea rubra	Pre	0.4 ± 0.4	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.6 ± 0.6	0.0 ± 0.0	1.2 ± 0.9	2.0 ± 1.7
		Post	0.4 ± 0.4	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0	0.1 ± 0.1	0.1 ± 0.1	2.2 ± 2.2	0.0 ± 0.0	2.5 ± 1.8	0.0 ± 0.0
	Apocynum androsaemifolium	Pre	2.0 ± 1.7	7.2 ± 4.6	5.8 ± 5.8	1.2 ± 0.9	3.3 ± 3.3	3.3 ± 3.3	1.1 ± 1.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
		Post	8.3 ± 6.1	6.1 ± 3.1	3.3 ± 3.3	1.8 ± 1.7	0.8 ± 0.8	0.8 ± 0.8	0.0* ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
	Aralia nudicaulis	Pre	15.6 ± 6.2	25.4 ± 8.7	12.1 ± 4.8	13.1 ± 3.5	20.4 ± 7.7	11.8 ± 3.8	18.4 ± 7.0	8.4 ± 3.1	11.4 ± 5.9	12.6 ± 6.0
		Post	14.4 ± 4.3	14.7* ± 5.9	9.3 ± 4.1	11.4 ± 4.2	15.9 ± 6.9	9.3 ± 2.8	17.1 ± 5.6	11.2 ± 4.5	14.4* ± 6.0	8.9 ± 4.1
	Aster ciliolatus	Pre	1.6 ± 0.9	0.9 ± 0.5	1.3 ± 0.9	1.8 ± 1.7	0.5 ± 0.4	2.0 ± 1.7	2.4 ± 1.1	2.4 ± 1.1	3.1 ± 1.1	10.5 ± 4.7
		Post	2.3 ± 1.7	2.3 ± 1.7	3.3 ± 2.2	1.2 ± 0.6	0.8 ± 0.8	2.6 ± 1.8	3.8 ± 2.3	6.7* ± 2.8	5.9 ± 2.3	12.9 ± 4.4
	Aster conspicuus	Pre	1.5 ± 0.6	2.9 ± 2.5	0.9 ± 0.8	5.9 ± 4.3	3.0 ± 2.5	0.0 ± 0.0	0.1 ± 0.1	0.4 ± 0.4	5.0 ± 5.0	0.0 ± 0.0
		Post	4.8* ± 2.5	2.9 ± 1.8	0.9 ± 0.6	2.1 ± 1.7	0.5 ± 0.3	0.1 ± 0.1	0.1 ± 0.1	0.0 ± 0.0	4.2 ± 3.4	0.1 ± 0.1
	Calamagrostis canadensis	Pre	0.6 ± 0.1	0.7 ± 0.1	0.8 ± 0.2	0.8 ± 0.1	0.8 ± 0.2	0.9 ± 0.2	1.0 ± 0.2	1.0 ± 0.2	0.9 ± 0.1	1.1 ± 0.1
		Post	1.3* ± 0.4	0.5* ± 0.2	1.0 ± 0.2	1.0 ± 0.2	1.2 ± 0.3	1.2 ± 0.3	1.6 ± 0.5	1.1 ± 0.3	1.4 ± 0.3	1.4 ± 0.3

Carex spp.	Pre	0,3 ± 0,1	0,3 ± 0,1	0,1 ± 0,1	0,3 ± 0,1	0,3 ± 0,1	0,3 ± 0,1	0,1 ± 0,1	0,1 ± 0,1	0,1 ± 0,1	0,1 ± 0,1
	Post	0,2 ± 0,1	0,3 ± 0,1	0,3 ± 0,1	0,2 ± 0,1	0,2 ± 0,1	0,1 ± 0,1	0,0 ± 0,0	0,1 ± 0,1	0,0 ± 0,0	0,1 ± 0,1
Cornus canadensis	Pre	4,2 ± 2,5	4,1 ± 1,8	6,8 ± 3,9	13,0 ± 6,1	12,1 ± 5,3	12,3 ± 5,2	3,2 ± 1,4	9,6 ± 4,1	2,8 ± 0,9	7,7 ± 3,4
	Post	4,4 ± 2,2	4,2 ± 1,7	6,9 ± 3,3	12,5 ± 5,5	11,2 ± 5,8	11,6 ± 5,7	5,9 ± 2,9	9,4 ± 3,8	3,4 ± 1,0	7,5 ± 2,2
Disporum trachycarpum	Pre	0,0 ± 0,0	1,7 ± 1,7	0,0 ± 0,0	0,1 ± 0,1	0,2 ± 0,1	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,2 ± 0,2
	Post	0,0 ± 0,0	0,8 ± 0,8	0,0 ± 0,0	0,2 ± 0,1	0,2 ± 0,1	0,0 ± 0,0	0,2 ± 0,2	0,0 ± 0,0	0,0 ± 0,0	0,1 ± 0,1
Epilobium angustifolium	Pre	1,7 ± 0,5	2,6 ± 0,9	2,0 ± 0,9	1,4 ± 0,5	1,3 ± 0,5	1,1 ± 0,4	1,1 ± 1,1	2,4 ± 0,7	2,0 ± 0,6	0,8 ± 0,4
	Post	2,4 ± 1,6	2,7 ± 1,1	0,9 ± 0,5	0,8 ± 0,3	1,1 ± 0,4	2,4 ± 1,7	0,3 ± 0,3	2,8 ± 1,0	1,8 ± 0,7	0,3* ± 0,2
Equisetum arvense	Pre	0,5 ± 0,2	0,3 ± 0,2	0,3 ± 0,2	0,4 ± 0,2	0,5 ± 0,3	0,5 ± 0,3	0,7 ± 0,4	0,0 ± 0,0	0,2 ± 0,1	0,3 ± 0,2
	Post	0,8* ± 0,4	0,2 ± 0,2	0,5* ± 0,3	0,4 ± 0,2	0,5 ± 0,3	0,5 ± 0,3	0,3* ± 0,2	0,1* ± 0,1	0,2 ± 0,1	0,2 ± 0,1
Equisetum pratense	Pre	0,2 ± 0,1	0,2 ± 0,1	0,1 ± 0,1	0,4 ± 0,2	0,2 ± 0,2	0,2 ± 0,2	0,0 ± 0,0	0,0 ± 0,0	0,1 ± 0,1	0,1 ± 0,1
	Post	0,2 ± 0,1	0,0 ± 0,0	0,0 ± 0,0	0,5 ± 0,2	0,4 ± 0,2	0,4 ± 0,2	0,1 ± 0,1	0,0 ± 0,0	0,1 ± 0,1	0,1 ± 0,1
Fragaria virginiana	Pre	2,9 ± 1,1	2,3 ± 0,9	2,9 ± 1,1	2,6 ± 1,1	3,9 ± 2,5	2,3 ± 0,8	1,3 ± 0,5	6,3 ± 2,3	2,6 ± 1,1	4,0 ± 1,2
	Post	2,8 ± 1,1	2,3 ± 0,9	4,3 ± 2,1	3,5 ± 1,7	3,5 ± 2,5	2,8 ± 1,6	1,4 ± 0,7	12,3* ± 4,0	2,5 ± 0,9	4,4 ± 1,2
Galium boreale	Pre	1,0 ± 0,3	0,9 ± 0,4	0,6 ± 0,2	1,2 ± 0,5	0,7 ± 0,2	0,6 ± 0,2	0,8 ± 0,2	1,0 ± 0,3	0,4 ± 0,1	0,8 ± 0,2
	Post	1,0 ± 0,3	1,0 ± 0,4	0,8 ± 0,4	1,4 ± 0,8	0,7 ± 0,2	0,7 ± 0,2	0,7 ± 0,2	0,9 ± 0,3	0,4 ± 0,1	0,8 ± 0,2
Galium triflorum	Pre	0,0 ± 0,0	0,2 ± 0,1	0,0 ± 0,0	0,2 ± 0,1	0,4 ± 0,3	0,4 ± 0,3	0,0 ± 0,0	0,1 ± 0,1	0,0 ± 0,0	0,0 ± 0,0
	Post	0,3 ± 0,3	0,2 ± 0,1	0,2 ± 0,1	0,1 ± 0,1	0,2 ± 0,2	0,2 ± 0,2	0,1 ± 0,1	0,1 ± 0,1	0,2 ± 0,2	0,0 ± 0,0
Lathyrus ochroleucus	Pre	2,9 ± 0,9	6,2 ± 2,0	5,8 ± 2,4	9,1 ± 3,1	7,1 ± 2,7	6,0 ± 2,5	1,0 ± 0,6	3,9 ± 1,3	6,4 ± 2,6	3,9 ± 1,0
	Post	5,6* ± 2,1	5,9 ± 2,2	4,4 ± 2,3	5,8 ± 2,1	6,7 ± 2,7	6,5 ± 4,1	6,4* ± 2,8	4,3 ± 2,1	9,4 ± 3,0	10,9* ± 3,0
Linnaea borealis	Pre	0,1 ± 0,1	0,3 ± 0,3	0,4 ± 0,2	4,4 ± 3,3	1,0 ± 0,6	9,3 ± 4,9	1,2 ± 0,6	7,0 ± 3,6	10,7 ± 5,0	11,7 ± 5,4
	Post	0,3 ± 0,3	0,4 ± 0,2	0,3 ± 0,2	6,8 ± 5,8	2,1 ± 1,7	9,8 ± 5,5	0,8* ± 0,4	8,0 ± 3,2	8,3 ± 4,0	9,5* ± 4,5
Lycopodium annotinum	Pre	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 ± 0,0	4,4 ± 4,4	0,8 ± 0,8	0,2 ± 0,2
	Post	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 ± 0,0	3,3* ± 3,3	1,7* ± 1,7	0,1* ± 0,1
Maianthemum canadense	Pre	3,6 ± 1,1	10,0 ± 3,4	11,6 ± 4,9	4,6 ± 1,6	4,8 ± 1,7	4,9 ± 1,7	3,7 ± 1,3	6,2 ± 3,0	2,9 ± 0,8	4,6 ± 1,2
	Post	7,6 ± 3,2	11,3 ± 3,4	11,2 ± 4,3	6,6 ± 2,1	7,0 ± 2,1	6,4 ± 1,7	3,0 ± 0,7	5,8 ± 2,0	4,0 ± 1,6	4,8 ± 1,2

Mertensia paniculata	Pre	1.3 ± 0.9	0.4 ± 0.4	1.8 ± 1.7	1.5 ± 0.9	2.5 ± 2.5	1.7 ± 1.7	0.8 ± 0.6	2.2 ± 1.1	1.8 ± 0.9	0.6 ± 0.4
	Post	1.3 ± 0.9	3.4 ± 3.3	0.8 ± 0.5	1.0* ± 0.8	2.9 ± 2.5	0.6 ± 0.4	1.1 ± 1.1	4.3 ± 2.2	4.1 ± 2.2	0.3* ± 0.1
Mitella nuda	Pre	0.2 ± 0.1	0.2 ± 0.1	0.4 ± 0.3	2.5 ± 1.1	1.2 ± 0.8	3.0 ± 1.2	1.1 ± 0.7	1.0 ± 0.5	1.1 ± 0.4	1.4 ± 0.5
	Post	0.3 ± 0.1	0.3 ± 0.1	0.6 ± 0.4	4.9 ± 2.5	1.3 ± 0.9	4.9 ± 2.2	0.6* ± 0.6	1.3 ± 0.7	1.6 ± 0.9	1.0* ± 0.5
Orthilia secunda	Pre	0.0 ± 0.0	0.0 ± 0.0	0.3 ± 0.3	0.2 ± 0.2	0.2 ± 0.1	0.3 ± 0.2	0.2 ± 0.1	0.0 ± 0.0	0.2 ± 0.1	0.2 ± 0.1
	Post	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.2	0.3* ± 0.3	0.2 ± 0.1	0.6* ± 0.3	0.2 ± 0.1	0.0 ± 0.0	0.1 ± 0.1	0.1 ± 0.1
Petasites palmatus	Pre	3.7 ± 1.4	1.8 ± 0.8	5.4 ± 3.3	3.4 ± 1.6	2.8 ± 1.6	2.3 ± 0.9	2.6 ± 1.1	3.6 ± 1.1	2.3 ± 0.9	6.6 ± 2.7
	Post	2.9 ± 1.1	3.6 ± 1.7	3.8 ± 2.2	2.6 ± 0.9	3.3 ± 1.0	4.5 ± 1.8	3.7 ± 2.1	6.4 ± 3.1	5.3 ± 2.8	7.0 ± 2.7
Pyrola asarifolia	Pre	0.3 ± 0.2	0.6 ± 0.3	0.8 ± 0.2	0.8 ± 0.6	0.2 ± 0.1	0.6 ± 0.4	0.2 ± 0.2	1.0 ± 0.6	0.4 ± 0.3	0.8 ± 0.8
	Post	0.0 ± 0.0	0.7 ± 0.3	0.9 ± 0.4	2.2* ± 1.1	0.2 ± 0.1	0.6 ± 0.3	0.2 ± 0.2	1.0 ± 0.6	0.5 ± 0.4	0.8 ± 0.8
Rubus pubescens	Pre	2.1 ± 0.9	1.3 ± 0.9	2.5 ± 1.7	7.3 ± 3.4	7.6 ± 3.1	4.6 ± 1.8	4.2 ± 2.3	5.6 ± 2.2	14.2 ± 4.9	5.0 ± 2.5
	Post	2.6 ± 1.6	2.2 ± 1.1	3.2 ± 1.8	6.3 ± 2.4	7.8 ± 2.3	5.5 ± 1.8	3.9 ± 2.3	8.3 ± 4.2	11.2 ± 4.6	4.0 ± 1.7
Thalictrum venulosum	Pre	0.4 ± 0.4	0.4 ± 0.4	0.0 ± 0.0	2.5 ± 1.8	0.2 ± 0.2	0.2 ± 0.2	0.3 ± 0.3	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
	Post	1.7* ± 1.7	0.2* ± 0.2	0.0 ± 0.0	2.6* ± 1.8	0.1* ± 0.1	0.1* ± 0.1	0.3* ± 0.4	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Trientalis borealis	Pre	0.2 ± 0.2	0.6 ± 0.4	0.2 ± 0.2	0.4 ± 0.3	0.0 ± 0.0	0.8 ± 0.8	0.3 ± 0.3	0.1 ± 0.1	0.4 ± 0.3	0.6 ± 0.4
	Post	0.2 ± 0.2	0.5 ± 0.4	0.4 ± 0.4	0.6 ± 0.4	0.0 ± 0.0	1.7 ± 1.7	0.2* ± 0.2	0.1 ± 0.1	0.3 ± 0.3	0.3 ± 0.2
Vaccinium vitis-idaea	Pre	0.2 ± 0.1	0.0 ± 0.0	0.2 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.2
	Post	0.2 ± 0.1	0.0 ± 0.0	0.1* ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.3* ± 0.3
Vicia americana	Pre	0.8 ± 0.5	1.8 ± 0.9	1.9 ± 1.1	0.5 ± 0.4	1.7 ± 0.6	1.8 ± 0.9	0.8 ± 0.5	0.9 ± 0.6	0.1 ± 0.1	1.8 ± 0.9
	Post	0.4 ± 0.3	0.7 ± 0.4	1.0 ± 0.5	0.4 ± 0.2	1.4 ± 0.6	0.6 ± 0.4	0.6 ± 0.6	0.1 ± 0.1	1.9* ± 1.7	0.8 ± 0.4
Viola spp.	Pre	0.1 ± 0.1	0.1 ± 0.1	0.2 ± 0.1	0.0 ± 0.0	0.1 ± 0.1	0.2 ± 0.2	0.1 ± 0.1	1.7 ± 1.2	0.1 ± 0.1	0.4 ± 0.4
	Post	0.2 ± 0.2	0.1 ± 0.1	0.1 ± 0.1	0.3 ± 0.3	0.0 ± 0.0	0.2 ± 0.2	0.4 ± 0.3	2.8 ± 2.2	0.0 ± 0.0	0.5 ± 0.4
Grass spp. [2]	Pre	0.8 ± 0.3	0.3 ± 0.1	0.3 ± 0.2	0.3 ± 0.1	0.6 ± 0.3	0.5 ± 0.3	0.7 ± 0.2	0.4 ± 0.2	0.3 ± 0.1	0.3 ± 0.1
	Post	0.7 ± 0.2	0.3 ± 0.1	0.3 ± 0.1	0.2 ± 0.1	0.4* ± 0.2	0.4 ± 0.2	0.3* ± 0.2	0.6 ± 0.2	0.3 ± 0.1	0.3 ± 0.2

[1] *Ribes oxyacanthoides* included *R. lacustre*.

[2] Grass included all grass species (including *Elymus innovatus*) except for *Calamagrostis canadensis*.

200m Buffer		Lake edge												Cut edge
		0	5	10	20	40	60	100	60	40	20	10	5	0
Shrubs														
Total	Pre	60 ± 10	64 ± 12	36 ± 8	37 ± 7	52 ± 12	52 ± 9	47 ± 9	46 ± 11	72 ± 12	55 ± 14	41 ± 8	59 ± 20	32 ± 9
	Post	53 ± 10	53 ± 10	26 ± 5	30 ± 6	44 ± 7	49 ± 8	58* ± 11	54 ± 9	60 ± 10	41 ± 6	39 ± 8	42 ± 14	23 ± 4
Alnus crispa	Pre	7,0 ± 5,2	1,0 ± 0,7	2,0 ± 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	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0
	Post	6,0 ± 5,0	2,2 ± 2,0	3,0 ± 3,0	0,0 ± 0,0	0,0 ± 0,0	3,0 ± 3,0	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 ± 0,0
Amelanchier alnifolia	Pre	10,3 ± 5,1	4,9 ± 3,9	4,5 ± 2,2	4,5 ± 2,6	4,1 ± 2,0	3,7 ± 1,5	2,5 ± 1,3	3,5 ± 1,3	2,5 ± 1,1	8,0 ± 2,4	4,9 ± 2,1	4,8 ± 2,1	3,5 ± 1,5
	Post	4,5 ± 2,6	1,4 ± 0,7	1,8 ± 0,7	2,0 ± 1,1	1,8 ± 0,7	3,1 ± 1,3	2,3 ± 1,3	2,9 ± 1,0	2,1 ± 0,7	5,6* ± 2,0	4,4 ± 2,0	2,6* ± 1,1	3,6 ± 1,5
Cornus stolonifera	Pre	0,0 ± 0,0	1,2 ± 1,0	1,1 ± 0,5	0,0 ± 0,0	1,0 ± 0,6	2,0 ± 1,3	3,5 ± 2,5	1,0 ± 0,7	2,2 ± 1,3	2,0 ± 2,0	2,2 ± 2,0	5,0 ± 4,0	0.0 ± 0,0
	Pre	0,0 ± 0,0	0,7* ± 0,5	1,1 ± 0,6	0,0 ± 0,0	0,8* ± 0,4	1,5* ± 1,1	5,0 ± 3,8	0,8* ± 0,6	1,4* ± 1,0	0,3* ± 1,0	4,2 ± 4,0	3,0* ± 2,1	0,0 ± 0,0
Corylus cornuta	Post	9,4 ± 9,0	8,0 ± 8,0	0,3 ± 0,2	0,0 ± 0,0	2,2 ± 2,0	8,0 ± 6,1	0,0 ± 0,0	0,9 ± 0,6	8,0 ± 4,2	5,0 ± 5,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0
	Post	9,5 ± 9,0	8,0 ± 8,0	0,3 ± 0,2	0,0 ± 0,0	2,5 ± 2,0	6,0 ± 4,3	0,0 ± 0,0	0,9 ± 0,6	12,0*± 6,6	4,0 ± 4,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0
Lonicera dioica	Pre	1,2 ± 0,6	2,4 ± 1,3	1,1 ± 0,5	1,2 ± 1,0	1,1 ± 0,5	1,6 ± 0,4	1,2 ± 0,5	2,1 ± 1,0	1,3 ± 0,5	1,4 ± 1,0	1,3 ± 0,4	0,4 ± 0,2	0,5 ± 0,3
	Post	1,0 ± 0,5	1,6 ± 0,7	0,6 ± 0,3	0,7 ± 0,5	0,8 ± 0,3	0,9 ± 0,2	1,3 ± 0,6	1,9 ± 0,9	1,7 ± 1,0	1,0 ± 0,4	0,8 ± 0,3	0,5 ± 0,3	0,5 ± 0,3
Lonicera involucrata	Pre	1,7 ± 1,0	9,0 ± 6,9	0,0 ± 0,0	2,5 ± 1,3	6,4 ± 3,3	4,7 ± 3,0	0,3 ±0,2	10,4 ± 6,1	10,9 ± 7,9	3,5 ± 3,0	4,0 ± 3,0	11,4 ± 7,6	0,0 ± 0,0
	Post	2,5 ± 1,3	10,2 ± 7,9	0,1 ± 0,1	2,0 ± 1,1	5,1* ± 2,7	5,5 ± 3,9	1,0* ± 0,4	9,3 ± 6,0	7,8* ± 5,9	1,5 ± 1,1	3,7 ± 3,0	9,2* ± 6,4	0,0 ± 0,0
Prunus spp. (*P. pensylvanica* and *P. virginiana*)	Pre	0,3 ± 0,3	1,0 ± 1,0	0,3 ± 0,3	0,0 ± 0,0	2,0 ± 2,0	0,0 ± 0,0	0,0 ± 0,0	0,1 ± 0,1	0,0 ± 0,0	1,0 ± 1,0	1,0 ± 1,0	0,5 ± 0,5	1,2 ± 1,2
	Post	0,3 ± 0,3	0,5 ± 0,5	0,1 ± 0,1	0,0 ± 0,0	1,0 ± 1,0	0,0 ± 0,0	0,0 ± 0,0	0,1 ± 0,1	0,0 ± 0.0	0,5 ± 0,5	0,5 ± 0,5	0,2 ± 0,2	0,5 ± 0,5
Ribes oxyacanthoides[1]	Pre	3,2 ± 1,6	1,2 ± 1,0	0,5 ± 0,5	0,7 ± 0,5	1,3 ± 1,0	1,0 ± 0,5	2,5 ± 0,9	2,2 ± 1,1	2,7 ± 1,0	3,7 ± 2,9	2,6 ± 2,0	1,8 ± 1,0	0,0 ± 0,0
	Post	2,0 ± 0,8	1,3 ± 1,0	0,6 ± 0,5	0,8 ± 0,5	1,2 ± 1,0	0,9 ± 0,4	2,7 ± 0,8	1,9 ± 1,0	2,7 ± 1,2	2,8 ± 1,9	2,5 ± 2,0	1,3 ± 0,7	0,0 ± 0,0
Ribes triste	Pre	2,6 ± 1,3	1,8 ± 1,0	0,6 ± 0,5	0,9 ± 0,6	4,6 ± 2,1	4,7 ± 2,0	3,2 ± 1,2	4,9 ± 2,9	4,7 ± 1,3	3,9 ± 1,9	3,5 ± 1,5	2,5 ± 1,0	1,3 ± 1,3
	Post	3,1 ± 2,0	2,1 ± 1,0	0,7 ± 0,4	0,9 ± 0,6	3,8 ± 1,9	7,4 ± 2,5	4,8* ± 1,5	9,8 ± 5,1	4,3 ± 1,2	3,7 ± 1,9	6,0 ± 2,7	3,1 ± 1,3	1,3 ± 1,3
Rosa acicularis	Pre	7,0 ± 3,8	6,6 ± 2,7	9,8 ± 3,8	10,7 ± 3,4	9,6 ± 3,2	7,1 ± 1,8	8,0 ± 3,6	8,8 ± 3.6	3,4 ± 4,2	6,4 ± 1,3	6,9 ± 1,7	18,9 ± 5.8	13,4 ± 6,8
	Post	4,5 ± 2,0	5,6 ± 1,8	6,1 ± 2,7	8,5 ± 2,2	7,2 ± 2,8	5,9 ± 1,2	7,8 ± 3,6	13,5*± 3,7	8,7 ± 2,2	6,4 ± 1,3	7,5 ± 2,3	10,7 ± 2,7	10,3 ± 3,5
Rubus idaeus	Pre	3,5 ± 1,9	3,8 ± 1,9	3,0 ± 1,0	2,8 ± 1,1	2,0 ± 1,1	4,7 ± 1,9	9,0 ± 4,8	1,4 ± 0,6	10,9 ± 6,8	6,0 ± 2,1	4,9 ± 1,9	4,9 ± 2,9	3,6 ± 1,2
	Post	6,6 ± 4,8	4,5 ± 2,9	2,7 ± 1,0	2,8 ± 1,1	1,9 ± 1,0	3,7 ± 1,2	8,7* ± 4,8	1,6 ± 0,6	5,0 ± 2,8	3,9 ± 1,1	4,0 ± 1,2	5,6 ± 3,9	2,5* ± 0,7
Salix spp.	Pre	3,0 ± 2,0	2,2 ± 2,0	0,0 ± 0,0	0,1 ± 0,1	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,5 ± 0,3	0,6 ± 0,4	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0.0	0,0 ± 0,0
	Post	3,5 ± 2,1	2,3 ± 2,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,4 ± 0,3	0,2 ± 0,1	0,0 ± 0.0	0,0 ± 0,0	0,0 ± 0.0	0,0 ± 0,0
Symphoricarpos albus (could include *S. occidentalis*)	Pre	1,9 ± 1,1	3,2 ± 2,1	1,6 ± 0,5	1,4 ± 0,6	1,3 ± 0,6	0,6 ± 0,2	1,2 ± 0,5	2,7 ± 0,6	1,4 ± 1,0	1,4 ± 0,4	1,4 ± 0,3	2,4 ± 0,9	4,1 ± 2,6
	Post	1,1 ± 0,5	2,2 ± 1,3	1,3* ± 0,4	0,8 ± 0,4	1,5 ± 0,6	0,7* ± 0,2	1,2 ± 0,5	2,6 ± 1,0	1,4 ± 1,0	1,7 ± 0,4	1,4 ± 0,3	1,5 ± 0,4	1,9 ± 1,3

Vaccinium myrtilloides	Pre	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	1,0 ± 1,0	0,4 ± 0,4	0,1 ± 0,1	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 ± 0,0
	Post	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	1,0 ± 1,0	0,4 ± 0,4	0,3 ± 0,3	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 ± 0,0
Viburnum edule	Pre	8,9 ± 3,9	17,7 ± 4,7	10,7 ± 3,4	11,2 ± 2,1	16,0 ± 4,2	11,9 ± 2,8	12,5 ± 3,3	7,0 ± 1,8	5.2 ± 2,1	13,1 ± 4,7	8,0 ± 3,2	6,6 ± 1,9	4,8 ± 2,3
	Post	8,8 ± 3,9	10,6*± 2,2	7,5 ± 1,8	10,7 ± 2,7	16,0 ± 3,6	10,1 ± 2,4	18,3*± 4,6	8,0 ± 3,1	4,2 ± 1,4	8,5 ± 2,2	3,8* ± 1,2	4,6* ± 1,1	2,9* ± 1,3
Herbs														
Total	Pre	53 ± 10	77 ± 10	85 ± 11	78 ± 9	67 ± 8	71 ± 8	62 ± 8	65 ± 7	60 ± 9	73 ± 10	59 ± 7	74 ± 9	63 ± 10
	Post	66 ± 14	73 ± 10	92 ± 11	93 ± 11	63 ± 5	78 ± 7	89* ± 9	71 ± 8	70 ± 12	84 ± 10	73 ± 8	84 ± 11	72 ± 8
Achillea millefolium	Pre	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,1 ± 0,1	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 ± 0.0	0.0 ± 0,0	0,0 ± 0,0
	Post	0,0 ± 0,0	0,0 ± 0,0	0,3 ± 0,3	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 ± 0,0	0,0 ± 0.0	0,0 ± 0.0	0,0 ± 0,0
Actaea rubra	Pre	0,0 ± 0,0	0,0 ± 0,0	0,3 ± 0,3	0,0 ± 0,0	1,4 ± 1,3	0,0 ± 0.0	0,4 ± 0,2	0,1 ± 0,1	1,7 ± 1,3	0,1 ± 0,1	0,7 ± 0,4	1,8 ± 0,9	0,0 ± 0,0
	Post	0,0 ± 0,0	0,0 ± 0,0	1,3 ± 1,3	0,0 ± 0,0	0,7* ± 0,7	0,0 ± 0,0	0,1* ± 0,1	0,1 ± 0,1	0,8* ± 0,7	0,4 ± 0,2	1,3 ± 0,7	1,3* ± 0,7	0,1 ± 0,1
Apocynum androsaemifolium	Pre	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 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0.0	0,0 ± 0,0	0.0 ± 0,0
	Post	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 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0.0	0,0 ± 0,0	0,0 ± 0,0
Aralia nudicaulis	Pre	13,7 ± 3,9	23,7 ± 5,1	29,3 ± 7,0	26,5 ± 5,8	20,3 ± 4,4	32,7 ± 8,0	21,7 ± 6,9	26,2 ± 5,4	23,8 ± 6,9	21,6 ± 5,6	20,3 ± 5,9	28,2 ± 6,4	19,6 ± 6,7
	Post	16,5 ± 5,7	18,2 ± 4,1	27,3 ± 6,4	24,5 ± 4,7	17,0 ± 3,3	31,9 ± 6,5	28,9*± 7,8	32,3*± 6,7	20.5 ± 5,2	24,1 ± 6,4	23.5 ± 6,0	25,0 ± 6,1	19,5 ± 6,4
Aster ciliolatus	Pre	2,3 ± 1,4	5,5 ± 2,1	5,0 ± 3,2	1,1 ± 0,4	3,3 ± 1,8	2,1 ± 0,9	1,8 ± 0,9	1,9 ± 0,7	2,9 ± 0,9	2,8 ± 1,5	1,7 ± 0.8	2,3 ± 1,1	4,0 ± 1,8
	Post	2,4 ± 1,4	6,3 ± 2,5	6,1 ± 3,7	4,8 ± 2,3	3,2 ± 1,8	2,9 ± 1,4	2,1 ± 0,9	4,0 ± 2,0	7,1 ± 2,3	5,6 ± 2,3	2,5 ± 1,1	4,9 ± 2,3	7,8 ± 3,4
Aster conspicuus	Pre	1,1 ± 0,7	1,3 ± 1,3	2,5 ± 1,4	1,4 ± 0,7	3,4 ± 1,9	3,1 ± 1,8	0,0 ± 0.0	0,0 ± 0,0	1,1 ± 0.7	2,7 ± 2,1	0,1 ± 0,1	2,8 ± 2,1	4,3 ± 2,3
	Post	2,4* ± 1,4	0,7 ± 0,7	1,7 ± 1,3	1,5 ± 0,6	1,7 ± 0,9	3,8 ± 2,3	0,0 ± 0,0	0,0 ± 0,0	0,1 ± 0,1	0,7 ± 0,7	0,3 ± 0,3	3,1 ± 2,7	4,2 ± 2,6
Calamagrostis canadensis	Pre	0,7 ± 0,1	0,7 ± 0,1	0,9 ± 0,1	1,2 ± 0,2	1,0 ± 1,0	1,0 ± 1,0	1,8 ± 0,4	0,9 ± 0,2	0,9 ± 0,1	0,9 ± 0,1	1,1 ± 0,2	0,8 ± 0,1	0,8 ± 0,1
	Post	1,4 ± 0,4	0,9 ± 0,2	1,9 ± 0,7	2,4 ± 0,7	1,3 ± 0,2	1,9 ± 0,4	7,4* ± 2,4	2,3 ± 1,3	1,3* ± 0,1	0,9 ± 0,1	2,3 ± 0,7	1,6 ± 0,4	0,9 ± 0,1
Carex spp.	Pre	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,1 ± 0,1	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,1 ± 0,1	0,1 ± 0,1	0,0 ± 0,0	0,0 ± 0,0
	Post	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,1 ± 0,1	0,0 ± 0,0	0,1 ± 0,1	0,0 ± 0,0	0,1 ± 0,1	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0
Cornus canadensis	Pre	1,7 ± 0,6	3,7 ± 0,9	5,2 ± 1,5	3,7 ± 1,1	7,3 ± 2,1	4,5 ± 1,6	2,4 ± 0,8	2,9 ± 1,4	6,7 ± 2,2	7,7 ± 2,4	6,4 ± 2,2	5,1 ± 1,5	9,9 ± 3,0
	Post	2,5 ± 0,8	4,3 ± 1,2	7,5 ± 2,2	6,1 ± 2,8	11,1 ± 3,5	6,1 ± 2,5	2,6 ± 0,9	3,7 ± 2,0	9,7 ± 3,5	10,6 ± 3,9	9.3 ± 3,2	10,1 ± 2,8	11,6 ± 3,8
Disporum trachycarpum	Pre	0,7 ± 0,7	0,3 ± 0,3	0,2 ± 0,2	0,1 ± 0,1	1,5 ± 1,3	3,3 ± 2,6	2,9 ± 1,7	0,0 ± 0,0	1,0 ± 0,7	0,8 ± 0,4	1,7 ± 0,9	0,9 ± 0,7	0,7 ± 0,4
	Post	0,3 ± 0,3	0,1 ± 0,1	0,2 ± 0,1	0,1 ± 0,1	0,9 ± 0,7	2,3 ± 2,0	2,9 ± 1,7	0,0 ± 0,0	0,6 ± 0,4	0,6 ± 0,3	1,7 ± 0,9	0,5 ± 0,4	0,3* ± 0,2
Epilobium angustifolium	Pre	1,0 ± 0,7	0,8 ± 0,4	0,5 ± 0,4	0,8 ± 0,4	0,5 ± 0,2	0,4 ± 0,3	0,8 ± 0,4	0,4 ± 0,3	0,9 ± 0,4	1,2 ± 0,7	0,7 ± 0,4	1,7 ± 0,8	0,9 ± 0,5
	Post	0,3 ± 0,3	1,1 ± 0,7	0,7 ± 0,4	0,8 ± 0,4	0,4 ± 0,2	0,6 ± 0,4	0,9 ± 0,4	0,0 ± 0,0	0,4 ± 0,3	1,4 ± 0,7	1,3 ± 0,7	3,4 ± 1,8	1,7 ± 0,9
Equisetum arvense	Pre	3,5 ± 2,0	1,3 ± 0,4	0,7 ± 0,2	0,1 ± 0,1	0,1 ± 0,1	0,1 ± 0,1	0,2 ± 0,1	0,1 ± 0,1	0,4 ± 0,2	0,0 ± 0,0	0,1 ± 0,1	0,2 ± 0,1	0,1 ± 0,1
	Post	2,1 ± 0,9	1,1 ± 0,4	0,5 ± 0,2	0,1 ± 0,1	0,1 ± 0,1	0,1 ± 0,1	0,2* ± 0,2	0,3 ± 0,1	0,3 ± 0,2	0,0 ± 0,0	0,1 ± 0,1	0,3 ± 0,2	0,2* ± 0,2
Equisetum pratense	Pre	0,1 ± 0,1	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,1 ± 0,1	0,0 ± 0,0	0,0 ± 0,0	0,3 ± 0,2	0,0 ± 0,0	0,0 ± 0,0	0,1 ± 0,1	0,0 ± 0,0
	Post	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0	0.1 ± 0.1	0.2 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1	0.1 ± 0.1

Fragaria virginiana	Pre	1,8 ± 0,8	1,9 ± 0,8	3,5 ± 1,8	3,3 ± 1,8	1,3 ± 0,7	0,8 ± 0,4	2,9 ± 1,7	2,1 ± 0,8	1,5 ± 0.7	2,9 ± 0,9	2,5 ± 1,3	2,1 ± 0,6	3,3 ± 1,2
	Post	1,9 ± 0,8	2,9 ± 1,0	5,2 ± 2,3	3,2 ± 2,0	1,8 ± 0,7	0,8 ± 0,4	3,3* ± 1,7	2,6 ± 1,1	1,9 ± 0,7	4,8 ± 1,8	4,7 ± 2,3	3,4 ± 1,4	3,0 ± 1,6
Galium boreale	Pre	0,5 ± 0,1	1,0 ± 0,4	0,8 ± 0,1	0,7 ± 0,2	0,4 ± 0,1	0,5 ± 0,1	0,4 ± 0,1	0,6 ± 0,1	3,1 ± 2,6	0,7 ± 0,1	0,6 ± 0,1	0,7 ± 0,1	0,8 ± 0,2
	Post	0,5 ± 0,2	0,9 ± 0,3	0,9 ± 0,2	0,7 ± 0,2	0,5 ± 0,1	0,6 ± 0,2	0,6 ± 0,2	0,6 ± 0,2	0,6 ± 0,1	0,7* ± 0.1	0.8 ± 0,1	0,8* ± 0,1	0,8 ± 0,2
Galium triflorum	Pre	0,2 ± 0,1	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,1 ± 0,1	0,1 ± 0,1	0,0 ± 0.0	0,3 ± 0,2	0,1 ± 0,1	0.0 ± 0,0	0,2 ± 0,1	0,1 ± 0,1	0,0 ± 0,0
	Post	0,5 ± 0,4	0,0 ± 0,0	0,1 ± 0,1	0,0 ± 0,0	0,1 ± 0,1	0,0 ± 0,0	0,0 ± 0,0	0,3 ± 0,2	0,1 ± 0.1	0.0 ± 0,0	0,1 ± 0,1	0,1 ± 0,1	0,0 ± 0,0
Lathyrus ochroleucus	Pre	3,5 ± 1,0	6,2 ± 1,8	8,5 ± 2,0	9,2 ± 2,2	5,5 ± 2,1	6,5 ± 2,1	3,3 ± 2,6	3,8 ± 1,4	2,3 ± 0,9	4,3 ± 1.0	5,1 ± 1,7	5,1 ± 1,5	6,3 ± 2,4
	Post	4,0 ± 1,4	3,9 ± 1,3	7,5 ± 2,3	16,1* ± 5,1	4,1 ± 1,4	3,7 ± 1,2	0,9 ± 0,5	1,3 ± 0,4	3,4 ± 2,0	4,6 ± 1,8	5,7 ± 2,2	5,5 ± 2,1	8,4* ± 3,1
Linnaea borealis	Pre	0,7 ± 0,7	3,7 ± 1,8	3,5 ± 2,0	6,1 ± 4,7	1,3 ± 0,5	1,7 ± 0,7	1,3 ± 0.8	0,5 ± 0,3	1,0 ± 0,7	5,1 ± 4,0	0,4 ± 0,2	0,9 ± 0,7	2,5 ± 1,6
	Post	0,7 ± 0,7	7,3 ± 3,7	5,3 ± 2,9	6,2 ± 3,7	1,1 ± 0,4	2,3 ± 1,3	2,4 ± 1,7	0,5 ± 0,3	0,7 ± 0.5	4,9 ± 4,0	0,2 ± 0,1	1,0 ± 0,7	1,5 ± 0,6
Lycopodium annotinum	Pre	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0.0	2,1 ± 1,4	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 ± 0,0	0,0 ± 0,0
	Post	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0.0	2,5* ± 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	0.0 ± 0,0	0,0 ± 0.0
Maianthemum canadense	Pre	2,7 ± 1,3	3.0 ± 1,4	3,7 ± 1,4	5,0 ± 1,4	3,5 ± 0,8	2,9 ± 0,9	1,4 ± 0,4	2,9 ± 1,0	1,7 ± 0,4	2,7 ± 0,7	2,3 ± 0,7	3,4 ± 1,0	1,7 ± 0,6
	Post	2,4 ± 1,3	3,2 ± 1,4	3,8 ± 1,0	3,8 ± 1,4	3,5 ± 0,8	3,6 ± 1,1	1,1 ± 0,4	3,1 ± 1,0	1,5 ± 0,5	2,9 ± 0,8	1,9 ± 0,4	2,5 ± 0,7	1,6 ± 0,5
Mertensia paniculata	Pre	2,5 ± 0,9	3,9 ± 2,0	2,3 ± 1,0	0,5 ± 0,4	0,5 ± 0,3	0,4 ± 0,2	6,2 ± 3,4	1,9 ± 0,9	3,5 ± 2,1	4,0 ± 1,8	0,2 ± 0,2	0,7 ± 0,7	0,8 ± 0,4
	Post	3,6 ± 1,5	4,1 ± 2,6	5,0* ± 1,9	1,2 ± 0,7	1,1 ± 0,7	1,2 ± 0,7	11,7* ± 4,3	4,7 ± 2,7	5,1 ± 2,9	3,7 ± 2,0	2,1 ± 2.0	0,3 ± 0,2	0,9 ± 0,8
Mitella nuda	Pre	1,5 ± 1,3	0,3 ± 0,2	0,5 ± 0,3	0,3 ± 0,2	0,7 ± 0,4	1,0 ± 0,7	1,9* ± 0,6	0,9 ± 0,2	1,4 ± 0,5	1,3 ± 0,4	0,9 ± 0,4	1,0 ± 0,4	0,4 ± 0,2
	Post	1,1 ± 0,7	0,9 ± 0,7	0,9 ± 0,7	0,4 ± 0,2	0,8 ± 0,4	1,1 ± 0,5	5,7 ± 1,9	2,1 ± 0,7	2,9 ± 1,4	1,6 ± 0,7	1,4 ± 0,5	2,6 ± 1,4	0.6 ± 0,4
Orthilia secunda	Pre	0,6 ± 0,4	0,7 ± 0,7	1,5 ± 1,3	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,4 ± 0,2	0,1 ± 0,1	0,7 ± 0,7	0,0 ± 0,0
	Post	0,3 ± 0,2	0,3 ± 0,3	1,4 ± 1,3	0,0 ± 0,0	0,0 ± 0.0	0,0 ± 0.0	0.1* ± 0.1	0,0 ± 0,0	0,0 ± 0,0	0,4 ± 0,3	0,0 ± 0,0	0,7 ± 0,7	0,0 ± 0,0
Petasites palmatus	Pre	7,9 ± 2,6	6,8 ± 2,0	3,0 ± 2,0	4,1 ± 1,5	3,2 ± 0,8	1,9 ± 1,3	4,6 ± 2,3	3,9 ± 1,5	2,1 ± 0,8	1,2 ± 0,4	3,8 ± 0,9	3,8 ± 2,0	1,4 ± 0,5
	Post	9,7 ± 3,7	4,4 ± 2,0	2,5 ± 1,3	4,1 ± 1,5	1,9* ± 0,5	1,0 ± 0,7	5,0 ± 2,2	3,3 ± 1,1	1,3 ± 0,4	2,3 ± 1,3	2,5 ± 0,9	3,8 ± 1,5	1,3 ± 0,5
Pyrola asarifolia	Pre	1,1 ± 0,4	1,7 ± 0,5	1,4 ± 0,5	0,8 ± 0,4	0,5 ± 0,2	0,3 ± 0,2	0,1 ± 0,1	0,2 ± 0,1	0,5 ± 0,3	0,2 ± 0,1	0,5 ± 0,3	0,3 ± 0,3	0,4 ± 0,2
	Post	1,6 ± 0,7	2,1 ± 0,7	1,6 ± 0,7	0,9 ± 0,4	0,9 ± 0,4	0,2 ± 0,1	0,2 ± 0,2	0,3 ± 0,2	0,5 ± 0,3	0,5 ± 0,3	0,5 ± 0,3	0,4 ± 0,3	0,7 ± 0,3
Rubus pubescens	Pre	3,4 ± 1,4	4,7 ± 2,0	6,6 ± 2,1	7,3 ± 2,2	4,5 ± 1,7	5,7 ± 1,7	3,2 ± 0,9	5,1 ± 1,7	4,6 ± 1,8	5,7 ± 2,2	5,1 ± 2,0	7,3 ± 2,9	2,7 ± 0,9
	Post	6,9 ± 2,4	4,8 ± 1,4	6,8 ± 2,1	7,9 ± 2,5	5,1 ± 1,4	7,5 ± 2,3	4,8 ± 1,7	6,7 ± 2,2	5,8 ± 2,5	7,9 ± 2,1	7,5 ± 2,1	9,1 ± 3,5	4,8 ± 1,7
Thalictrum venulosum	Pre	0,1 ± 0,1	0,0 ± 0,0	0,0 ± 0.0	0,2 ± 0,2	0,0 ± 0,0	0,6 ± 0,4	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,1 ± 0,1	0,0 ± 0,0	0,0 ± 0,0
	Post	0,1 ± 0,1	0,0 ± 0,0	0,1* ± 0,1	0,3* ± 0,3	0,0 ± 0,0	2,5* ± 2,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,1* ± 0,1	0,2* ± 0,2	0,0 ± 0,0	0,0 ± 0,0
Trientalis borealis	Pre	0,0 ± 0,0	0,1 ± 0,1	0,0 ± 0,0	0,0 ± 0,0	0,1 ± 0,1	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 ± 0,0	0,0 ± 0,0
	Post	0,0 ± 0,0	0,1 ± 0,1	0,0 ± 0,0	0,0 ± 0,0	0,1 ± 0,1	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 ± 0,0	0,0 ± 0,0
Vaccinium vitis-idaea	Pre	0,0 ± 0,0	0,0 ± 0,0	0,1 ± 0,1	0,9 ± 0,7	0,1 ± 0,1	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 ± 0,0	0,0 ± 0,0
	Post	0,0 ± 0,0	0,0 ± 0,0	0,1 ± 0,1	1,0* ± 0,7	0,1 ± 0,1	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 ± 0,0	0,0 ± 0,0
Vicia americana	Pre	0,8 ± 0,4	2,1 ± 0,9	2,3 ± 0,8	1,2 ± 0,4	0,3 ± 0,2	0,3 ± 0,2	0,0 ± 0,0	0,3 ± 0,2	0,8 ± 0,3	1,1 ± 0,4	1,7 ± 0,5	1,2 ± 0,5	1,9 ± 0,6
	Post	1.3 ± 0.4	1.0 ± 0.3	1,1* ± 0.4	1.7 ± 0.7	0.1 ± 0.1	0.4 ± 0.3	0.0 ± 0.0	0.2 ± 0.2	0.9 ± 0.4	0.7 ± 0.2	1.1 ± 0.3	1.6 ± 0.7	1.1 ± 0.3

Viola spp.	Pre	0,1 ± 0,1	0,3 ± 0,2	0,8 ± 0,7	0,1 ± 0,1	4,1 ± 2,1	0.5 ± 0.2	3,6 ± 1,8	0,6 ± 0,4	1,5 ± 0,5	2,3 ± 1,3	2,1 ± 1,4	1,9 ± 1,3	0,8 ± 0,5
	Post	0,2 ± 0,1	0,5 ± 0,3	0,6 ± 0,3	0,1 ± 0,1	3,4 ± 1,8	0,9 ± 0,4	5,0 ± 2,6	1,5 ± 1,3	3,4 ± 1,5	4,0 ± 1,5	2,0 ± 1,5	1,9 ± 1,4	1,1 ± 0,8
Grass spp.[2]	Pre	0,7 ± 0,3	0,6 ± 0,3	0,5 ± 0,2	0,5 ± 0,2	0,2 ± 0,1	0,1 ± 0,1	0,0 ± 0,0	0,2 ± 0,1	0,0 ± 0,0	0,2 ± 0,1	0,3 ± 0,1	0,1 ± 0,1	0,0 ± 0,0
	Post	0,9 ± 0,5	1,7 ± 0,9	0,8 ± 0,3	1,1 ± 0,7	0,4 ± 0,2	0,3 ± 0,1	0,0 ± 0,0	0,4 ± 0,2	0,1 ± 0,1	0,3 ± 0,1	0,2 ± 0,1	0,2 ± 0,1	0,3* ± 0,1

[1] *Ribes oxyacanthoides* included *R. lacustre.*

[2] Grass included all grass species (including *Elymus innovatus*) except for *Calamagrostis canadensis.*