Edge Effects at Clearcut, Fire and Riparian Buffers in the Boreal Forest of Northwestern Ontario

by

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Abstract

In the boreal forest of northwestern Ontario clearcutting and fire are two common edge-creating disturbances. Fundamental knowledge regarding the ability of fire and clearcut edges to minimize edge effects, preserve interior habitat, and provide sources of vegetative growth is lacking. Development of sustainable forest management strategies that emulate natural disturbance relies upon such information. This thesis examines edge effects in the boreal forest of northwestern Ontario at conifer clearcut, deciduous clearcut, and conifer fire edges. Riparian buffers with an upland clearcut edge and an upland-riparian ecotone were also studied. Edge effects were explored on a number of scales ranging from landscape-level to stand-level to small-scale bryophyte response. Residual patch, core area and edge were assessed in 1000 ha and 250 ha windows in both clearcut and fire disturbance. At the stand-level canopy and understory conditions were sampled along transects (60 m) placed across edges and buffers, in comparison to transects in the interior forest or at undisturbed stream edges. Edge characteristics and the depth of edge influence (DEI) were determined using the critical values approach, multiple response permutation procedure, analysis of covariance and other nonparametric tests. Conifer and deciduous clearcut edges had many similarities. Species response across conifer fire edges was different from clearcut edges due to shading provided by standing dead trees and a pre-existing moisture gradient at burnt edges. Most buffers maintained a similar species composition to undisturbed stream edges, but changes in species abundance were detected at the stream edge. The DEI was greatly decreased for most response variables 10 m past the edge; however, a significant DEI was found for some response variables at 40 m or up to the stream edge, which was the greatest distance measured.

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General Introduction

Forest edge is an important landscape element that can be described as a boundary line or narrow transition zone between communities (Chen *et al.,* 1992). Boundaries in a landscape may occur as a direct result of edaphic patterns, or may reflect changes in the underlying pattern due to physical disturbances (Wiens *et al.,* 1985). An edge is a purely structural or spatial entity, whereas an ecotone is defined by dynamic processes (Jeffers *et al.,* 1989). Ecotones occur at edges arising from both anthropogenic and natural sources. An ecotone is a zone of transition between adjacent ecological systems in which species of adjacent plant communities meet their limits (Delcourt & Delcourt, 1992; Lachavanne & Juge, 1997). Differences in vegetation establishment are often related to abrupt discontinuities in environmental conditions or environmental boundary zones (Curtis 1959; Van der Maarel, 1989).

The term edge effects refers to all of the abiotic and biotic changes that occur as a result of the juxtaposition of two different habitat types (Schlaepfer & Gavin, 2000). The microclimatic conditions and resulting species distribution in clearcut and burnt areas is different from the conditions and distribution found under an undisturbed canopy. Edge effects can be considered on three levels: the abiotic changes initiated by edge creation, first-order biological changes that are a direct response to abiotic changes, and higher-order biological interaction based upon changes in the first two levels (Murica, 1995; Schlaepfer & Gavin, 2000).

In this thesis edge effects were examined across clearcut edges, fire edges and riparian buffers. The amount of edge that has been created through cutting has increased several-fold over the past 25 years in comparison to the amount of edge that has been created by fire, which has remained relatively constant (Perera & Baldwin, 2000). Wildfires create a landscape pattern that is more spatially complex, with a greater range in patch size and more irregular disturbance boundaries (Delong & Tanner, 1996). Clearcut areas, however, tend to be more spatially homogeneous due the complete or near complete removal of structure within cuts and abrupt linear edges. Understanding how edges differ between anthropogenic (clearcut) and natural (fire) disturbance is essential in creating management plans that can better emulate natural edge creation. In addition, there is still much debate regarding the characteristic features of ecotones (Walker *et al.*, 2003). Changes in plant physiognomy, species richness and the existence of ecotonal species and distinctive vegetation communities across edges have not been confirmed, and will be explored in this thesis.

The importance of edge effects is emphasized in small forest fragments, like riparian buffers, because there is a greater potential for the loss of interior habitat, declining long-term stability and alteration of riparian environments. Riparian buffers are uncut forest strips retained adjacent to hydrological features after forest harvesting. Although buffers are widely regarded as necessary in the protection of streams and other aquatic resources, buffer width requirements are still highly debated (Castelle *et al.*, 1994). The preservation of riparian areas (communities occurring between the open water and the upland forest) is essential because these highly productive habitats provide high levels of biodiversity and important ecosystem services. Riparian areas have a complexity of soils, topography and microclimate and are defined by a unique array of edaphic influences and frequent natural disturbances related to the water body itself

(Macdonald *et al.,* 2004). Riparian buffers further provide a unique opportunity to explore the effects of both induced edges, created through harvesting, and inherent edges, reflective of natural ecotonal gradients. Inherent edges are ecotones that are often related to topographic differences, edaphic gradients, presence of open water and geomorphic factors (Bannerman, 1998). Due to the complexity of edge effects across riparian buffers this thesis includes a fine scale examination of microclimatic change and bryophyte response across both riparian buffers and undisturbed stream edges. Bryophytes have unique life history characteristics and poikiolohydrous water relations (Longton, 1984), which make them excellent indicators of the habitat conditions. Determining the habitat conditions in riparian buffers is essential not only for the protection fluvial features, but also to ensure the maintenance of biodiversity in buffers (Hylander *et al.,* 2002).

The structure and function of edges are scale-dependent. At a landscape-level ecotones are zones where spatial and temporal rates of change in ecological structure and function are rapid relative to rates of change across the landscape as a whole (di Castri & Hansen, 1992). The appropriate scale of investigation depends on the research question, organisms of interest and temporal parameters (Wiens *et al.,* 1993). Efforts to understand spatial patterns occurring in Ontario forests have just begun, and there is a limited knowledge about how these spatial patterns relate to stand-level dynamics (Perera & Baldwin, 2000). Ecological landscape-scale research aims to determine the relationships between landscape pattern and ecological processes. Due to the broad spatial-temporal scales involved, experimentation and hypothesis testing becomes more challenging at a landscape-scale. Results from studies conducted at relatively fine scales, therefore, may need to be extrapolated to broader scales to obtain insights about pattern-process relationships (Turner, 1989; Weins *et al.*, 1993). By employing a multi-scale approach, both a local and regional understanding of edge effects can be gained.

There are four chapters in this thesis each exploring the different aspects of edge effects discussed above. The specific questions that are addressed in the four chapters are:

1) What are the edge characteristics and the depth of edge influence in relation to canopy structure, canopy composition and understory species composition at conifer clearcut, deciduous clearcut and fire edges? What management strategies could be employed to best emulate natural disturbance patterns at edges?

2) How do the upland-riparian dynamics in buffers affect edge characteristics and depth of edge influence? Are there certain species that are effective ecotonal indicators? What is the response of upland and riparian species across narrow (30 m or less) and wide (40 m or greater) buffers with respect to undisturbed stream edges?

3) Does the influence of edge effects allow for the maintenance of undisturbed conditions in 40 m buffers with respect to microclimatic conditions and the biological response of two bryophyte species? How do microclimatic factors and life strategies of bryophytes interact to influential bryophyte growth and vitality?

4) How does incorporation of stand-level data affect our understanding of the ecological implications of landscape pattern? How does the structural legacy left by clearcutting and fire disturbance differ? Are landscape-level changes detected at a 1000 ha scale and a 250 ha scale consistent? What management strategies would encourage the emulation of natural disturbance patterns?

Chapter 1

Edge characteristics of clearcuts and fires in the boreal forest of northwestern Ontario

Abstract

In the boreal forest of northwestern Ontario clearcutting and fire are two common edge-creating disturbances. However, little is known regarding the edge characteristics and depth of edge influence across fire and clearcut edges in the boreal forest. Further research is needed for the development of forest management strategies that emulate natural disturbance. The goal of this study was to quantify, characterize and compare edges resulting from clearcutting and fire in conifer and deciduous forests. Three types of edges were compared: conifer clearcut edges, deciduous clearcut edges and conifer fire edges. Thirty sites (i.e. ten of each edge type) were sampled with two edge transects placed 20 m into the clearcut or burn and 40 m towards the interior forest. At each site an interior forest transect was placed at least 100 m from any edge and was used to represent the undisturbed condition. Multiple response permutation procedure (MRPP and its variant MRBP), Indicator Species Analysis and the critical values approach were used to characterize edges and determine the depth of edge influence (DEI). Clearcut edges were characterized by a high number of weedy shade-intolerant species in the cut and at the edge. Fire edges had distinct vegetation communities across the edge, primarily in response to pre-existing soil moisture gradients. The DEI was greatly decreased for most response variables 10 m past the edge towards the interior forest, however, a significant DEI was found for some response variables at 40 m, which was the greatest distance measured.

Introduction

Ecotones occur at edges arising from both anthropogenic and natural sources. An ecotone is a zone of transition between adjacent ecological systems in which species of adjacent plant communities meet their ecological limits (Delcourt & Delcourt, 1992; Lachavanne & Juge, 1997). Interpretation of the plant communities occurring at boundaries is considered of basic importance in vegetation ecology (van der Maarel, 1989). Understanding edge characteristics and depth of edge influence has further implications for effective forest management.

In the boreal forest of northwestern Ontario clearcutting and fire are two common edge-creating disturbances. The amount of edge that has been created through cutting has increased several-fold over the past 25 years in comparison to that created by fire, which has remained relatively constant (Perera & Baldwin, 2000). In order to develop forest management strategies that emulate natural disturbance, the ecological processes that occur at clearcut and fire edges need to be better understood. Therefore, research is needed regarding the comparative ability of fire and clearcut edges to minimize adverse edge effects, preserve interior habitat, and act as sources of vegetative growth.

Microclimatic gradients formed across forest edges, create a physical environment that differs between the open area (clearcut or burn) and the forest interior (Ranney *et al.*, 1981). Solar radiation, air temperature, soil temperature, relative humidity, soil moisture and wind velocity can all be altered by the creation of edge (Brosofske *et al.*, 1997). An intact canopy reduces light intensity (Hutchinson & Matt, 1977; Ranney *et al.*, 1981), buffers temperature flux (Geiger, 1957) and maintains an environment with high relative humidity and soil moisture, through reducing air flow and evapotranspiration (Ranney *et* *al.,* 1981). Structural diversity at forest edges may also be important in supporting both plant and animal species not found on either side of the edge (Wales, 1972; Galli *et al.,* 1976; Shugart, 1990).

The differences in microclimatic conditions are amplified by various plant responses to environmental gradients (Ranney *et al.,* 1981). Edge effects appear to extend further for secondary responses (understory structure and composition) than for primary responses (forest structure) (Williams-Linera, 1990a; Chen *et al.,* 1992; Harper & Macdonald, 2001). Differential response of species to changes in the physical environment may result in localized shifts in species composition (Murica, 1995).

Numerous studies have investigated the zonation of species across edges (Ranney et al., 1981; van der Maarel, 1989; Delcourt & Delcourt, 1992; Auerbach & Schmida, 1993; Carter, 1994; Harper & Macdonald, 2001;Walker et al., 2003). A number of studies have classified species across edges based upon their characteristic spatial position (e.g. edge positive versus edge negative, ecotonal versus interior). Interactions between plants and the environment are variable and these characteristic spatial positions may shift. A functional classification based upon the inherent physiological and life history characteristics that determine how plants respond to varying environmental conditions may provide insight into edge dynamics and the characteristics of different edge types.

In this study the spatial distribution of species across edges was examined based on their life history characteristics with special attention to adaptive strategies of plants to light and soil moisture conditions. Under different resource conditions the functional strategies of resource use allow plants to fill different ecological roles (Smith & Huston, 1989). Most plants may reach their physiological optimum under conditions of abundant light and moisture. Due to species interactions in natural communities, however species are distributed towards their ecological optimum (Smith & Huston, 1989).

The goal of this study was to quantify, characterize and compare edges resulting from clearcutting and fire in conifer and deciduous forests. The study had three specific objectives:

i) to quantify the depth of edge influence in relation to canopy and composition and understory species composition at clearcut and fire edges,

ii) to characterize species distribution across edges as a function of expected microclimatic gradients and species life history characteristics, and

iii) to identify potential management strategies that best emulate natural disturbance patterns by comparing the edge characteristics and depth of edge influence of the different edge types.

Methods

Study area

The study area was located between 30 and 150 km northwest of Thunder Bay, Ontario (latitude 48”22’ N; longitude 89”19’ W and elevation 199 m a.s.l.). The area was characterized by low rolling relief with underlying bedrock composed of primarily Precambrian granite and gneiss. In many areas bedrock was overlain with glacial till and Podzol and thick Organic soils. January and July mean temperature ranges were from –26 to –22° C and from 21 to 25°C respectively. Total annual precipitation varied from 700 to 850 mm (Baldwin *et al.,* 2000).

Study sites

Three different edge types were compared in this study: conifer clearcut edges, deciduous clearcut edges and conifer fire edges. To reduce site-to-site variation, all sites in a single treatment were located in either conifer or deciduous dominated stands. Similarity in elevation, slope and soil type were also considered during site selection. Due to difficulties in finding older edges in the study area and determining the precise edge location, only relatively young edges were used. In this study most clearcut sites were approximately 3-7 years of age, which corresponds with the age of edges created by fire (4-5 years). Similar time since disturbance allowed for a comparison between conifer and deciduous clearcut edges and between conifer clearcut edges and conifer fire edges. In total 30 forest sites were studied, 10 sites of each edge type and two transects were placed at each site (Table 1).

Conifer clearcut edges and deciduous clearcut edges were located in four different watersheds, the Poshkokagan river watershed, the Black Sturgeon watershed, the Current river watershed and the Mackenzie river watershed (Figure 1). Conifer fire edges were all located in the Black Sturgeon watershed and within the 1999 Nipigon 10 burn. Conifer clearcut and conifer fire sites were upland *Picea mariana* dominated stands with common tree species associations including *Pinus banksiana, Abies balsamea* and in wetter areas, *Larix laricina* and *Thuja occidentalis*. Deciduous clearcut sites were dominated by *Populus tremuloides* and *Populus balsamifera* with common tree species associations including *Betula papyifera, P. mariana* and *A. balsamea* (Thompson, 2000). Further details regarding the study sites can be found in Appendix I.

Table 1. Number of sites and transects, edge ages and % of dominant canopy trees at conifer clearcut, deciduous clearcut and conifer fire edges. * Total number of conifer or deciduous live stems expressed as a percent of total live sampled in canopy plots.

Edge type	Number of sites	Number of transects	Age class of edge (yrs.)	% Dominant canopy trees*
Conifer clearcut	10	20	3-6	91
Deciduous clearcut	10	20	3-7	81
Conifer fire	10	20	4-5	88

Sampling design

Most studies have found edge effects to disappear within 50 m of the edge (Murica, 1995), therefore, transects were placed perpendicular to the edge and extended 40 m into the forest and 20 m into the clearcut or burn (Figure 2). In addition to sampling edges that have been exposed to disturbance, reference data representative of the mature interior undisturbed forest condition was required both as a control and as an essential aspect of the analytical techniques. Interior forest transects (60 m) were placed at least 100 m from any edge (Figure 2). To reduce variability and allow for more meaningful comparisons, all edge transects had a corresponding interior transect in mature forest at the same site.

Edge orientation was considered in this study, because edge effects fluctuate based on aspect with north-facing edges showing weaker edge effects than south-facing edges (Kapos, 1989; Matlack, 1993; Murica 1995; Chen et al.; 1995, Burton, 2002). Following a similar protocol to Harper & Macdonald, (2001, 2002) only south-facing edges (± 45°) were selected.

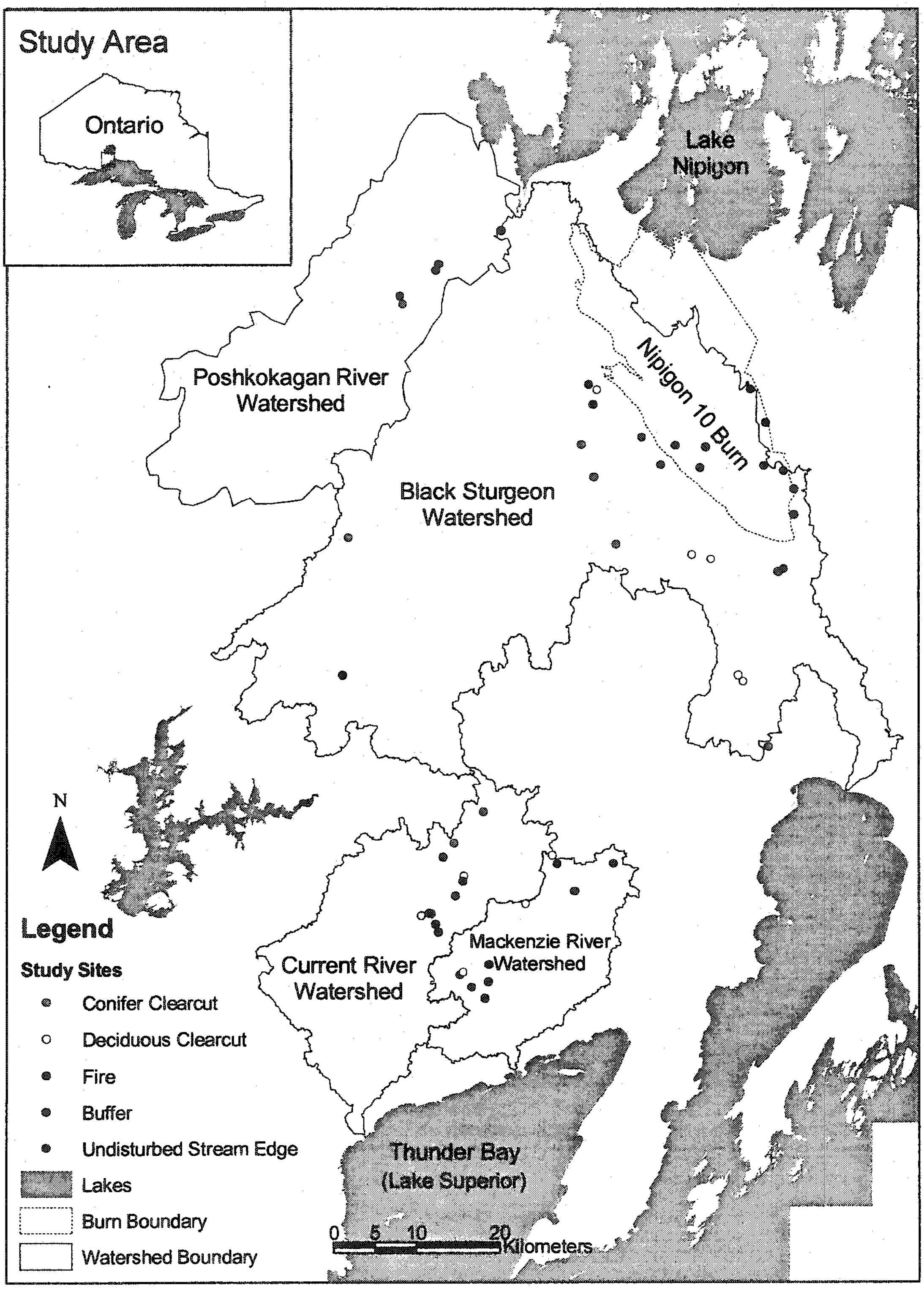


Figure 1. Study area with conifer clearcut, deciduous clearcut, fire, buffer and undisturbed stream edges in the Poshkokagan river, Black Sturgeon, Current river and Mackenzie river watersheds.

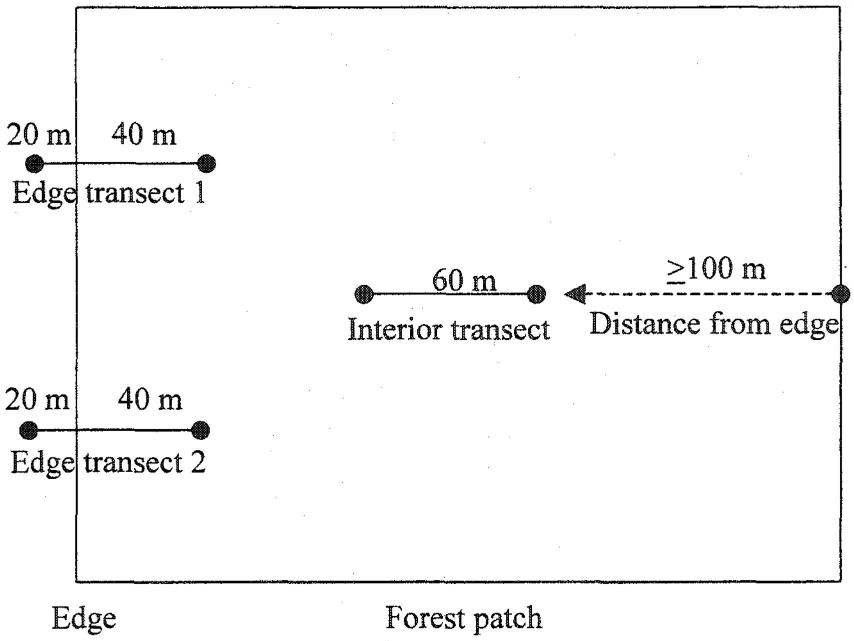


Figure 2. Sampling design with 60 m edge transects with 20 m placed in the burn or clearcut and 40 m into the forest. In each site a 60 m interior transect was placed 100 m from any edge.

Edge effects are not necessarily monotonic, therefore, a fine enough scale of sampling must be used to give precise estimates and to identify significant fluctuations (Murica, 1995). Large sampling intervals allow for longer transects, however, in the process smaller trends and patterns may be missed. Therefore, in this study a relatively small sampling interval (5 m) and shorter transect length (60 m) was used.

Percent cover for all understory plants was determined by ocular estimation to the nearest percent in 1 x 1 m quadrats at 4 m intervals (Figure 3). Following a method similar to Chen *et al.,* (1992), canopy cover was recorded at each understory quadrat location as a discrete variable: 0 indicating the complete absence of canopy above the quadrat and 1 indicating presence of canopy above the quadrat. Basal diameter (for species with dbh ≥ 5 cm) and stem density of canopy species were determined in 20 x 5 m plots placed at 15 m intervals. All field sampling occurred from June 19^{h} to August 28 2002 and from July 4 to August 27 2003.

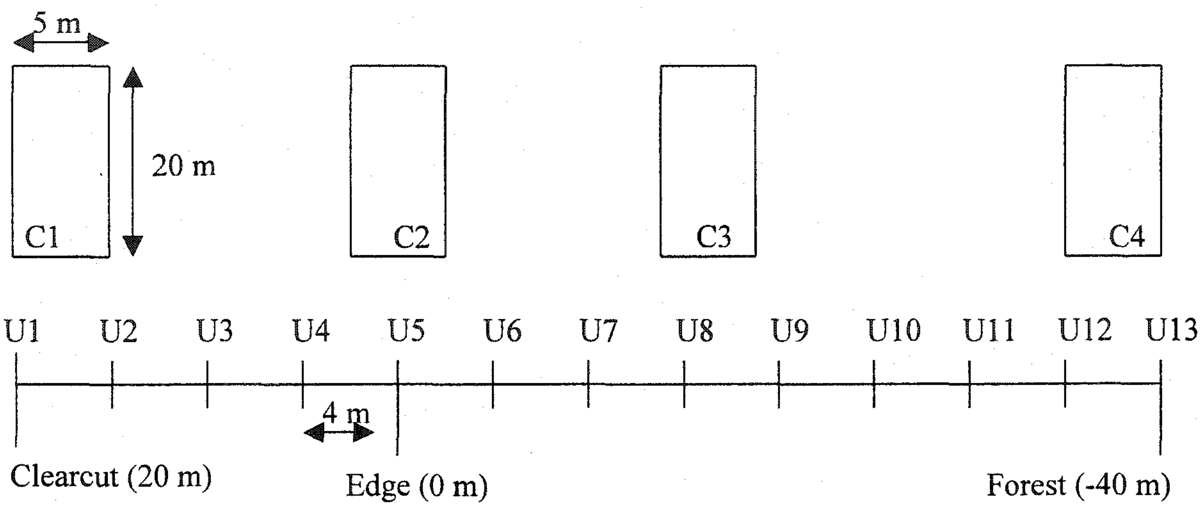


Figure 3. Sampling design along a 60 m transect placed perpendicular to the edge with 1 x 1 m understory plots (U1-13) placed every 4 m and 5 x 20 m canopy plots (C1-4) placed every 15 m.

Most plants were identified to the species level. Plants that were difficult to identify with certainty in the field were collected and later identified in the lab. Voucher specimens are available at the Lakehead University Claude Garton Herbarium (LKCGH). Nomenclature followed Newmaster *et al.*, (1998). Some of the willow, sedge and bryophyte species were lumped prior to some analyses (Appendix II).

Data analysis

To determine the characteristics of edge types and the depth of edge influence (DEI) two different methods were used. Multivariate community level analyses were performed using Multiple Response Permutation Procedure and its variant Blocked Multiple Response Permutation Procedure with Indicator Species Analysis. Individual species response was assessed using the critical values approach.

MRPP, MRBP and Indicator Species Analysis

Multiple Response Permutation Procedure (MRPP) is a non parametric procedure that tests the null hypothesis of no difference between two or more *a-priori* groups (McCune *et al.*, 2002). Assumptions of normal distribution and homogeneity of variance do not have to met in a MRPP (Zimmerman *et al.*, 1983). MRPP calculates the observed delta, which is the linear combination for all groups of the average pairwise distances between each sample within a particular group. The observed delta is compared to the expected delta, which is the null distribution of all possible permutations of samples into groups of the same size. A test statistic T is calculated from a Pearson type III distribution to derive the probability of having a delta the same size or smaller than the observed delta. An A statistic is also calculated from the observed and expected deltas and is used to measure the homogeneity within groups. An A value of greater than 0.3 is fairly high, and in community ecology A values below 0.1 are common even when the observed delta is significantly different than the expected delta (McCune & Mefford, 1999).

Blocked Multiple Response Permutation Procedure (MRBP) is a variant of MRPP, which is often used with paired sample data. Both MRPP and MRBP have the same assumptions (i.e. the distance measure represents variation of interest in the data, sample units are independent and the relative weighting of variables has been controlled), but with MRBP a more complex dataset can be analyzed effectively (McCune *et al.*, 2002). An MRBP considers not only differences among treatments as in a MRPP, but focuses the analysis on within block differences, presumably due to treatment alone (McCune *et al.*, 2002). A MRBP was used to test the null hypothesis of no significant difference in understory plant community composition between the different edge types. There were 149 understory species and 120 plots used in the analysis. The plots were arranged in three groups (1 = Conifer clearcut, 2 = Deciduous clearcut, 3 = Conifer fire) and four blocks relating to transect location (1 = cut/burn 20 to 5 m, 2 = near edge 0 to –15 m, 3 = far edge –20 to –35 m, 4 = interior forest ≥100 m). The observed values were randomly reassigned to different treatments within a block. The inclusion of blocking, therefore, allows for a comparison between sites while maintaining the spatial properties of the data (McCune & Mefford, 1999). Since a balanced design was required to perform the MRBP, the last quadrat on each edge transect (-40 m) was not used and eight of the 13 interior quadrats were randomly selected. For each site the mean value of the eight understory quadrats per blocking group were used in the analysis. The distance measure used was Euclidean and median alignment was performed.

While MRBP provides one method of exploring a more complex design, MRPP can still be useful in investigating complex datasets when analysis is conducted in a piecewise manner. Dividing complex datasets in various ways allows a number of different questions to be answered (McCune *et al.,* 2002). Due to the complexity of the dataset, MRPP was used to further investigate differences among the edge types after performing a MRBP. A MRPP was performed to test for the null hypothesis of no difference in conifer clearcut, deciduous clearcut and fire edges. A total of 149 species and 120 plots were used in the MRPP analysis. For all MRPP tests the Euclidean distance measure and default weighting of groups (C(I) = n(I)/sum(n(I))) were used. Differences across the edges for each site were explored separately. Data was divided into the blocking groups used in the MRBP and a MRPP was used to test for the hypothesis of no difference between different spatial locations across the edge. In the analyses there were 131, 112 and 127 species in 40 plots of the conifer clearcut, deciduous clearcut and conifer fire edges respectively.

One of the aims of plant community analysis is to identify different species that can detect and describe environmental conditions, levels of disturbance or experimental treatments (McCune *et al.,* 2002). Indicator Species Analysis provides a method for combining information about species abundance and frequency within a particular group (Dufrene & Legendre, 1997). Using a Monte Carlo randomization technique, indicator values are tested for statistical significance. Indicator Species Analysis is commonly used in conjunction with an MRPP, because it provides information regarding the characteristics of different groups. In this study an Indicators Species Analysis was used to characterize clearcut and fire edges. The response variable used in the MRBP, the MRPP and the Indicator Species Analysis was mean percent cover for all understory species. All multivariate tests were carried out using the PC-ORD program version 4 (McCune & Mefford, 1999).

Critical Values Approach

Assessing the distance/Depth of Edge Influence (DEI) is essential for determining the amount of interior forest remaining in forest fragments (Harper & Macdonald, 2001). The DEI has been determined by Analysis of Variance with single or multiple factors (Wales, 1972; Chen *et al.,* 1992; Laurance *et al.,* 1998), regression including multiple linear, stepwise and non-linear models (Ranney *et al.,* 1981; Laurence, 1991; Chen *et al.,* 1992; Jose *et al.,* 1996; Cadenasso *et al.* 1997), curve-fitting (Laurence *et al.,* 1998) and non-parametric procedures such as, Kruskal-Wallis, Detrended Correspondence Analysis (DCA) and cluster analysis (Fraver, 1994; Matlack, 1994;). Assumption of a particular response model and spatial autocorrelation, which violates the assumption of independence, limits the precision and explanatory power associated with many of these methods. Methods of analyzing edge effects have been further limited by failing to include interior forest reference values or by using subjective means to quantify interior forest (Harper, 1999). Due to the inherent heterogeneity of forest conditions in the boreal forest, inclusion of this variation is essential to provide appropriate reference values. In addition, non-normal and autocorrelated data are common in research concerning ecotones (Gosz, 1991; Harper & Macdonald, 2001).

Harper & Macdonald, (2001) introduced a new method for determining DEI known as the critical values approach. The critical values approach incorporates the inherent variability in interior forest, does not have the assumptions of most parametric tests and reduces the effect of spatial autocorrelation in quantifying the distance of edge influence. In the critical values approach, DEI is a set of distances from the edge where a given variable is significantly different from the inherent variability of the interior forest.

Critical values are determined through randomization tests on interior forest data. Randomization tests were performed for interior response variables using the critical values program in Visual Basic, Microsoft Excel 1997 (Harper & Macdonald, 2002b). Mean values at different distances from the edge are considered to be significant or show an edge effect if they lay outside the critical values. The null hypothesis for the critical values approach is: the average of values observed at a particular distance from the edge is no different than would be expected by chance in the reference forest (Harper, 1999). DEI, therefore, can be defined as the set of two or more consecutive distances for which mean values are significantly different than the reference forest (Harper & Macdonald, 2002).

A modification of the critical values approach also allows for the comparison of two different edge types. To control for site-to-site variation, interior forest values from both forest types are used to create critical values through randomization test and *t* values are determined at different edge distances with edge data (Harper & Macdonald, 2002). The critical values for all tests were the 2.5 and 97.5 percentiles of the 5000 permuted averages (2 tailed test, sig. = 0.05).

Edge characteristics were identified and the mean depth of edge was estimated and compared for each of the treatment groups with respect to a number of response variables (Table 2). Differences in canopy species structure and composition, and understory species richness and abundance were determined both at the edges within each treatment and between the treatments. Standing dead trees (snags), live trees and recently fallen trees were all considered in the canopy response variables. Both upright stem density (stems/ha), including both live and dead stems, and live stem density (stems/ha) were examined to give a more comprehensive understanding of the canopy conditions. Using a similar approach to Burton (2002), the number of snags and the number of fallen trees were calculated as a percentage of upright stems.

Table 2. Response variables used in the critical values analysis including canopy composition and structure, and understory species richness and composition.

Type of response	Response variables
Canopy	Canopy cover
	Upright stem density (stems/ha)
	Live stem density (stems/ha)
	Basal area (m^2/ha)
	Snags (% of upright stems)
	Recently fallen trees (fallen trees/ha)
	Recently fallen trees (% of upright stems)
	Number of stems per species (stems/ha)
	Mean live stem diameter at breast height (dbh)
	Mean dbh of snags
	Mean dbh per species
Understory	Richness
	Percent cover for all species
	Total cover
	Percent cover of coarse woody debris

Understory species were further divided into several groups. Using a descriptor-based classification of functional types the main basis for group division was physiognomy: saplings, shrubs, herbs, vascular cryptogams, grasses, sedges, mosses, liverworts and lichens. Some of these groups were further divided based on physiognomy, such as conifer and deciduous saplings, tall and low-growing shrubs and acrocarpous, pleurocarpous and sphagnum mosses. The herb group was further divided based upon shade-tolerance and association with soil moisture (Rowe, 1983; Legasy *et al.*, 1995; Ringus & Sims, 1997). Species commonly occurring in very moist habitats or requiring high moisture conditions for growth were deemed indicators of moisture. Shade-tolerance and habitat preferences (i.e. open and disturbed versus upland forest) were used to divide the remaining herb species into the shade-tolerant and shade-intolerant groups. Species were grouped in this manner to explore the application of the trade-off model developed by Smith & Huston, (1989).

The trade-off model has three premises, which were further explored in relation to edge characteristics: i) plants that can grow rapidly under high light conditions are unable to survive at low light levels (i.e. shade-intolerant) and conversely plants that are able to grow in low light (shade-tolerant) have a low maximum growth rate under high light conditions, ii) plants that can grow rapidly under high soil moisture conditions are unable to survive under dry conditions and conversely plants that are adapted to dry conditions cannot grow rapidly under high soil moisture availability, iii) tolerances to conditions of low light and low moisture are independent and inversely correlated. Adaptations that allow a plant to grow at low light, therefore, restrict its ability to survive under dry conditions.

Results

Characterizing edges- MRBP, MRPP and Indicator Species Analysis

The MRBP showed no significant difference between the different edge types (p= 0.327) and the within-group homogeneity was very low (A = 0.009)(Table 3). The MRPP showed a significant difference between the three edge types (p = 0.000) and the within-group homogeneity was moderately high (A = 0.139) (Table 4). The MRPP showed a significant difference between the edge locations for conifer clearcuts (p = 0.003), deciduous clearcuts (p = 0.002) and fires (p = 0.000) (Table 5). The within-group homogeneity was highest for fire edges (A=0.125) and lower for conifer clearcut (A= 0.092) and deciduous clearcut edges (A=0.045) (Table 5).

Table 3. MRBP showed no significant difference between conifer clearcut, deciduous clearcut and fire edges. The observed delta was determined from the data and the expected delta was obtained from the null distribution. The difference of the observed and expected delta divided by the square root of the variance in deltas is the T test statistic. The chance-corrected within-group agreement (A) indicates within-group homogeneity compared to random expectation. The p value indicates the probability of having a more extreme observed delta and is significant at (<0.05).

Edge types	MRBP statistics				
	Observed delta	Expected delta	T	A	p
Conifer clearcut Deciduous clearcut Fire	28.2586	28.5325	-0.4059	0.0095	0.3273

Table 4. MRPP showed a significant difference between conifer clearcut, deciduous clearcut and fire edges. Refer to Table 3 for details regarding all MRPP statistics.

Edge types	MRPP statistics				
	Observed delta	Expected delta	T	A	p
Conifer clearcut Deciduous clearcut Fire	47.8193	55.5395	-34.1668	0.1390	0.0000

Table 5. Three separate MRPP analyses showed a significant difference in understory species at different edge locations for conifer clearcut, deciduous clearcut and fire edges. Refer to Table 3 for details regarding all MRPP statistics.

Edge types	MRBP statistics				
	Observed delta	Expected delta	T	A	p
Conifer clearcut	42.5325	46.8789	-5.0337	0.0927	0.0003
Deciduous clearcut	41.2636	43.2158	-3.6810	0.0451	0.0027
Fire	46.6526	53.3633	-8.0678	0.1257	0.0000

An indicator species analysis was performed to identify species as indicators of change at the different edge locations for each of the edge types. The largest number of indicator species for all three edge types occurred at edge location 1 in the cut or burn. Conifer and deciduous clearcut edges had indicator species for only two edge locations, whereas three edge locations were identified with indicators at fire edges (Appendix III).

Conifer and deciduous clearcuts had a relatively high number of weedy shade-intolerant herbs (e.g. *Hieracium caespitosum, Polygonum cilinode* and *Taraxacum* spp.), and grasses (e.g. *Bromus ciliatus* and *Calamagrostis canadensis*) in the clearcut (edge location 1). Fire edges had species indicative of fire disturbance (e.g. *Epilobium angustifolium, Vaccinium myrtilloides* and *Ceratodon purpureus*) in the burnt area (edge location 1). Conifer clearcut edges had two indicators (*Gaultheria hispidula* and *Sphagnum* spp.) for the far edge location (3) and deciduous clearcut edges had one indicator (*Athyrium felix-femina*) of the interior location (4). Fire edges had two indicators (*Dicranum* spp. and *Pluerozium schreberi*) for the interior location (4) and two indicators (*Sphagnum* spp. and *Thuja occidentalis*) for the far edge location (3).

Indicator species occurring at the same edge location at more than one edge type indicated similarities between the different edges (Table 6). *Epilobium angustifolium, Rubus idaeus* and *Taraxacum* spp. were indicators of the disturbed locations (clearcut or burn) for all three edge types. Conifer and deciduous clearcut edges also shared a number of additional indicators in the clearcut. Burnt areas and deciduous clearcuts both had indicators that were tall shrubs. *Sphagnum* spp. was an indicator at the far edge location of both conifer clearcut and fire edges. Deciduous clearcut edges had the largest number of indicators in common with other sites.

Table 6. Indicator species occurring at more than one edge type at the same edge location (1= clearcut/burn 20 to 5 m, 2= near edge 0 to –15 m, 3= far edge –20 to –35 m, 4= interior ≥100 m).

Indicator species at more than one edge type	Indicator species	Edge location (Max grp)
All edge types	*Epilobium angustifolium*	1
	Rubus idaeus	1
	Taraxacum spp.	1
Conifer clearcut and deciduous clearcut	*Betula papyifera*	1
	Bromus ciliatus	1
	Hieracium caespitosum	1
	Polygonum cilinode	1
Conifer clearcut and fire	*Sphagnum* spp.	3
Deciduous clearcut and fire	*Polytrichum* spp.	1
	Prunus pensylvanica	1
	Salix spp.	1
	Anaphalis margaritacea	1

Characterizing edges and determining the DEI - Critical values approach

Canopy structure and composition

Compared to their respective interior conditions all edge types had less canopy cover in the clearcut or burnt area (Appendix IV). However, only deciduous clearcut edges had less canopy cover at the edge (0 m) and 5 m past the edge compared to the interior forest.

Coarse woody debris (CWD) was higher in the clearcut or burnt area as well as across edges, however only at deciduous clearcut edges was CWD significantly higher (Appendix IV). Significantly higher CWD occurred from 10 m within the clearcut to 15 m past deciduous clearcut edges towards the interior.

There were numerous differences in the canopy structure both between each edge type and its interior as well as between the three edge types (Table 7). Compared to the interior condition, deciduous clearcut edges had a lower upright stem density, live stem density and basal area at the edge (0 m). Fire edges had a higher upright stem density, but a lower live stem density at the edge when compared to the interior. Conifer clearcut edges had lower upright stem density at the edge (0 m) and lower live stem density 20 m past the edge compared to fire edges.

Compared to the interior, the number of snags (as a percent of all upright trees) was higher at deciduous clearcut edges (0 m). Fire edges had a greater number of snags in the burnt area and at the edge in comparison to the interior condition and in comparison to conifer clearcut edges. All three edge types had a higher number of recently fallen trees at the edge (0 m) when compared to their respective interior conditions. Conifer and deciduous clearcuts also had a larger number of recently fallen trees (as a percent of upright stems) in the clearcut. Conifer clearcut edges had fewer recently fallen trees in the clearcut area than fire edges had in the burnt area, however conifer clearcut edges had larger number of recently fallen trees (as percent of upright stems) at the edge.

Fire edges had lower mean live stem dbh, specifically dbh of *Picea mariana* stems, in the burnt area and at the edge compared to the interior. Compared to conifer clearcut edges, fire edges had lower mean live stem dbh in the burnt area and up to 20 m past the edge towards the interior. Snags at deciduous clearcut edges (0 m) had a larger dbh than snags in the deciduous interior and than snags across conifer clearcut edges (from 20 to –20 m).

Table 7. Differences in canopy structure at edge locations and between edge types for conifer clearcut, deciduous clearcut edges and conifer fire edges. * A significant DEI is indicated when mean values are above (+) or below (-) critical values. † A significant difference between edge types is indicated when *t* values are greater (+) or less (-) than critical values. ns = No significant edge influence was observed. Transect location 20 m is within the clearcut or burn with 0 m located at the edge and with negative values occurring towards the interior forest. Where mean or *t* values occurred outside of the critical values only in the clearcut or burn (20 m) results are not shown.

Canopy response variable	Edge type	Location of significant DEI*	Significant difference between edge types†
Upright stem density	Deciduous clearcut	- (0)	ns
(stems/ha)	Fire	+ (0)	Conifer – (0)
Live stem density	Deciduous clearcut	- (0)	ns
(stems/ha)	Fire	- (0)	Conifer – (-20)
Basal area (m^2/ha)	Deciduous clearcut	- (0)	ns
Snags (% of total upright	Deciduous clearcut	+ (0)	ns
stems)	Fire	+ (20 to 0)	Conifer – (20 to 0)
Recently fallen trees	Conifer clearcut	- (20) + (0)	ns
(trees/ha)	Deciduous clearcut	- (20) + (0)	ns
	Fire	+ (20 to 0)	Conifer – (20)
Recently fallen trees	Conifer clearcut	+ (20 to 0)	ns
(% of upright stems)	Deciduous clearcut	+ (20 to 0)	ns
	Fire	+ (20)	Conifer – (20) + (0)
Mean live stem dbh	Fire	- (20 to 0)	Conifer + (20 to –20)
Mean snag dbh	Deciduous clearcut	+ (0)	Conifer – (0 to –20)
Mean *Picea mariana* dbh	Fire	- (20 to -20)	Conifer + (0)

Tree species composition at conifer and deciduous clearcut edges was not significantly different from interior composition. Fire edges, however, had a higher number of *Thuja occidentalis* (-20 m) and *Fraxinus nigra* (-20 to –40 m) stems in comparison to the interior (Table 8). The number and mean dbh of shrub species was greater at all edge types compared to their respective interiors (Table 8). Both conifer clearcut edges and deciduous clearcut edges had a larger number and size of *Alnus incana* compared to their respective interior conditions. In comparison to deciduous clearcut and fire edges, conifer clearcut edges had a larger number and size of *A. incana* at the edge (0 m), but fewer and smaller *A. incana* 40 m past the edge. Deciduous clearcut edges had a larger number and size of *Prunus virginiana* at 40 m past the edge in comparison to the deciduous interior and conifer clearcut edges. Deciduous clearcut edges also had fewer and smaller *Acer spicatum* in the clearcut (20 m) and up to 20 m past the edge compared to the interior. Fire edges had a larger number and size of *Salix* spp. 20 m past the edge towards the interior.

Understory species

Analysis of the understory plant response using the critical values approach provided the most information regarding the depth of edge influence (DEI) and edge characteristics. For all understory response variables the DEI was considered to be significant only if two consecutive values were above or below the critical values.

Table 8. Differences in canopy composition at edge locations and between edge types for conifer clearcut, deciduous clearcut and conifer fire edges. Refer to Table 7 for details.

Canopy response variable	Edge type	Location of significant DEI	Significant difference between edge types
Total number of *Fraxinus nigra*	Fire	+ (-20 to –40)	Conifer – (-20 to – 40)
Total number of *Thuja occidentalis*	Fire	+ (-20)	Conifer – (-20)
Total number and mean dbh of *Alnus incana*	Conifer clearcut	+ (0) + (-40)	ns
	Deciduous clearcut	+ (-40)	Conifer + (0) – (-40)
	Fire	ns	Conifer + (0) – (-40)
Total number and mean dbh of *Prunus virginiana*	Deciduous clearcut	+ (-40)	Conifer – (-40)
Total number and mean dbh of *Acer spicatum*	Deciduous clearcut	- (20 to –20)	Conifer + (0 to –20)
Total number and mean dbh of *Salix* spp.	Fire	+ (-20)	ns

Understory species richness and total cover

At deciduous clearcut edges understory species richness was not significantly different from the interior forest or from conifer clearcut edges. Conifer clearcut edges had significantly higher richness in the clearcut area and fire edges had significantly higher richness from 5 to 10 m past the edge in comparison to their respective interior conditions (Figure 4a). Fire edges had higher richness compared to conifer clearcut edges from 5 to 10 m past the edge toward the interior forest.

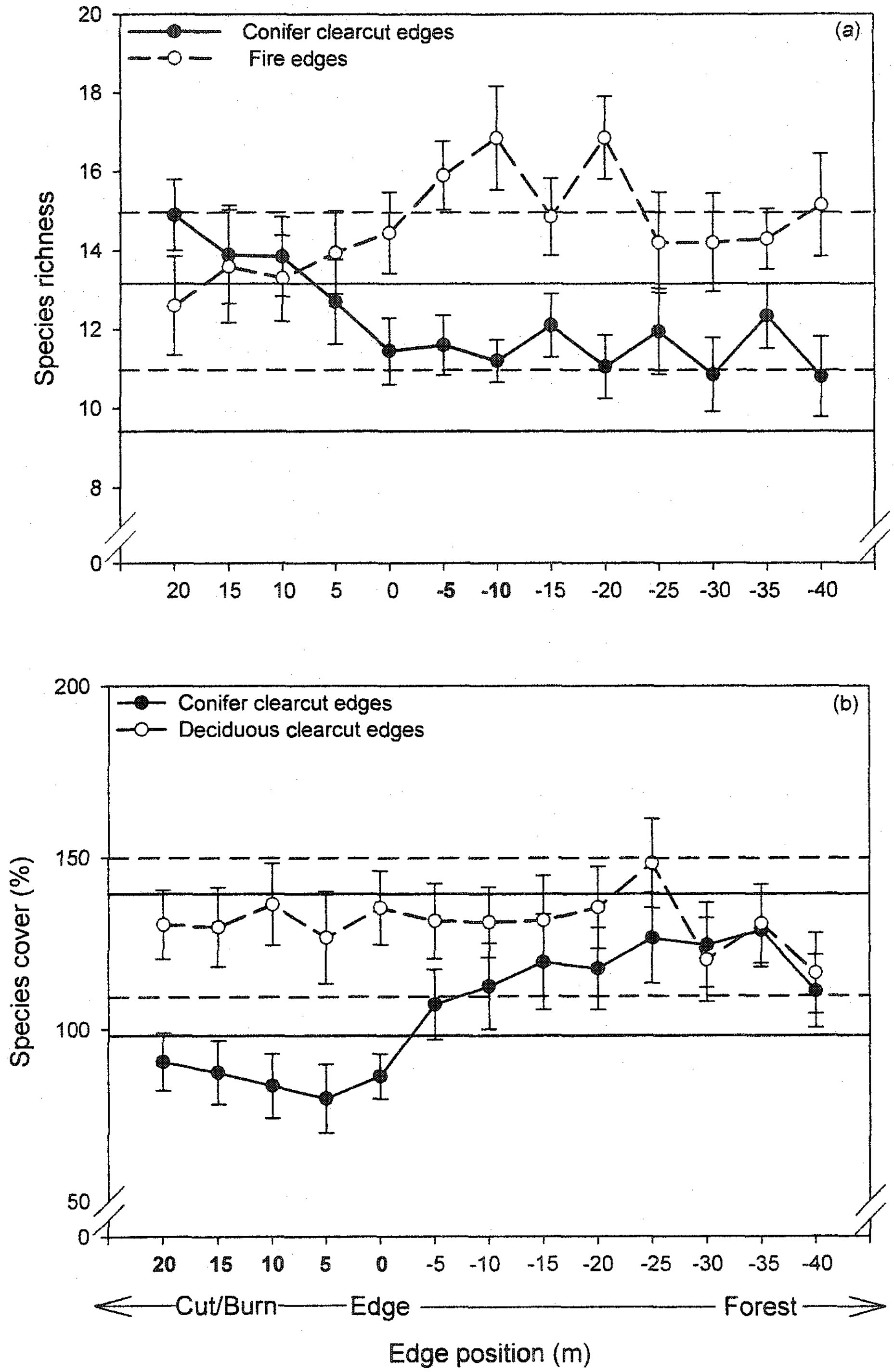


Figure 4. Mean species richness at conifer clearcut and fire edges (a) and mean total cover at conifer clearcut and deciduous clear-cut edges in comparison to their respective interior conditions and each other. Interior conditions represented as critical values are shown as solid (conifer) or dashed (fire, deciduous) lines. Significant values are those occurring outside of the critical values and bars represent mean ±1 SE. Bold values on the x-axis indicate where edge types are significantly different determined by *t* values that occur outside the critical values.

Total cover of understory species was not significantly different at fire edges compared to the interior forest conditions. Lower species cover was found in the conifer clearcut area and at the edge (0 m) compared to the interior forest (Figure 4b). Conifer clearcut edges also had significantly lower cover in the clearcut and at the edge compared to the deciduous clearcut edges.

The general response of understory species across the three edge types was compared using the percentage of species at each edge type that had a significant DEI (Figure 5). Conifer and deciduous clearcut edges had a similar trend in the number of species with a significant DEI in the clearcut and across the edge. Fire edges had fewer species showing an edge effect in the burnt area, but a higher number of species with a significant DEI from 10 to 30 m past the edge.

DEI at conifer clearcut edges

In general conifer clearcut edges had a rapid decrease in the number of species with a significant DEI from the clearcut area to the edge (0 m). A large number of species belonging to the low-growing shrub, shade-tolerant herb and shade-intolerant herb groups had a significant DEI (Figure 6). Low-growing shrubs had a complex pattern with a higher abundance for some species and a lower abundance for others both in the clearcut and up to 30 m past the edge towards the interior forest (Appendix V). Among the low-growing shrubs some species (e.g . *Ribes glandulosum, Ribes hirtellum* and *Rubus idaeus*) had high abundance in the clearcut while others (e.g. *Chamaedaphne calyculata, Gaultheria hispidula* and *Vaccinium oxycoccos*) were more abundant in the moist and closed canopy conditions.

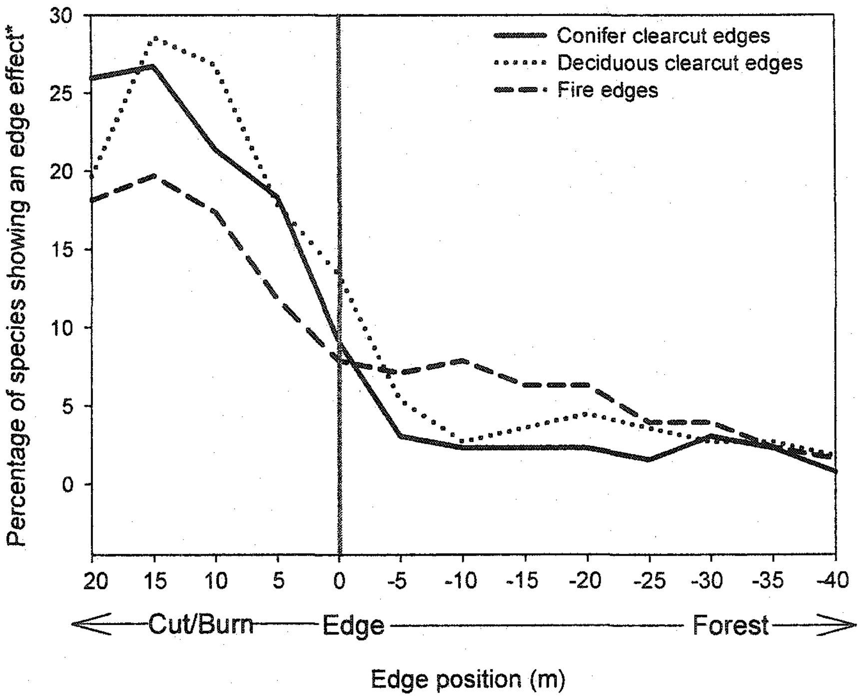


Figure 5. Percentage of species showing an edge effect at a given edge location for conifer clearcut, deciduous clearcut and fire edges. *Number of understory species with a mean abundance above or below the critical values for a given edge location divided by the total number of understory species at each edge type.

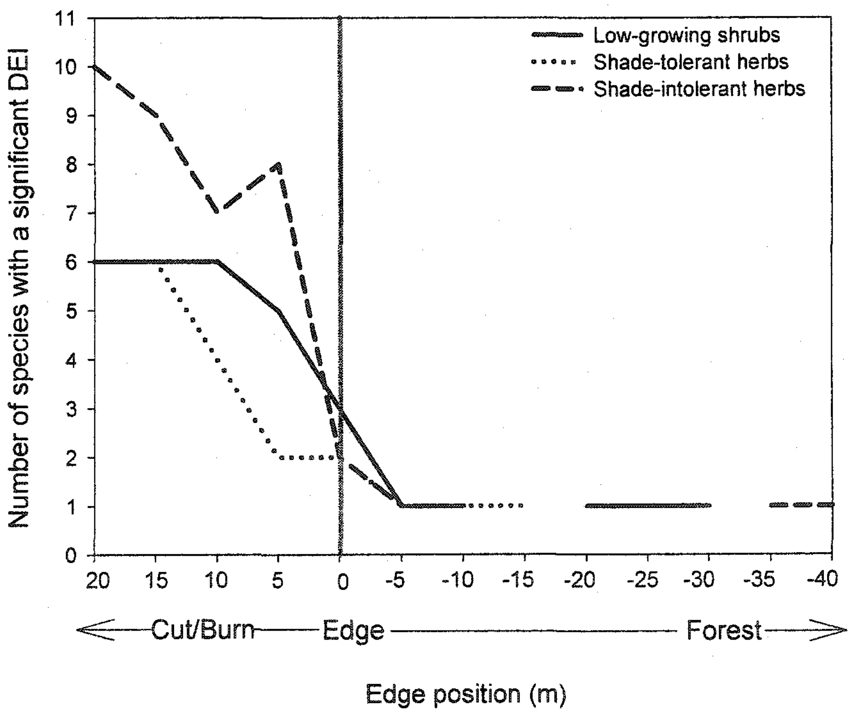


Figure 6. Number of low-growing shrubs, shade-tolerant herbs and shade-intolerant herbs with a significant DEI across conifer clearcut edges.

Shade-tolerant herbs that had a significant DEI were habitat generalists (e.g. *Cornus canadensis, Maianthemum canadense, Anemone quinquefolia* and *Melampyrum lineare)* with high abundance in the clearcut area (Appendix V). For species such as *Cornus canadensis*, a high abundance also occurred up to 15 m past the edge towards the interior forest. Shade-intolerant herbs had the largest number of species with a significant DEI at conifer clearcut edges (Appendix V). Shade-intolerant species were commonly found in open and disturbed habitats (e.g. *Aster ciliolatus, Epilobium angustifolium, Taraxacum* spp., *Achillea millefolium,* and *Hieracium caespitosum*) and did not have a high abundance beyond the edge (0 m); with the exception of *Fragaria virginiana* (DEI up to 10 m past the edge) and *Aster puniceus* (DEI from 35 to 40 m past the edge).

A number of other species groups also had a significant response across conifer clearcut edges. Conifer saplings, deciduous saplings, tall shrubs, grasses and sedges had a higher abundance and moss species a lower abundance in the clearcut compared to the interior forest (Figure 7). Low-growing shrubs, shade-tolerant herbs, and grasses had a higher abundance that extended beyond the edge. Vascular cryptogams and species associated with high soil moisture conditions had a higher abundance at locations past the edge towards the interior forest.

DEI at deciduous clearcut edges

Deciduous clearcut edges had a rapid decrease in the number of species with a significant DEI from the clearcut area to the edge (0 m). In comparison to conifer clearcut edges, however, deciduous edges had a larger number of species with DEI

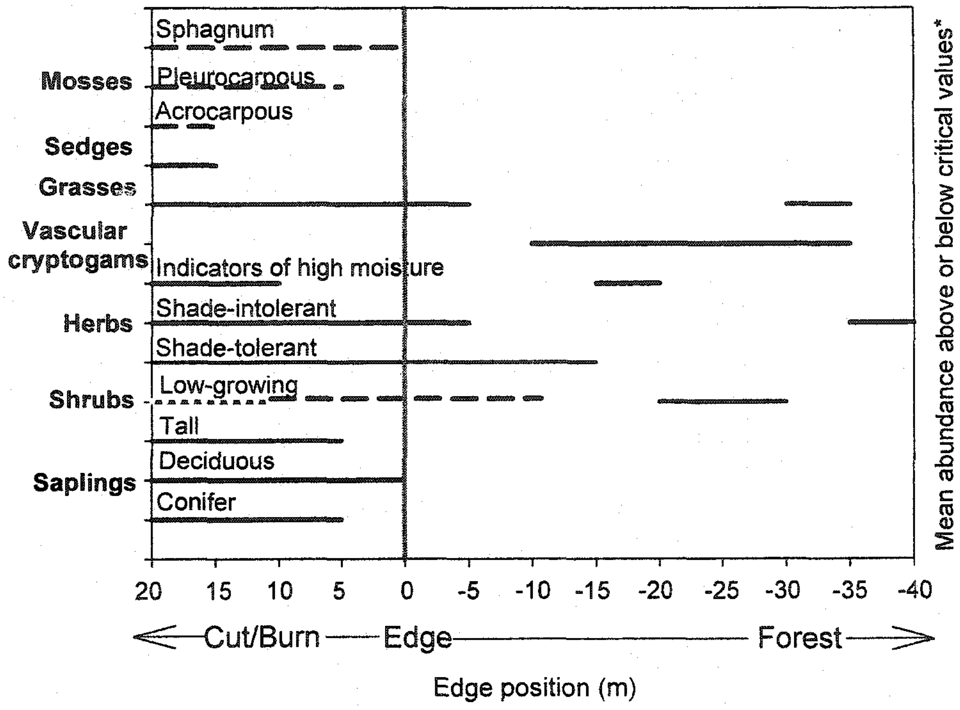


Figure 7. Mean understory species abundance above or below critical values at conifer clearcut edges. *Two or more consecutive mean values above or below critical values (representative of interior forest) are deemed to show DEI at a given edge location. Solid black lines represent means above, dashed lines represent means below and dotted lines represent means both above and below the critical values.

extending from the clearcut area to 5 m past the edge. Within the clearcut at deciduous edges there is a peak in the number of species with a significant DEI between 15 and 5 m. Similar trends are also found in the clearcut and burnt areas of conifer edges. Tall shrubs, shade-tolerant and shade-intolerant herbs had the largest number of species with a significant DEI (Figure 8). Tall shrub species had both a higher and lower abundance in response to deciduous clearcut edges compared to the interior conditions (Appendix VI). Shrub species common in open and disturbed areas (e.g. *Prunus pensylvanica* and *Salix* spp.) had a high abundance in the clearcut and up to 10 m past the edge; whereas species found to form a sub-canopy in deciduous stands (e.g. *Acer spicatum*) had a low abundance in the clearcut.

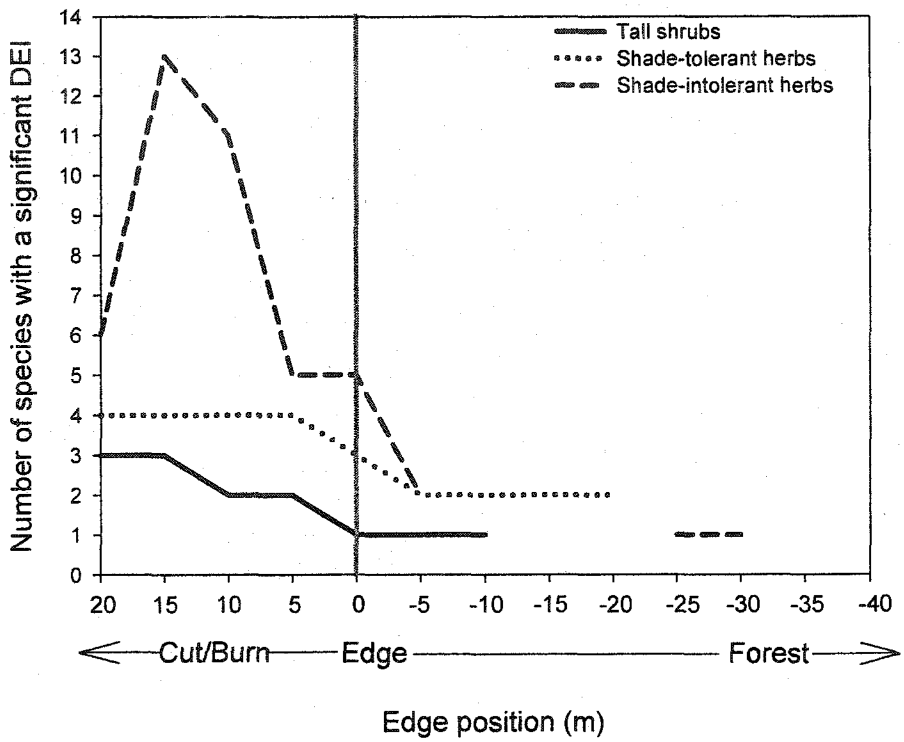


Figure 8. Number of tall shrubs, shade-tolerant and shade-intolerant herbs with a significant DEI across deciduous clearcut edges.

At deciduous clearcut edges shade-tolerant species were common habitat generalist (e.g. *Cornus canadensis* and *Melampyrum lineare*) and had a similar distribution to shade-tolerant herbs at conifer clearcut edges, with a higher abundance both in the clearcut and up to 10 m past the edge (Appendix VI). There were however, three shade-tolerant species (*Aralia nudicaulis, Clintonia borealis* and *Trientalis borealis*) that had a lower abundance in the clearcut area than the forest interior. Shade-intolerant herbs had the largest number of species with a significant DEI at deciduous clearcut edges. The majority of shade-intolerant species did not have a significant DEI past the edge (0 m). Some species (e.g. *Polygonum cilinode, Galeopsis tetrahit*, *Taraxacum* spp. and *Aster ciliolatus*), however, had a significant DEI that extended 5 or 10 m past the edge towards the interior forest (Figure 8).

Other species groups such as, conifer and deciduous saplings, low-growing shrubs, grasses, sedges, acrocarpous mosses and Sphagnum had a higher abundance in deciduous clearcuts compared to the interior condition (Figure 9). For most of these species groups the DEI extended approximately 5 m past the edge towards the interior forest. Vascular cryptogams had a lower abundance in the clearcut area. A higher abundance of low-growing shrubs, shade-intolerant herbs, vascular cryptogams, grasses and mosses was observed at locations 15 to 40 m past the edge.

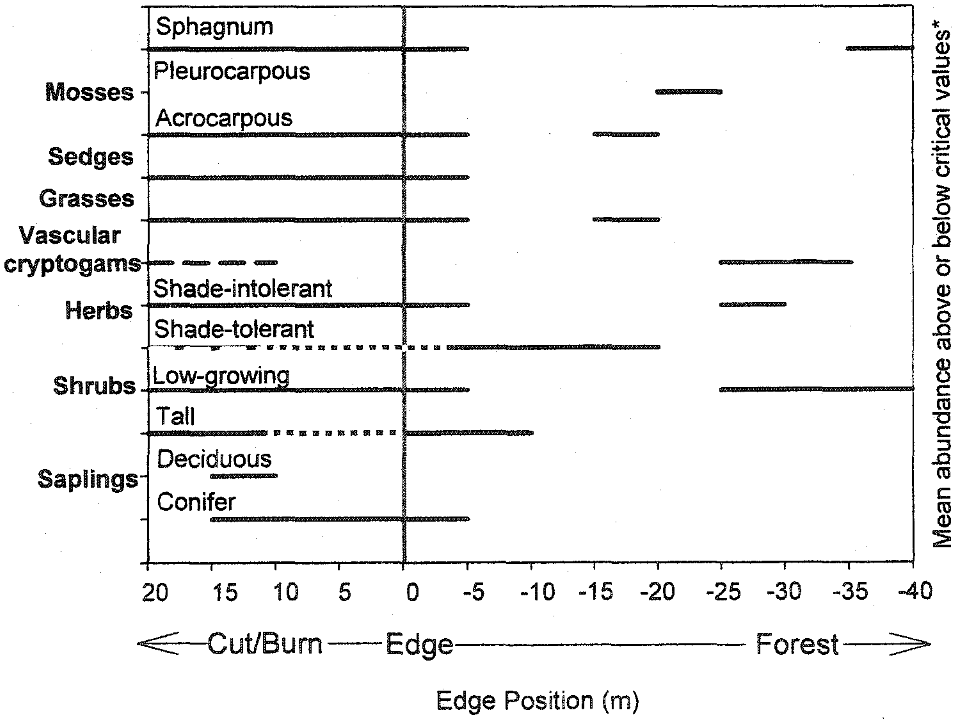


Figure 9. Mean understory species abundance above or below critical values at deciduous clearcut edges. *Two or more consecutive mean values above or below critical values (representative of interior forest) are deemed to show DEI at a given edge location. Refer to Figure 7 for details.

DEI at fire edges

The general distribution pattern of understory species was different at fire edges than at conifer and deciduous clearcut edges. There was a decrease in the number of shade-intolerant herbs with a significant DEI from the burnt area to the edge (0 m). However, low-growing shrubs, vascular cryptogams and species indicative of high moisture conditions showed distinct patterns of increased abundance past the edge (Figure 10). Low-growing shrub species common in burnt areas (*Linnaea borealis, Ribes glandulosum, Ribes triste, Rosa acicularis, Rubus idaeus, Vaccinium angustifolium* and *Vaccinium myrtilloides*) had a higher abundance only in the burn, except for *Vaccinium angustifolium,* and *Rubus idaeus*, which had a significant DEI up to 30 m past the edge towards the interior forest (Appendix VII). Low-lying shrub species associated with a higher moisture regime had a significant DEI from 5 to 15 m past the edge (*Viburnum trilobum* and *Viburnum edule*) and from 30 to 40 m past the edge (*Lonicera villosa*). Moisture loving herbs (*Mertensia paniculata, Eupatorium maculatum* and *Lycopus uniflora*) also had a higher abundance either at the edge or from 20 to 30 m past the edge compared to interior conditions (Appendix VII). In addition, a higher abundance of vascular cryptogams (*Equisetum arvense*, *Athyrium felix-femina* and *Phegopteris connectilis*) occurred at the same edge locations as shrubs and herbs with a significant DEI that were indicative of high moisture conditions. Among the three edge types fire edges had the largest number of vascular cryptogams with a significant DEI.

Unlike conifer and deciduous clearcut edges, shade-intolerant herbs did not have the largest number of species with a significant DEI at fire edges. In addition, none of the shade-intolerant herbs had a significant DEI past the edge at fire edges.

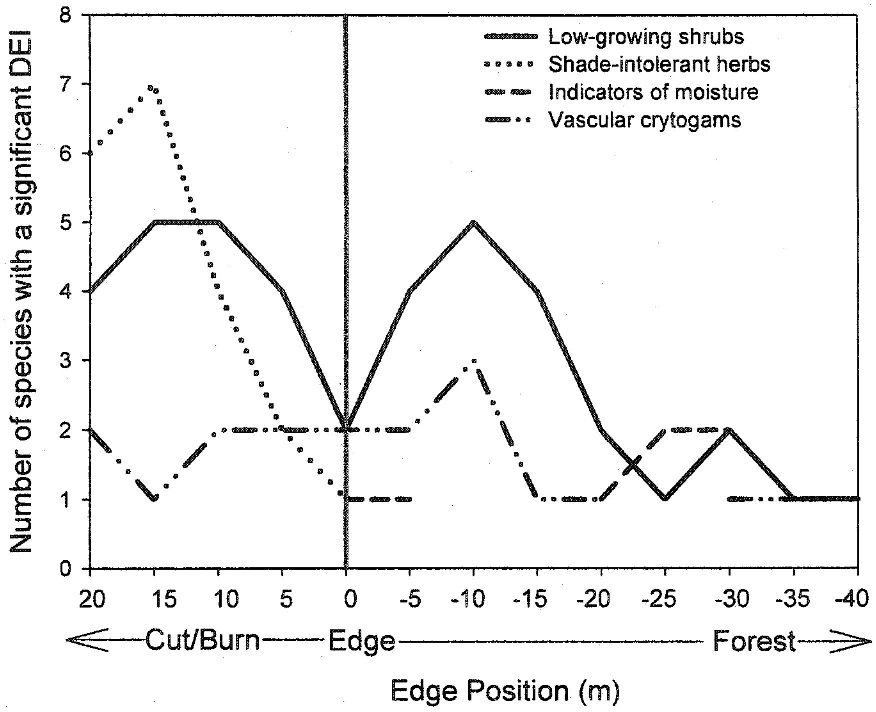


Figure 10. Number of low-growing shrubs, shade-intolerant herbs, species indicative of high moisture and vascular cryptogams with a significant DEI across fire edges.

However, there were still a number shade-intolerant species (*Fragaria virginiana, Taraxacum* spp., *Hieracium caespitosum*, *Epilobium angustifolium* and *Epilobium ciliatum*) with a high abundance in the burnt area (Figure 10).

A number of the other species groups had a higher abundance at fire edges compared to the interior including, deciduous saplings, tall shrubs, shade-tolerant herbs, sedges, acrocarpous mosses and lichens (Figure 11). Conifer saplings, pleurocarpous mosses and *Sphagnum* spp. had a lower abundance in the burnt area compared to interior forest conditions. From approximately 15 m to 30 m past the edge deciduous saplings, grasses, sedges, acrocarpous mosses and liverworts had a higher abundance.

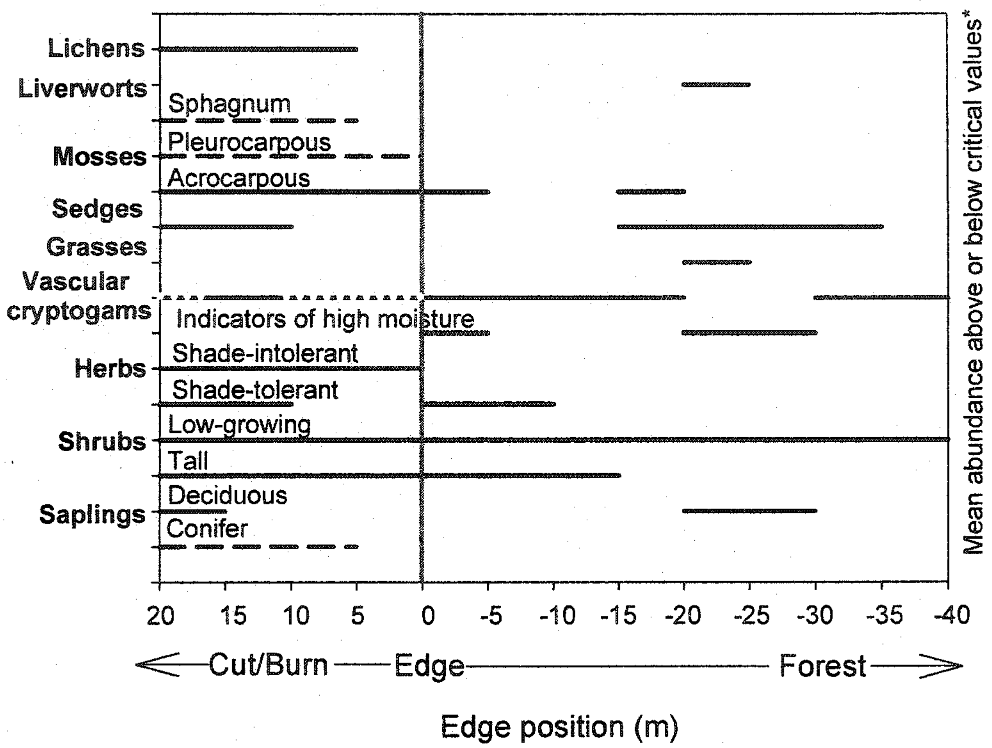


Figure 11. Mean understory species abundance above or below critical values at fire edges. *Two or more consecutive mean values above or below critical values (representative of interior forest) are deemed to show DEI at a given edge location. Refer to Figure 7 for details.

Discussion

There were both similarities and differences in the edge characteristics of conifer clearcut, deciduous clearcut and conifer fire edges. Canopy structure was different between burnt and clearcut areas, as well as between the two clearcut edge types. Differences in canopy composition were limited to changes in shrub composition at clearcut edges, and changes in tree species composition were found only at fire edges. Understory species response at clearcut edges was largely confined to the clearcut with a sharp decline in the number of species with a significant DEI up to 10 m past the edge. The understory at fire edges had a different pattern of response with distinct communities arising past the edge towards the interior forest. Due to many similarities in the understory response across the three edge types, detection of edge effects using a MRBP was difficult. General similarities and differences, however, were detected using the MRPP and indicator species analysis. Finer scale edge characteristics and the DEI were best determined by using the critical values approach.

Characterizing edges- MRBP, MRPP and Indicator Species Analysis

None of the exploratory analytical techniques were as effective at characterizing edges as the critical values approach. Comparison of the exploratory techniques used, however, does reveal important similarities and differences between the edge types and lends support to the trends detected by the critical values approach. No significant difference was found between the three edge types when comparisons were constrained by spatial location (i.e. relative edge location). Compositional similarities at edge locations (i.e. within the blocks) most likely masked the more subtle edge type differences. Although A values from all of the MRPP analyses were relatively low, both edge type and spatial locations across each edge type were significantly different. The indicator species analysis provided insight into the similarities at edge locations across all three edge types, the characteristics of the different edge types and the edge locations that can be most easily differentiated.

Removal of the canopy can lead to similar micro-environmental conditions at the different edge types, which in turn results in a similar understory composition. *Epilobium angustifolium, Rubus idaeus* and *Taraxacum* spp. were indicators of the clearcut/burn location (edge location 1) at all three edge types. These species are common and often highly competitive in disturbed areas; for example, *Epilobium angustifolium*, which is colonized from windblown seeds, is an aggressive invader of disturbed areas in the boreal forest (Rowe, 1983; Schimmel & Granstrom, 1995). Conifer clearcuts and deciduous clearcuts share a number of additional indicator species for edge location one, which are primarily grasses and weedy shade-intolerant herbs common in disturbed areas.

Deciduous clearcut and fire edges share tall shrub species (*Prunus pensylvanica* and *Salix* spp.), *Anaphalis margaritacea* and *Polytrichum* spp. as indicators of edge location one. Tall shrub species may be prevalent in deciduous or conifer-deciduous mixed stands prior to harvesting and able to rapidly recolonize after harvesting, outcompeting other species due to vertical and horizontal competition strategies (Mallik *et al.,* 1997). In addition, Rowe & Scotter (1973) suggested that shrub species, such as *Salix* spp., can replace themselves at a rapid rate within burns by wind disseminated seeds and sprouting from underground stem bases and roots that are not damaged during fire. *Polytrichum* spp. and *Anaphalis margaritacea* are common in rocky areas with exposed mineral soil and would be expected at burnt sites due to removal of the organic layer (Legasy *et al.,* 1995). Deciduous clearcut edges may share *Polytrichum* spp. and *A. margaritacea* as a result of post-harvest scarification at some sites.

Although more similar in canopy composition, conifer clearcut and fire edges do not exclusively share any indicator species in the disturbed area. The mechanism of disturbance may be crucial in defining the subsequent understory composition. In comparison to both conifer and deciduous clearcut edges, fire edges had fewer weedy shade-intolerant herbs as indicators of edge location one. *Sphagnum* spp. was an indicator of the far edge location (edge location 3) at both fire and conifer clearcut edges, most likely due to similar site conditions under *P. mariana* canopies. *Sphagnum* spp. are often abundant in well-established *P. mariana* stands (Brumelis & Carleton, 1988).

Many of the same indicator species were identified at more than one edge type. Deciduous clearcut edges had the lowest within-group homogeneity value (0.0451), and also shared the largest number of indicator species with the two other edge types. Fire edge had the highest within-group homogeneity value (0.1257) and also the largest number of edge locations (1, 3 and 4) differentiated through the indicator species analysis. Conifer fire edges in the boreal forest may have a more complex ecotone with a number of distinct communities distributed across the edge. Studies of natural forest edges, particularly fire edges are limited. However, Harper et al. (2004), found that in the boreal forest of northwestern Quebec fire edges had more extensive structural change and difference species composition than cut edges.

There were no indicator species for the near edge location (edge location 2). Only two edge locations were detected at conifer clearcut edges and at deciduous clearcut edges. Clearcut edges, therefore, may not support a series of distinctive communities associated with the edge, but major community differences may be more reflective of the clearcut and interior conditions. Community mosaicity (i.e. the occurrence of a spatial vegetational mosaic) has been recognized from the origin of the ecotone concept (Walker *et al.,* 2003). However, this study suggests that clearcut edges in the boreal forest do not appear to support unique communities across the edge. Walker *et al.,* (2003) also found mosacity was not an inherent ecotonal feature.

Important shifts in community composition may have not been detected, because blocks were subjectively created and may not represent natural ecotonal patterns or break points associated with understory species tolerance ranges. Arranging the transects into artificial blocks also may have contributed to difficulties in detecting differences between edge types (MRBP) and may partially account for low within-group homogeneity for edge locations. The critical values approach was more effective in determining the fine-scale shifts in species composition across edges.

Characterizing edges and determining the DEI - Critical values approach

Canopy structure and composition

Significantly lower canopy cover was observed primarily in the clearcut/burn at all three edge types. Deciduous clearcut edges, however, appeared to have the greatest amount of structural damage at the edge due lower live stem density, lower basal area, more snags, more fallen trees and more coarse woody debris (CWD). Harper & Macdonald (2002) found similar results at *Populus*-dominant boreal mixed-wood forest edges in Alberta: Canopy cover was lower at edges 16 years old (DEI = 5-10 m), a lower density of dominant tress occurred at edges 5 years and older (DEI = 0-5 m), and edges had larger amounts of recently accumulated CWD (DEI = 0-20 m) compared to interior conditions.

Compared to conifer clearcut edges, deciduous clearcut edges did not have a significantly larger number of fallen trees, but did have a higher amount of CWD. CWD may be more widely distributed at deciduous edges due to larger snags and wide spread branches, whereas the conical shape of conifer trees may result in a more constrained distribution of CWD.

Burton (2002) found strong differences in canopy openness and light between interior forest conditions and within 10 m of south-facing forest edges in the sub-boreal spruce forest of northwest-central British Columbia. In this study, conifer clearcut edges showed the least amount of structural damage with no significant differences in structural variables beyond the edge (0 m), although canopy sampling was only measured in 15 m intervals. All edge types, however, exhibited some structural damage either through lower live stem density or an increase in the number of fallen trees at the edge. Burton (2002) reported fewer stems in canopy edge plots compared to the interior forest, primarily due to increased numbers of recently fallen trees (Burton, 2002).

In all but the most severe cases, fire events leave standing dead trees, which cast partial shade ameliorating the forest floor microclimate during hot, dry summer conditions (Carelton & MacLellan, 1994). Snags can intercept relatively high percentages of full light. Coniferous species intercept more light than deciduous species (Poulin *et al.,* 2002). The presence of standing burnt trees at fire edges led to higher upright stem density at the edge and a larger number of snags in the burn compared to both the clearcuts and the edge of conifer clearcuts. Conifer clearcut edges, however had a larger number of fallen trees (as a percent of upright stems) at the edge (0 m) compared to fire edges. Patterns of wind damage indicate that winds are deflected along the edges of clearcuts (DeWalle, 1983), standing burnt trees may act as a buffer to lessen or redirect winds.

Results from this study indicate that radial growth reduction does not occur at recently created edges. Burton (2002) studied 9 to 21 year old clearcut edges and also detected no significant radial growth reduction of spruce on south-facing edges. In this study lower dbh of *P. mariana* stems was observed at fire edges, which may be due to competition from shrubs and other moisture-loving species. *Cornus stolonifera*, which had a higher abundance at the edge, is often found at edges on water-receiving sites and can be a significant competitor of coniferous trees on wet, shrub dominated sites (Ringus & Sims, 1997). Other species associated with a high soil moisture regime (*Thuja occidentalis*, *Fraxinus nigra* and *Salix* spp.) were also found in significantly higher abundance at fire edges.

In this study changes in canopy composition across the three edge types were primarily restricted to changes in shrub species. Increases in the number of shrub species is more likely indicative of increased growth of shrubs at edge locations in comparison to interior conditions. Young and Mitchell (1994) found a higher density of young individuals in the forest interior, yet mature individuals were only found at the edge. Some species may disperse to and germinate in the forest interior, but continued growth and establishment can only occur at the edge. *Alnus incana* is often present at low density prior to cutting and enters a phase of rapid expansion in the absence of other woody vegetation (Brumelis and Carleton, 1988). Shortly after logging, fast-growing shrubs (e.g. *Alnus* spp., *Rubus* spp., and *Salix* spp.) can invade the clearcut and inner edge of adjacent forest stands, taking advantage of increased light availability and may rapidly decrease light "sealing" newly formed edges (Wales, 1972; Matlack, 1994; Mesquita *et al.,* 1999; Burton, 2002). At recent edges, such as those included in this study, where canopy closure has not yet occurred, increases in sub-canopy shrubs may be the initial development of a side canopy. *Acer spicatum* was the only shrub species with fewer and smaller stems in the clearcut compared to the interior forest. *Acer spicatum* is common in deciduous stands often forming a conspicuous sub-canopy in the understory (Legasy *et al.,* 1995). Removal of the canopy by clearcutting, therefore, would disrupt its preferred habitat with partial shade.

In this study the DEI for canopy structure variables did not extend beyond 20 m and was often limited to the clearcut /burnt area (20 m) or edge (0 m). Other studies have also found primary canopy responses to be confined within 10 and 20 m past the edge (Pallik and Murphy, 1990; Harper and Macdonald, 2002). In this study the DEI for canopy composition variables extended further than for canopy structure variables. Increases in shrub growth were detected up to 40 m past the edge towards the interior forest.

Understory response

Species richness and total cover

Of the three edge types included in this study only fire edges had higher species richness at the edge. Due to the juxtaposition of different habitat types at edges, these transition zones have traditionally been expected to have higher diversity (Wiens, 1985; Harris, 1988). Some studies have found an increase in species diversity at the ecotone (Ranney *et al.,* 1981; Young & Mitchell, 1994), whereas other studies suggest higher richness is not an intrinsic ecotone feature (Matlack, 1994; Lloyd *et al.,* 2000; Harper & Macdonald, 2002; Walker *et al.,* 2003). Llyod *et al.,* (2000) found that species richness at ecotones was similar to the community on one side, but significantly greater than the community on the other side. For example, an ecotone between a lawn habitat and a plantation had similar richness to the lawn area, but significantly higher richness than the plantation.

In this study conifer clearcut edges had higher richness in the clearcut and near the edge compared to the interior condition. Schoonmaker & McKee (1988) found richness of shrub and herb species peaked in the clearcut two to five years after logging, which was also accompanied by a peak in invading herbs. During mesic succession shade-intolerant functional types that compete successfully in the high light conditions of early succession are eventually excluded by shade-tolerant functional types (Smith & Huston, 1989). Decreasing richness across the conifer clearcut edges is based upon the same process with exclusion of weedy shade-intolerant herbs as light diminishes with greater canopy closer towards the interior. Deciduous clearcut edges did not exhibit the same trend likely due to the higher light conditions under deciduous canopies, which allowed for a greater range of light-use strategies (i.e. functional types) to persist.

Fire edges did not have higher understory species richness in the burnt area, but did have higher richness from 5 to 10 m past the edge compared to both the interior condition and conifer clearcut edges. Higher richness at fire edges is most likely due to the response of functional groups to the area of high moisture observed at the edge. Under wetter conditions species diversity within habitats may be higher because more light-use strategies are viable (Smith & Huston, 1989). Contradictory findings from previous studies may be symptomatic of variation in the stand-level characteristics of edges included in the study. Clearcut edges that lack a moisture gradient across the edge may not support higher richness.

Significantly lower total species cover in the clearcut at conifer clearcut edges was primarily the result of moss species dynamics. Most boreal landscapes have an abundance of well-developed moss communities in areas with dominant conifer canopies (Weetman & Timmer, 1967; Longton, 1984; Vitt, 1990). However, many pleurocarpous mosses, such as *Ptilium crista-castrensis*, lack underground tissue and cannot rapidly recover from above ground disturbance. Many mosses cannot retain water and cease to photosynthesis in hot dry conditions often encountered in clearcuts (Callaghan *et al.*, 1978). At deciduous clearcut edge moss species did not contribute as much to understory cover, therefore, cover in the clearcut was not as effected. Burnt areas were able to maintain higher cover because fire-adapted bryophytes (acrocarpous mosses) quickly colonize burnt areas (Rowe & Scotter, 1973; Foster, 1985; Per-Anders *et al.*, 1992). A significantly higher abundance of acrocarpous mosses, such as *Ceratodon purpureus* and *Polytrichum* spp. and a significantly lower abundance of *Pleurozium schreberi, Sphagnum* spp. and *Cladina* spp. were found in the burnt area. Granstrom & Schimmel, (1996) found that fire altered forest floor vegetation more than understory vegetation. *Polytrichum* spp. and *C. purpureus* were dominant and pleurocarpous mosses and fruticose lichens were absent in burnt areas during their five year study. Several other studies have also reported the rapid increase in acrocarpous mosses following fire and a similar successional pattern of ground vegetation recovery (Rowe & Scotter, 1973; Foster, 1985; Per-Anders *et al.*, 1992).

Understory Composition

P. mariana saplings did not have a high abundance in the clearcut or burnt area at any of the edges, however, a number of deciduous saplings and shrubs (*Betula papyifera, Populus* spp., *Salix* spp. and *Prunus pensylvanica)* had a significant DEI in the clearcut or burn. This apparent lack of regeneration of *P. mariana* in clearcuts and shift towards deciduous species dominance has been found by a number of other studies (Brumelis & Carleton, 1988; Harvey & Bergeron, 1989; Carleton & MacLellan, 1994). Mechanically logged stands place fast-growing species at a competitive advantage over *P. mariana* and can cause a wholesale conversion of conifer dominated stands to mixed or hardwood stands (Brumelis & Carleton, 1988; Carleton & MacLellan, 1994). The relative growth rate of woody plants < 2 m has been demonstrated to be twice as rapid on experimental edges than in the interior forest (Williams-Linera, 1990b). The increase in abundance of saplings and tall shrubs, however, did not extend beyond edge in this study. Lower abundance of *P. mariana* saplings at fire edges is surprising as fire is considered a cycling agent of woody vegetation leading to rapid establishment of conifer stands (Foster, 1985). The lower abundance of *P. mariana* in this study may be a result of a number of small *P. mariana* trees in the interior, which provide a greater cover than the 4-5 year old seedlings in the burn.

In this study the majority of indicator species and species with a significant DEI in the clearcut area at both conifer and deciduous clearcut edges were grasses, sedges, weedy shade-intolerant herbs and shrubs. Brumelis and Carleton (1989) also found peak abundances of *Calamagrostis canadensis* and *Carex vaginata* (included in *Carex* group 2) in *P. mariana* dominated clearcuts. Other studies have found shade-intolerant herbs and shrubs (*Achillea millefolium, Epilobium angustifolium, Vicia americana, Taraxacum officinale, Ribes* spp., *Rubus* spp., *Prunus pensylvanica* and *Salix* spp.) at a high abundance or exclusively in five year-old clearcuts or at five year-old edges (Schoonmaker & McKee, 1988; Brumelis & Carleton, 1989; Harper & Macdonald, 2002). In this study only a few shade-intolerant species had a significant DEI extending greater than 5 m past the edge and edge effects initiating in the clearcut appear to be limited to within 10 m past the edge. Due to less canopy cover and a lower stem density at deciduous clearcut edges it is not surprising that more species had a DEI that extended further towards the interior forest. At fire edges none of the shade-intolerant herbs had a higher abundance past the edge (0 m) and there were < 50 % as many shade-intolerant species with significantly higher abundance compared to clearcut edges.

A number of shade-tolerant species (*Aralia nudicaulis, Clintonia borealis* and *Trientalis borealis*) had a lower abundance in the clearcut compared to the interior conditions. Harper and Macdonald, (2002) also found *Aralia nudicaulis* to have a significantly lower abundance up to 10 m past the edge at five year-old edges. Species, such as *Clintonia uniflora* are strongly associated with late-successional stands and have been shown to go locally extinct in logged areas (Halpern & Spies, 1995). The reproductive organs of *Trientalis borealis* tend to be restricted to the litter layer (Flinn & Wein, 1977), therefore, aboveground disturbance would greatly limit its reproductive ability. Lower abundance in the clearcut was also noted for other species (e.g. *Lycopodium dendroideum*) with growing points on or only slightly below the surface of the litter.

Some shade-tolerant generalists appear to be able to take advantage of both the increased light conditions in the clearcut or burn and the shaded areas along the ecotone. *Maianthemum canadense* is a generalist species with a clonal guerilla life strategy possessing an extensive underground root and rhizome system and *Cornus canadensis*, which was more abundant in the burnt area, has underground reproductive tissues that are usually found in the mineral soil (Silva *et al.,* 1964; Sobey & Barkhouse, 1977; Flinn & Weins, 1977). Survival of the underground system and rapid growth following disturbance due to favourable environmental conditions can result in flower production and abundance often exceeding pre-disturbance levels.

A decrease of opportunistic shade-intolerant species and an increase of shade-tolerant species from the edge towards the interior are commonly found across edges (Ranney *et al.*, 1981; Pallik & Murphy, 1990). Due to tradeoffs involved in premise one (see p. 20) there is an inevitable shift in the competitive ability of functional types over successional time. The shift in competitive ability is due to the decrease in light at ground level as plant height and leaf area increase (Smith & Huston, 1989). Shifts in community composition across edges can be viewed in a similar manner (i.e. different species will have a competitive advantage at different edge locations). Findings from this study suggest that shade-intolerant functional types may outcompete shade-tolerant species in the clearcut or burn, however shade-tolerant species appear to regain the competitive advantage between the edge and 10 m past the edge.

In both the clearcut and burnt areas there was a peak in the number of species with a significant DEI from 15 to 5 m. In addition, there were a number of species at conifer and deciduous clearcut edges that had a significant DEI from approximately 15 to

35 m past the edge and from approximately 25 to 40 m past the edge, respectively. Due to the interaction of edge effects it is unrealistic to assume that edge effects vary monotonically with distance from the edge (Murica, 1995). Numerous studies have found a similar result with peaks and depressions of edge effects around the intermediate distance of 20-30 m past the edge (Kapos, 1989; Pallik & Murphy, 1990; Matlack 1994; Williams-Linera, 1998).

These trends are not only a result of different light conditions with distance from the edge, but are also associated with moisture regime and other habitat factors. *Ledum groenlandicum* is shade-intolerant, a moderate indicator of moist to wet moisture regimes and is commonly associated with *Sphagnum* spp. (Ringus & Sims, 1997), both of which had a significantly higher abundance between 25 and 40 m past deciduous clearcut edges. Both *Equisetum arvense* and *Equisetum sylvaticum* prefer moist clearings and had a higher abundance between 15 and 35 m past conifer clearcut edges. An increase in moisture past the edge may reflect the practical limitations of logging in wet areas and the maintenance of high moisture conditions under the canopy.

Understory species at fire edges had the strongest association with soil moisture conditions across the edge. A number of shrubs associated with higher moisture (*Cornus stolonifera, Lonicera villosa, Rubus pubescent, Viburnum edule* and *Viburnum trilobum*) had a high abundance between 0 and 20 m past fire edges. In addition, *Schizachne purpurascens, Carex aquatilis, Eupatorium maculatum, Lycopus uniflora, Mertensia paniculata* and *Gallium triflorum* had higher abundances past the edge compared to the interior forest and are common in wet clearings and moist thickets (Legasy *et al.*, 1995).

Under dry conditions, often experienced in exposed disturbed areas, the possible light-use strategies are limited to those that are relatively shade-intolerant (i.e. premise three) (Smith & Huston, 1989). Fewer shade-intolerant species at fire edges was likely the result of a more shaded environment, due to standing dead trees, and higher soil moisture. Early-successional transients that are shade-intolerant but tolerant to low water availability do not persist when water availability is high. As moisture availability increases shade-tolerance becomes a more viable strategy often leading to a complex vertical stratification of forest structure (Smith & Huston, 1989).

In comparison to both conifer and deciduous clearcut edges, fire edges had fewer species with a significant DEI in the disturbed area, but a greater number of species with a significant DEI past the edge. Fire edges appear to have a more complex ecotone with a pre-existing gradient of moisture beyond the edge. This area of high moisture logically coincides with where fire could no longer travel, creating patches of upland conifer that are buffered by low-lying areas of high moisture. The high moisture conditions also appear to contribute to the reduction of edge effects, disallowing weedy shade-intolerant species to penetrate into remaining stands.

Conclusions and Management Implications

Similar to many studies, this study found the DEI for understory variables was greater than that of overstory variables (Palik & Murphy, 1990; Williams-Linera 1990a; Chen *et al.,* 1992; Malcolm, 1994; Harper & Macdonald, 2001; Harper & Macdonald, 2002). The DEI determined is therefore greatly affected by the response variables under consideration.

The canopy at conifer clearcut edges was least effected with only a larger number of fallen trees present at the edge compared to the interior forest. Deciduous canopy structure was most effected with a large number of large snags and high canopy openness. A large number of burnt snags at fire edges decrease light penetration and perhaps even redirect winds, reducing the number of fallen trees at the edge.

The present standard for snag management suggests that a minimum of 6 large living trees and 19 snags, dying or living trees, must be left on all sites (Ontario Ministry of Natural Resources, 2002). This study found that conifer clearcut edges had no more snags than the interior forest, which is likely a result of low mortality in edge trees but also due to a lack of standing stems being left by harvesting practices. To emulate the structural legacy left by fires, discourage weedy species invasion and provide faunal habitat, more standing stems should be left, especially near edges.

Increasing understory diversity may not be an appropriate management goal or indicator of ecosystem health, not only because this study suggests that terrestrial edges are not inherently species rich, but also because many plants in the most diverse herb and shrub stages after disturbance are common persistent weedy species that are unlikely to become threatened (Schoonmaker & McKee, 1988; Peltzer *et al.,* 2000).

High moisture conditions at fire edges appeared to buffer edge effects. To buffer edge effects forestry practices have often increased the buffer width on wet ground, but edge effects appear to be less pronounced in wet habitats (Hylander *et al.,* 2002). Current guidelines suggest that the placement of residual patches and clearcuts should follow natural landscape contours, forest stand boundaries and local fire history (Ontario Ministry of Natural Resources, 2002). From the stand-level observations made in this study it appears that inclusion of higher ground moisture at clearcut edges may be paramount to emulating natural fire disturbance.

In this study the DEI was greatly decreased for most response variables 10 m past the edge, however, a significant DEI was found for some response variables at 40 m, which was the greatest distance measured. Although edges in the boreal forest of northwestern Ontario appear to be relatively effective at buffering edge effects, compositional changes did occur up to at least 40 m. Residual patches or peninsulas left on the landscape to emulate natural fire disturbance must allow for at least 40 m of edge habitat on their southern border if they are to maintain interior conditions.

Chapter 2

Edge effects at wide and narrow buffers in northwestern Ontario

Abstract

The study of edge effects across riparian buffers provides a unique opportunity to explore the effects of both induced edges, created by forest harvesting, and inherent edges, reflective of natural ecotonal gradients. The aim of this study was to determine the upland and riparian species response across narrow ($\leq$ 30 m) and wide ($\geq$ 40 m) buffers with respect to undisturbed stream edges. Two 60 m transects were laid perpendicular to the stream at 12 undisturbed stream edges and across 12 buffers. The critical values approach and split-moving window analysis were used to compare canopy and understory conditions in upland and riparian areas of buffers, with upland and riparian areas of undisturbed stream edges. Several species had a significant depth of edge influence (DEI) across the entire width of buffers. Species with a significant DEI at the stream edge of buffer sites, however, were common riparian species. An increase in abundance and diversity of riparian plants at the stream edge of buffers may be due to light penetrating from the clearcut allowing enhanced opportunities for establishment and growth. Some species had a response to both induced and inherent edges at narrow buffers, but only to induced edges at wider buffers. Narrow buffers may have an interaction between the clearcut edge and the riparian-upland ecotone. Current buffer guidelines may allow for the maintenance of understory communities representative of undisturbed riparian area, but may not effectively mitigate microclimatic change leading to changes in species abundance at the stream edge.

Introduction

Edge effects in riparian buffers merit special attention, because of the importance of maintaining riparian habitats, and because edges created by anthropogenic activities (induced edge) differ from those created by natural disturbance (inherent edge) (Williams-Linera *et al.,* 1998). Two main sources of induced edge in the boreal forest are clearcutting and fire. Inherent edges are ecotones often related to topographic differences, edaphic gradients, presence of open water and geomorphic factors (Bannerman, 1998). Riparian buffers (uncut forest strips retained adjacent to hydrological features after forest harvesting) of the boreal forest have both induced and inherent edges.

Riparian areas (communities occurring between the open water and the upland forest) with natural riparian-upland ecotones maintain high biodiversity due to intermediate levels of disturbance and provide a diverse array of microhabitats and ecological services (Naiman & Decamps, 1990; Gregory *et al.,* 1991; Jonsson, 1997; Naiman & Decamps, 1997; Hylander *et al.,* 2002). Although riparian areas have been recognized for their high biodiversity, over 80 % of riparian corridor area in Europe and North America has disappeared in the last 200 years (Naiman *et al.,* 1993). Buffer strips that border streams have both an upland edge created by clearcutting and encompass riparian habitats near the stream.

Riparian buffers have been largely viewed in terms of their ecological services in preventing stream sedimentation and maintaining fish habitats. Riparian vegetation, specifically the density of the riparian canopy, plays a major role in modifying solar inputs and influencing stream temperature (Barton *et al.,* 1985; Gregory *et al.,* 1991).

Altering microclimate near streams by forest harvesting in the upland, can alter the function of the riparian zone, changing plant composition, diversity and succession near streams, and may reduce landscape connectivity (Brosofske *et al.,* 1997). The habitat value of buffer strips themselves needs to be further investigated to determine if current buffer widths can maintain an environment similar to intact riparian forests (Hylander *et al.,* 2002).

A number of studies have explored the alteration of microclimatic parameters or biotic change across riparian buffers (Castelle *et al.,* 1994; Hibbs & Giordano, 1996; Brosofske *et al.,* 1997; Dong *et al.,* 1998; Williams-Linera *et al.,* 1998; Hylander, 2002). Williams-Linera (1998) found increased canopy openness, air temperature and soil temperature from the stream towards the open area. Brosofske *et al.,* (1997) suggested that harvesting affects riparian gradients by increasing temperatures and decreasing humidity along the gradient. The width of buffers did not appear to affect air temperature and wind speed at the stream. However, total solar radiation decreased with increasing buffer width and relative humidity displayed a positive exponential relationship with buffer width.

Changes in species composition measured from lakeshores into the upland were significantly different within 20-40 m and up to 60 m or greater for some species (Harper & Macdonald, 2001). Hibbs & Giordano, (1996) suggested that buffer strips may become increasingly dominated by shrubs, which may suppress future tree regeneration. Using a multivariate approach, Lamb *et al.,* (2003) found the composition of riparian plant community at coldwater streams in northwestern Ontario was not significantly altered by disturbance in the upland. However, there were increases in the abundance of some riparian species. In this study both the critical values approach and a split moving window analysis, which may be more effective at detecting subtle changes, were used to examine species response in both the upland and the riparian area of buffers. Increased transpiration rates from riparian vegetation across the landscape may cumulatively affect the hydrological budget of the watershed (Dong *et al.,* 1998). While a heterogeneous environment may conserve multiple habitats, fluctuations may exceed the adaptive range of certain organisms resulting in mortality. Species responses to a variable environment near the stream need to be studied (Dong *et al.,* 1998).

Although there is no quantitative agreement among different studies regarding the microclimatic or biotic changes that occur within buffers, some general trends are evident. Disturbed areas (i.e. clearcuts) often have higher light and lower soil moisture than buffers, which have intermediate light and soil moisture. Riparian areas often have higher light conditions due to a lack of canopy trees, but are also able to maintain high moisture conditions due to close proximity to the stream.

The current guidelines regarding forest harvesting near waterbodies in Ontario are intended to protect aquatic ecosystems that support fish populations (Ministry of Natural Resources, 1988). Shorelands under timber management operations that are adjacent to fish habitats are identified as areas of concern. The width of an area of concern (here referred to as a buffer) is based upon slope and slope angle ranging from 30 to 90 m in width. Coldwater streams including tributaries to coldwater lakes, such as those included in this study, require more protection due to the sensitivity of coldwater fish species. Shade requirements are particularly important for coldwater species, which may necessitate the maintenance of standing timber adjacent to streams. The management guideline suggest that no road construction, placement of landings or mechanical site preparation should occur within coldwater stream and lake buffers and harvesting should be severely restricted (Ministry of Natural Resources, 1988). The guidelines further suggest that blowdown be considered when creating relatively narrow strips of forest in the landscape. Beyond this suggestion, however, the guidelines do not take into consideration the penetration or variability of edge effects. Conventional management guidelines providing static buffers zones fail to consider the inherent variability of riparian areas and may not be sufficient in countering the dynamic nature of forest edges (Gascon *et al.,* 2000; Macdonald *et al.,* 2004). The appropriate buffer width may vary from 3 m to 200 m depending on the specific function of the buffer and the site-specific conditions (Castelle *et al.,* 1994).

The aim of this study was to determine the upland and riparian species response across narrow ($\leq$ 30 m) and wide ($\geq$ 40 m) buffers with respect to undisturbed stream edges. This was approached by a) characterizing and quantifying edge effects across riparian buffers, b) investigating the upland-riparian dynamics that occur within buffers and c) identifying ecotonal indicators associated with upland and riparian environments.

Methods

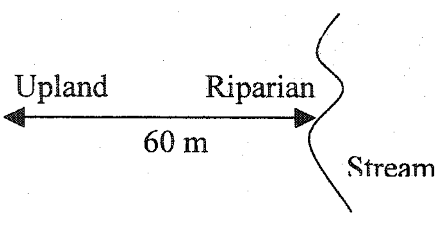
Site selection

All riparian sites, including buffers and undisturbed stream edges, were located within the northwestern Ontario study area previously described in Chapter 1 (Figure 1). In total 24 riparian sites were studied, consisting of 12 stream sites that had an adjacent clearcut with buffer (hereafter referred to as buffer sites) and 12 stream sites with undisturbed forest (hereafter referred to as undisturbed stream edges). All the sites were dominated by *Picea mariana* and had a south-facing aspect (± 45 °). Ages of the buffer sites varied from recently disturbed (one year) to approximately 10 years since disturbance. The coldwater streams at both buffer and undisturbed sties were predominately small having a watershed area of less than 10 km^2. The slope from the stream into the upland was gentle ($< 20^o$) at most sites. Although inclusion of differently aged buffers and different stream sizes increased site-to-site variability, similarity in other site characteristics such as width of riparian zone, topography, soil and vegetation were considered during site selection. The location of the upland-riparian transition was visually estimated as the area where the most rapid change from riparian vegetation to upland vegetation occurred. The upland-riparian transition was approximately 10 m from the stream edge at all sites. Further details regarding study sites can be found in Appendix I.

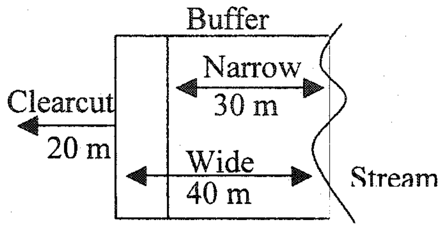
Sampling design

Two transects were located at each of the 12 buffer sites and 12 undisturbed stream edges at least 50 m apart with most transects being 100 m apart. Transects were placed from the stream up to 60 m into the upland forest at undisturbed stream edges and from the stream, across the buffer and 20 m into the clearcut at buffer sites (Figure 12).

Cover for all understory plants was determined in 1 x 1 m quadrats at 4 m intervals (Figure 13). Canopy cover was assessed visually at each understory quadrat location.



Undisturbed sites



Buffer sites

Figure 12. Transect placement at undisturbed reference sites and disturbed narrow (30 m) and wide (40 m) buffer sites.

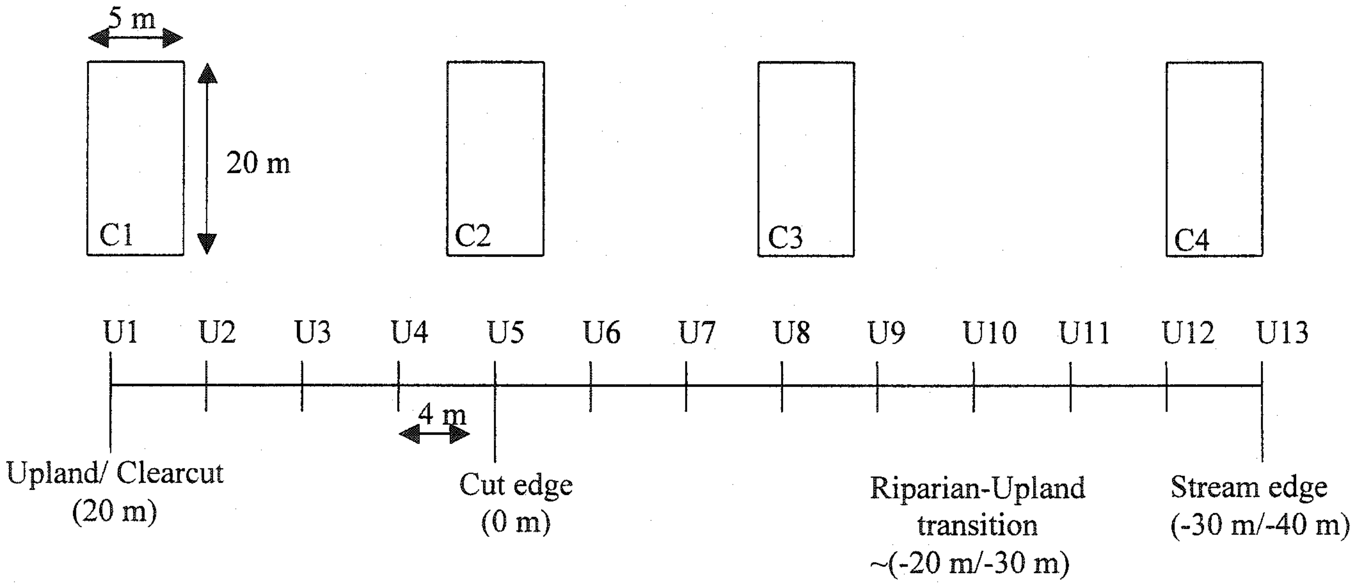


Figure 13. Sampling design along a 60 m transect placed perpendicular to the stream edge or buffer with 1 x 1m understory plots (U1-13) placed every 4 m and 5 x 20 m canopy plots (C1-4) placed every 15 m.

Following a method similar to Chen *et al.*, (1992), cover was determined as a discrete variable with 0 indicating the absence of canopy and 1 indicating the presence of canopy. Basal diameter (for species with dbh $\geq$ 5 cm) and density of canopy species were determined in 20 x 5 m plots at 15 m intervals. All field sampling occurred from June 19 to August 28 2002 and from July 4 to August 27 2003.

Data analysis

Buffer transects were divided into two groups: wide buffers, 40 m or greater in width and narrow buffers, 30 m or less in width. Where buffer widths were neither 30 nor 40 m, interior buffer values were averaged or averaged and repeated. Buffer width groups of 30 and 40 m were selected as they most closely represented the majority of buffers reducing the number of interior values requiring alteration. Each of the two buffer width groups (narrow and wide) had 12 transects. Due to variable buffer width at a single site each buffer transect was considered independent, with some buffer sites having one transect in the wide group and one transect in the narrow group.

Critical Values Approach

The critical values approach was used to quantify the depth of edge influence (DEI). The critical values for all tests are the 2.5 and 97.5 percentiles of the 5000 randomly permuted averages of the undisturbed stream edge transects (2 tailed test, sig.= 0.05). Randomization tests were performed for undisturbed stream edge data using the critical values program in Visual Basic, Microsoft Excel 1997 (Harper & Macdonald, 2002b). The null hypothesis for the critical values approach was: the average of values observed at a particular distance from the edge is no different than would be expected by chance in the reference forest (Harper, 1999). For further details regarding the critical values approach see Chapter 1.

Due to high variability within the data, buffer transects (12 wide and 12 narrow) were compared with critical values generated from twice the number of undisturbed stream edge transects (24). The larger reference dataset provided greater power in determining ecologically significant trends while limiting significant results that were an artifact of variability. The reference data had inherent spatial properties because it spanned both riparian and upland communities; therefore, three different reference data sets were used. The division of the reference data was used to explore differences in the upland and riparian communities, but also to ensure that buffer means are compared with appropriate critical values. The reference data sets were: (1) all undisturbed stream edge reference data, which included the entire transect; (2) upland undisturbed stream edge reference data, which included data from 30 to 60 m from the stream; (3) riparian undisturbed stream edge reference data, which included data from the stream edge up to 25 m from the stream.

Mean values at each buffer distance for both wide and narrow buffers were compared to the critical values of the three reference data sets. Entire buffer transects were compared with entire undisturbed transects (reference values 1). Upland buffer means within the clearcut to 10 m past the clearcut edge (20 to –10 m) were compared with the upland portion of undisturbed transects (reference values 2). Riparian buffer means 15 m past the clearcut edge to the stream edge (–30 m or –40 m) were compared with the riparian portion of undisturbed transects (reference values 3). Mean values at different buffer transect locations were considered to be significant or show an edge effect if they lay outside the critical values.

Buffers were compared to undisturbed conditions with respect to 14 response variables (Table 9). Differences in canopy species structure and composition, and understory species richness and abundance were investigated.

Table 9. Response variables used in the critical values analysis including canopy composition and structure, and understory species richness and composition.

Type of response	Response variables
Canopy	Canopy cover Upright stem density (stems/ha) Live stem density (stems/ha) Basal area, (m^2/ha) Snags (% of total upright stems) Recently fallen trees (% of upright stems) Number of stems per species (stem/ha) Mean live stem diameter at breast height (dbh) Mean dbh of snags Mean dbh per species
Understory	Richness Total cover Percent cover for all species Percent cover of coarse woody debris

Split Moving Window Analysis

Split moving window analysis (SMW) was used to examine the response of selected species with a significant DEI at narrow (30 m) and wide (40 m) buffers. A split moving window analysis can help detect the spatial location of an ecotone based upon the magnitude of change. A window of a given size (x) is placed at the beginning of the data series; the window is split into two equal halves and the average for each variable within each half calculated. A measure of dissimilarity (D) is then calculated between the two halves of the window and the process is repeated as the window is moved along the transect one quadrat at a time (Cornelius & Reynolds, 1991; Turner *et al.,* 1991; Harper & Macdonald, 2001).

The selected scale of analysis, or window size, and the spatial resolution of the data can strongly affect the accuracy of the delineated boundary (Fortin, 1994; Fortin & Edwards, 2001). A small window may contain too much noise and not hold enough of the community to detect meaningful changes, whereas a larger window may have too much environmental heterogeneity and can smooth over important vegetation change (Fortin; 1999, Walker *et al.,* 2003).

In this study understory species cover data were used to determine the magnitude of the rates of change in dominance. Understory quadrats in this study were not contiguous but spaced at 4 m intervals; therefore, the analysis was limited to changes that can be detected at a resolution of greater than 4 m. Two different window sizes (x) were selected to compare the effect of scale on ecotone detection. Fine scale changes were examined in a 6 m window, which corresponds to the width of two understory sampling quadrats and the distance between them. Larger scale changes were examined in a 16 m window, which includes four understory quadrats in each window (Figure 14).

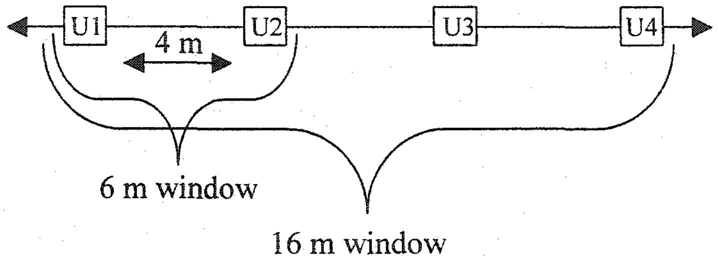


Figure 14. Split moving window analysis with a 6 m window with two understory quadrats and a 16 m window with four understory quadrats.

The dissimilarity measure (D) used in this study was the absolute difference in mean cover or abundance. For each half of the window the mean abundance was calculated for each buffer width. The dissimilarity between the two halves of the window was then determined. For each analysis the results were standardized (i.e. mean is equal to 1) to allow for comparison between different species (Harper & Macdonald, 2001). The split moving window analysis was performed in a Microsoft Excel 2000 spreadsheet. Due to the presence of both a clearcut edge and an upland-riparian ecotone, investigation of the magnitude of change across the transect provides information on the area of maximum response in regards to these two features.

Results

Characterizing buffer edges

Canopy structure and composition

Canopy cover was lower in the clearcut and at the edge (20 to 0 m) for both wide and narrow buffers compared to the undisturbed condition (Appendix VIII). Canopy cover was higher from 15 to 20 m past the edge in wide buffers, but lower at the stream edge (-30 m) in narrow buffers.

CWD was not a strong response variable, because no two consecutive means lay outside of the critical values. However, compared to undisturbed stream edges, coarse woody debris (CWD) was significantly higher at the clearcut edge (0 m) and riparian-upland transition (-25 m) in narrow buffers (data not shown).

Canopy structure at wide and narrow buffers was compared to canopy structure at undisturbed stream edges. Wide buffers had higher stem density and basal area from the clearcut edge up to 20 m and 40 m past the edge respectively (Table 10). Snags, as a percentage of total stems, were higher at the clearcut edge of both wide and narrow buffers, but lower at the stream edge of wide buffers. A larger number of recently fallen trees were present in the clearcut and across the entire width of narrow buffers. Compared to undisturbed stream edges, the average dbh of all stems was higher at the clearcut edge and up to 20 m past the edge at wide buffers and from the clearcut edge to the stream edge at narrow buffers. The average dbh of live stems was higher at the clearcut edge and up to 20 m past the edge at wide buffers, but was only higher at the stream edge for narrow buffers. The average dbh of snags was higher at both buffer widths with the exception of the stream edge at wide buffers. Compared to the undisturbed condition, wide buffers had a higher average dbh of *Abies balsamea*, *Picea mariana*, and *Pinus banksiana* at various locations across the buffer. Narrow buffers had a higher average dbh of *A. balsamea* and *P. banksiana*, but a lower average dbh of *P. mariana* at the clearcut edge.

Table 10. Differences in canopy structure across wide (40 m) and narrow (30 m) buffers compared to undisturbed stream edges. * A significant edge influence is indicated when mean values are above (+) or below (-) critical values in comparison to the respective upland or riparian undisturbed conditions. Transect location 20 m is in the cut with 0 m located at the edge and negative values occurring towards the stream edge. Where mean values occurred outside of the critical values only in the cut (20 m) results are not shown.

Structural canopy response variable	Buffer width (m)	Location of significant edge influence*
Upright stem density, (stems/ha)	40	+(0 m to –20 m)
Live stems density, (stems/ha)	40	+(0 m to –20 m)
Basal area, (m^2/ha)	40	+ (0 m to –40 m)
Snags, (% total upright stems)	40	+(0 m), - (-40 m)
Recently fallen trees, (% of upright stems)	30	+(20 m to –30 m)
	40	+(20 m to 0 m), - (-40 m)
Mean dbh of live stems	30	+ (-30 m)
	40	+ (0 m to –20 m)
Mean dbh of snags	30	+ (0 m to –30 m)
	40	+(0 m to –20 m), - (40 m)
Mean dbh of *Abies balsamea*	30	+ (0 m)
	40	+ (-20 m)
Mean dbh of *Picea mariana*	30	-(0 m)
	40	+ (0 m to –40 m)
Mean dbh of *Pinus banksiana*	30	+ (-30 m)
	40	+ (0 m to –20 m)

Canopy composition at wide and narrow buffers was compared with canopy composition at undisturbed stream edges. Fewer *A. balsamea* and *Alnus incana* stems occurred up to 20 m past the edge in wide buffers and fewer *Larix laricina* stems occurred across the entire width of 40 m buffers (Table 11). Narrow buffers had fewer *A. incana* and *Betula papyifera* in the clearcut and at the clearcut edge.

Compared to the undisturbed condition, a larger number of *Populus balsamifera* stems were found across the entire width of narrow buffers, but only at the clearcut edge (0 m) of wide buffers. Similarly, a larger number of *Picea glauca* occurred across the entire width of narrow buffers, but only from the clearcut edge to 20 m past the cut edge at wide buffers. A larger number and size of *Prunus pensylvanica* was found 20 m past the clearcut edge at narrow buffers. Wide buffers had a larger number and size of *Thuja occidentalis* across the entire buffer width.

Table 11. Differences in canopy composition across wide (40 m) and narrow (30 m) buffers compared to undisturbed stream edges. * A significant edge influence is indicated when mean values are above (+) or below (-) critical values in comparison to the respective upland or riparian undisturbed conditions

Compositional canopy response variable	Buffer width (m)	Location of significant edge influence*
Total number of *Abies balsamea*	40	-(20 m to –20 m)
Total number of *Alnus incana*	30	-(20 m to 0 m)
	40	-(20 m to –20 m)
Total number of *Populus balsamifera*	30	+ (0 m to –30 m)
	40	+(0 m)
Total number and average dbh of *Betula papyifera*	30	- (20 m to 0 m)
Total number and average dbh of *Larix laricina*	40	- (20 m to –40 m)
Total number and average dbh of *Picea glauca*	30	+(0 m to –30 m)
	40	+ (0 m to –20 m)
Total number and average dbh of *Prunus virginiana*	30	+ (20 m)
Total number and average dbh of *Thuja occidentalis*	40	+ (20 m to –40 m)

Understory

Species richness and total cover

Critical values for both species richness and total cover generated from the riparian undisturbed stream edge data (-15 to –40 m) were higher than the critical values generated from the upland undisturbed stream edge data (20 to –10 m). Comparison of the critical values for the upland (2) and riparian (3) areas separately provide further insight into species richness at undisturbed steam edges. Out of a total of 176 species, 91 species had critical values where the lower and upper confidence intervals were twice as high in the riparian area compared to the critical values for the upland area. Only eight species had lower and upper confidence intervals that were twice as high in the upland compared to critical values for the riparian area.

Wide and narrow buffers had a similar pattern of species richness, with a peak in richness at –15 m and –20 m respectively and a peak in richness at the stream edge (Figure 15a). Narrow buffers had significantly higher richness values in the clearcut (20 to 5 m) and at the stream edge (-30 m) compared to the undisturbed condition. Wide buffers had significantly higher richness 20 m past the clearcut edge and at the stream edge (-40 m). Narrow buffers had slightly higher richness across the entire buffer compared to wide buffers.

Wide and narrow buffers had a similar pattern of total species cover past the clearcut edge (Figure 15b). In the clearcut, however, narrow buffers had higher total cover than wide buffers. Wide buffers had significantly lower total cover in the clearcut (20 to 0 m) and in the riparian area between 20 and 35 m past the clearcut edge.

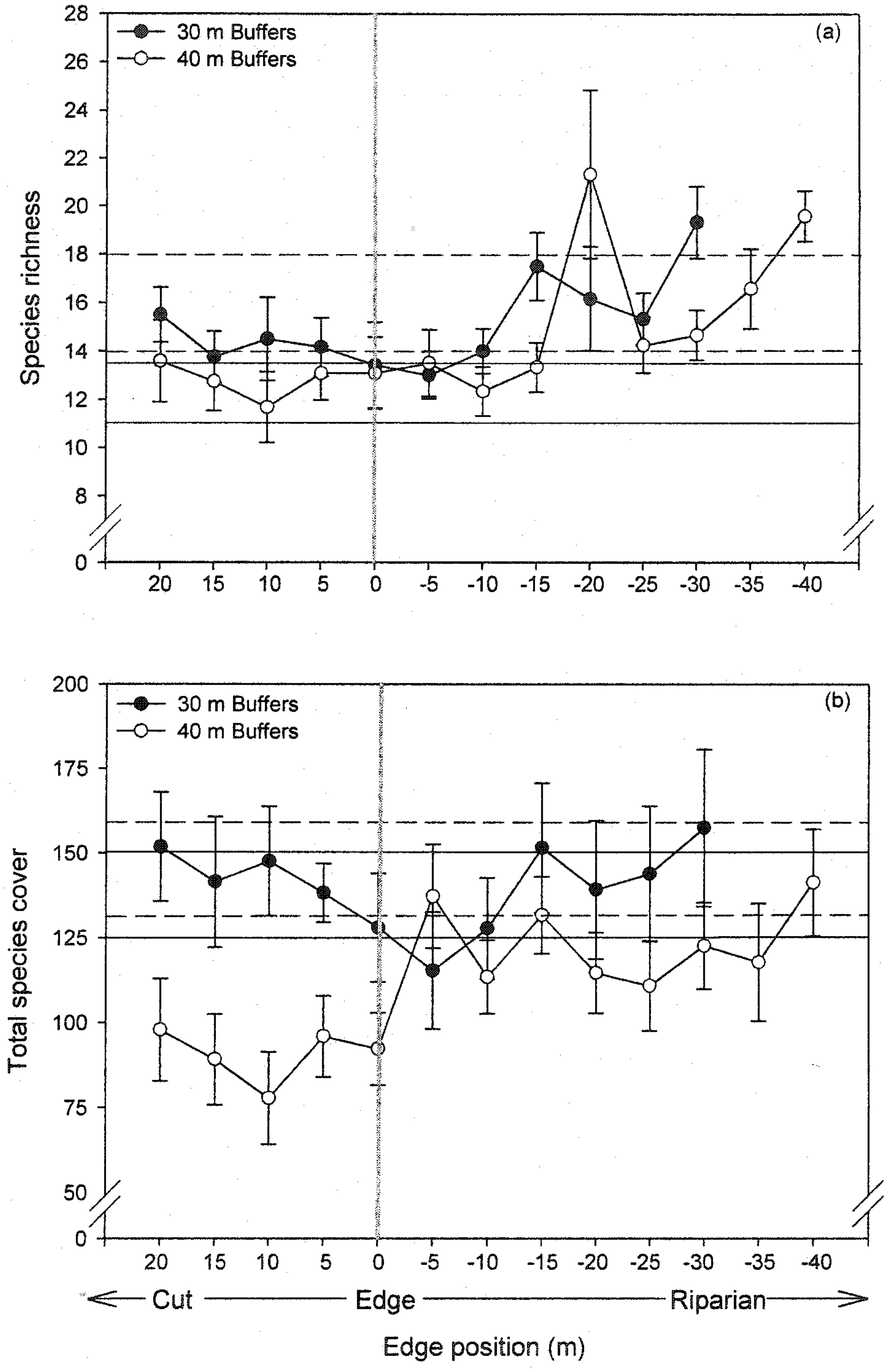


Figure 15. Mean species richness (a) and mean total species cover (b) at wide (40 m) and narrow (30 m) buffers in comparison to undisturbed stream edge conditions. Undisturbed upland (solid line) and riparian (dashed line) conditions are represented as critical values. Significant values are those occurring outside of the critical values and bars represent mean ±1 SE. The grey solid line represents the upland buffer edge.

Individual species cover

Individual species cover at each edge location in both narrow and wide buffers was compared with all three sets of the reference data (Appendix IX & X). Compared to the entire undisturbed transect (reference values 1), species with a higher abundance across the entire width of narrow buffers were tall and low-growing shrubs, grasses, sedges and weedy shade-intolerant herbs. Species with a lower abundance across the entire width of narrow buffers were mosses and shade-tolerant shrubs and herbs. Across the entire width of the buffer, a lower abundance of moss species, shade-tolerant herbs and conifer saplings were observed. Compared to reference values 1, all species had a unidirectional response (i.e. either higher or lower abundance) at narrow buffers with the exception of the bryophyte spp. group, which had lower abundance in the clearcut and higher abundance at the stream edge. At wide buffers, however, five species had a bi-directional response (i.e. both higher and lower). *Mertensia paniculata* and *Rubus pubescens* had a higher abundance in the clearcut and a lower abundance in the riparian area. *Coptis trifolia, Cornus canadensis* and *Pleurozium schreberi* had a lower abundance in the clearcut and a higher abundance in the riparian area.

Compared to the upland portion of the undisturbed transects (reference values 2), narrow buffers had a higher abundance of deciduous saplings, grasses and shade-intolerant weedy herbs in the clearcut. Shade-intolerant herbs and *Lycopodium dendroideum* had a lower abundance in the clearcut. In the clearcut at wide buffers, tall and low-growing shrubs, poplar saplings, and weedy shade-intolerant herbs had a higher abundance and *Lycopodium* spp. had a lower abundance.

Compared to the riparian portion of the undisturbed transects (reference values 3), species with a higher or lower abundance in the riparian area of narrow buffers were mostly common riparian species (e.g. *Salix* spp., Thalose liverworts, *Mentha arvense, Caltha palustris, Anemone quinquefolia* and *Climacium dendroides*). Species with a high and low abundance in the riparian area at wide buffers were similar to those at narrow buffers and were primarily common riparian species (e.g. *Lonicera villosa, Rhamnus alnifolia, Circaea alpina, Alnus incana, Thalictrum dasycarpum* and the Leafy liverworts).

Upland/Riparian dynamics

Narrow buffers had 78 species and wide buffers had 62 species with a significant DEI compared to the entire undisturbed transect (reference values 1). Narrow buffers had eight species and wide buffers had 15 species with a significant DEI compared to only upland (reference values 2) or only riparian (reference values 3) areas. Therefore, 91% (narrow buffers) and 81% (wide buffers) of species with a significant DEI had abundance values that were different from any location across undisturbed stream edges.

There were 25 species at narrow and wide buffers that were not found at undisturbed stream edges, 15 of which had a significant DEI. The upland area (20 to –10 m) of narrow buffers had the highest number of "foreign" species (Table 12).

In both wide and narrow buffers a large number of species had a significantly higher abundance, whereas relatively few species had a significantly lower abundance compared to the undisturbed stream edge (Figure 16). Both buffer widths had a similar pattern in the number of species with a significant DEI across the buffer. The clearcut and riparian area had a much higher percentage of species showing an edge effect compared to the buffer interior.

Table 12. The number and percentage of species with a significant DEI found exclusively at narrow and wide buffers. *Percentage is determined by dividing the number of "foreign" species with a significant DEI by the total number species with a significant DEI showing the same trend (higher or lower cover) at the same buffer location.

Buffer width (m)	Buffer location	Number of species with a significant DEI not found in undisturbed stream edges	Percentage of species per location with a significant DEI not found in undisturbed stream edges*
40	Entire buffer	1	14
	Upland area	2	18
	Riparian area	2	8
30	Entire buffer	1	6
	Upland area	7	30
	Riparian area	2	8

Compared to wide buffers, narrow buffers had more species with a significantly higher abundance across the entire buffer and differences were most pronounced in the clearcut and riparian areas (Figure 16a). Wide buffers had a slightly more species with a significantly lower abundance across the entire buffer (Figure 16b).

Ecotonal indicators

Compared to the undisturbed condition, *Bromus ciliatus* was the only species with a significantly higher abundance across the entire width of narrow and wide buffers (Table 13).

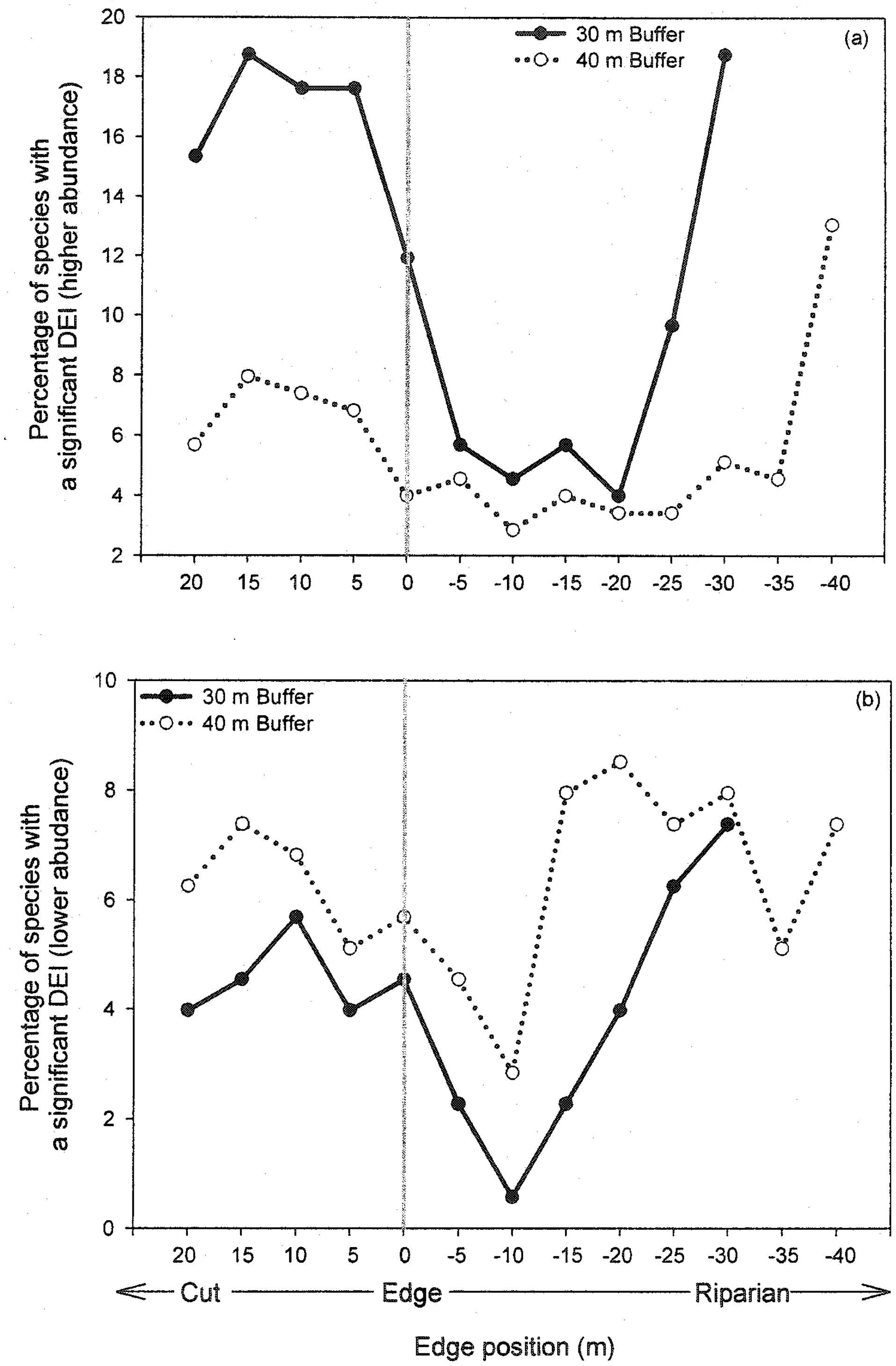


Figure 16. Percentage of species with a significant DEI due to higher (a) or lower (b) abundance at wide (40 m) and narrow (30 m) buffers. The grey solid line represents the upland edge of the buffer.

Table 13. Species with a significant DEI at both narrow (30 m) and wide (40 m) buffers. The response at different widths indicates a significantly higher (+) or lower (-) abundance.

Response at different buffer widths	Species with a significant DEI at both buffer widths	Edge location of significant increase and/or decrease in abundance
40 m Buffer (+)	*Bromus ciliatus*	Upland and Riparian
30 m Buffer (+)		Upland and Riparian
40 m Buffer (-)		Upland and Riparian
30 m Buffer (-)	*Acer spicatum*	Upland and Riparian
	Cladina spp.	
	Dicranum spp.	
40 m Buffer (-)	Bryophyte spp. group	Upland and Riparian
30 m Buffer (-, +)		Upland and Riparian
40 m Buffer (+, -)	*Mertensia paniculata*	Upland and Riparian
30 m Buffer (+)		Upland only
40 m Buffer (-, +)	*Rubus pubescens*	Upland and Riparian
30 m Buffer (-)		Upland only
40 m Buffer (+)	*Epilobium angustifolium*	Upland only
30 m Buffer (+)	*Oryzopsis asperifolia*	Upland only
	Populus spp.	
	Pinus banksiana	
	Picea glauca	
40 m Buffer (-)	*Lycopodium dendroideum*	Upland only
30 m Buffer (-)		Upland only
40 m Buffer (+)	*Prunus pensylvanica*	Upland only
30 m Buffer (+)	*Rubus idaeus*	Upland and Riparian
	Taraxacum spp.	
40 m Buffer (-)	*Lycopodium annotinum*	Upland only
30 m Buffer (-)		Upland and Riparian
40 m Buffer (+)	*Aster puniceus*	Riparian only
30 m Buffer (+)	*Aster umbellatus*	Riparian only
	Lonicera villosa	
	Salix spp.	
	Glyceria striata	
	Pyrola spp.	
	Sagittaria cuneata	
	Viburnum edule	
40 m Buffer (-)	*Anemone quinquefolia*	Riparian only
30 m Buffer (-)		Riparian only
	Corylus cornuta	
	Leafy liverwort group	
	Streptopus roseus	
40 m Buffer (+)	*Carex aquatilis*	Riparian only
30 m Buffer (+)		Upland and Riparian

Across the entire width of both narrow and wide buffers, *Acer spicatum, Cladina* spp., and *Dicranum* spp. had significantly lower abundance. The bryophyte spp. group had a lower abundance in the clearcut and a higher abundance at the stream edge of narrow buffers, but a lower abundance across the entire width of wide buffers. *Rubus pubescens* and *Mertensia paniculata* had a bi-directional response (i.e. both higher and lower abundance) in wide buffers, but only a lower or higher abundance in the upland of narrow buffers. *Prunus pensylvanica, Rubus idaeus* and *Taraxacum* spp. had a higher abundance and *Lycopodium annotinum* had a lower abundance across the entire width of narrow buffers, but at wide buffers the response for these species was confined to the upland area.

Compared to the undisturbed condition, *Populus* spp., *Pinus banksiana, Picea glauca, Epilobium angustifolium* and *Oryzopsis asperifolia* had a significantly higher abundance in the upland area at both narrow and wide buffers. At both buffer widths *Lycopodium dendroideum* was the only species with a significantly lower abundance in the upland area. Two *Aster* spp., *Lonicera villosa* and *Salix* spp. had higher abundances and *Anemone quinquefolia, Corylus cornuta* and the leafy liverworts had lower abundances in the riparian area at wide and narrow buffers compared to the undisturbed condition.

Spatial pattern analysis

The species selected for pattern analysis were those identified as ecotonal indicators (Table 13). Results from the split moving window analysis supported the findings of the critical values approach

Moving window analysis conducted with the 6 m window resulted in a similar pattern to that resulting from analysis using a 16 m window. The pattern was highly variable in the 6 m window, however, making detection of the area of maximum change difficult (Figure 17). The 16 m window was chosen as the optimum window size based upon an investigation of the pattern and the length of the sampling transect.

Epilobium angustifolium had a significant DEI with a higher abundance in the upland area at both buffer widths compared to undisturbed stream edges. The maximum change in abundance occurred at the clearcut edge in wide buffers and 5 m past the clearcut edge in narrow buffers (Figure 17b). There was also a second area of maximum change in narrow buffers at the upland-riparian transition.

Bromus ciliatus showed a similar pattern in both wide and narrow buffers with the maximum amount of change coinciding with the clearcut edge, and a secondary peak in change occurring at the respective riparian-upland ecotones (Figure 18a). At both buffer widths, *Lonicera villosa* and *Aster umbellatus* had a significant DEI in the riparian area and showed a similar response in the split moving window analysis with a maximum change in abundance at the riparian-upland transition (Figure 18b & c).

The bryophyte spp. group, *Carex aquatilis, Rubus idaeus* and *Taraxacum* spp. had different responses in narrow buffers than in wide buffers (Figure 19). At narrow buffers, maximum changes in abundance were found at both the clearcut edge and riparian-upland transition. At wide buffers, the maximum change for *Carex aquatilis* and the bryophyte spp. group occurred only in the riparian area, corresponding with the areas where a DEI was detected. The area of maximum change for *Rubus idaeus* and *Taraxacum* spp. occurred at the clearcut edge of wide buffers, which also corresponds with the areas where a significantly higher abundance was detected.

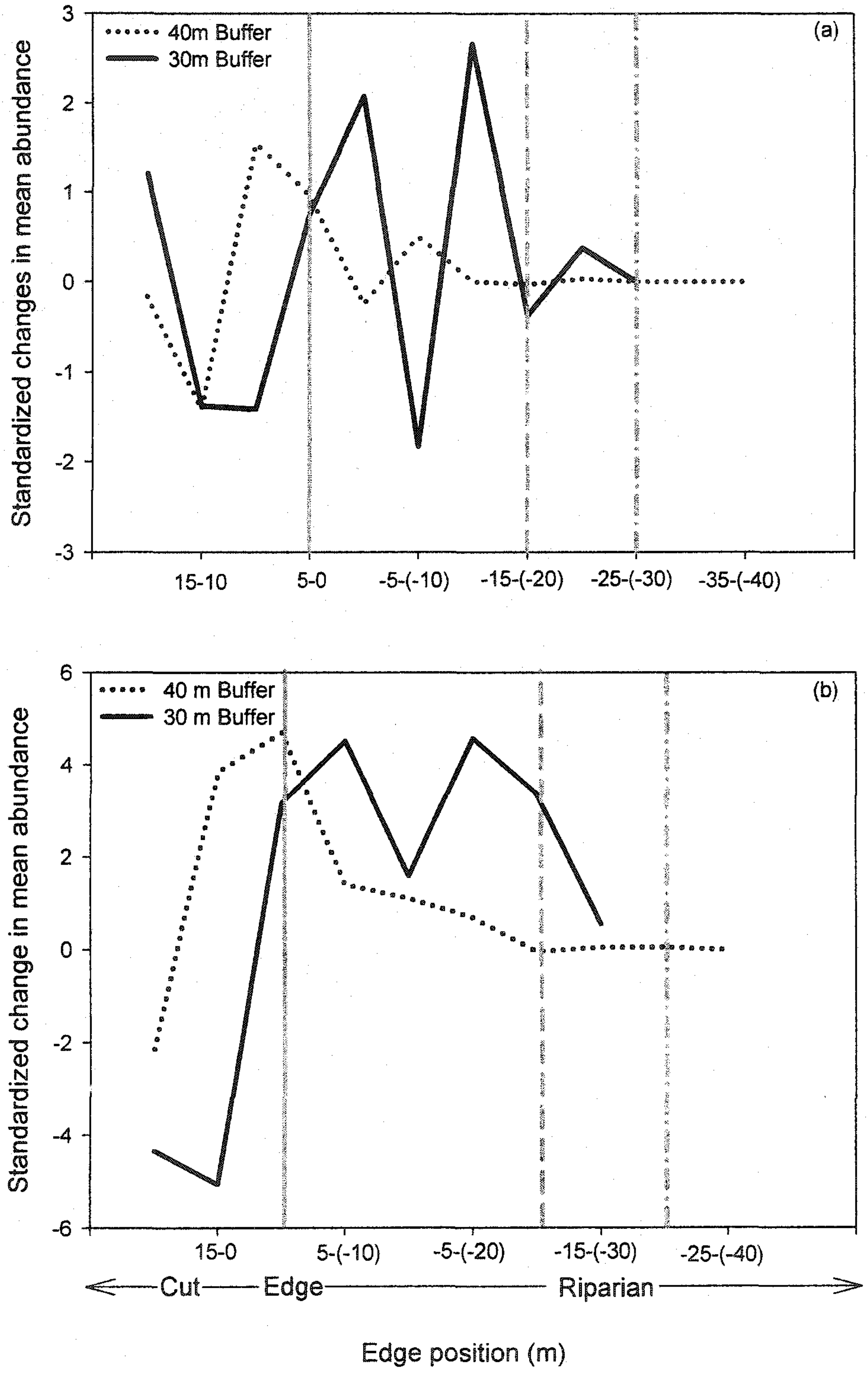


Figure 17. Changes in the mean abundance of *Epilobium angustifolium* across wide (40 m) and narrow (30 m) buffers detected in a splitting moving window analysis with a 6 m window (a) and 16 m window (b). The grey lines represent upland buffer edge (solid), the riparian-upland transition at narrow buffers (dashed) and the riparian-upland transition at wide buffers (dash-dot).

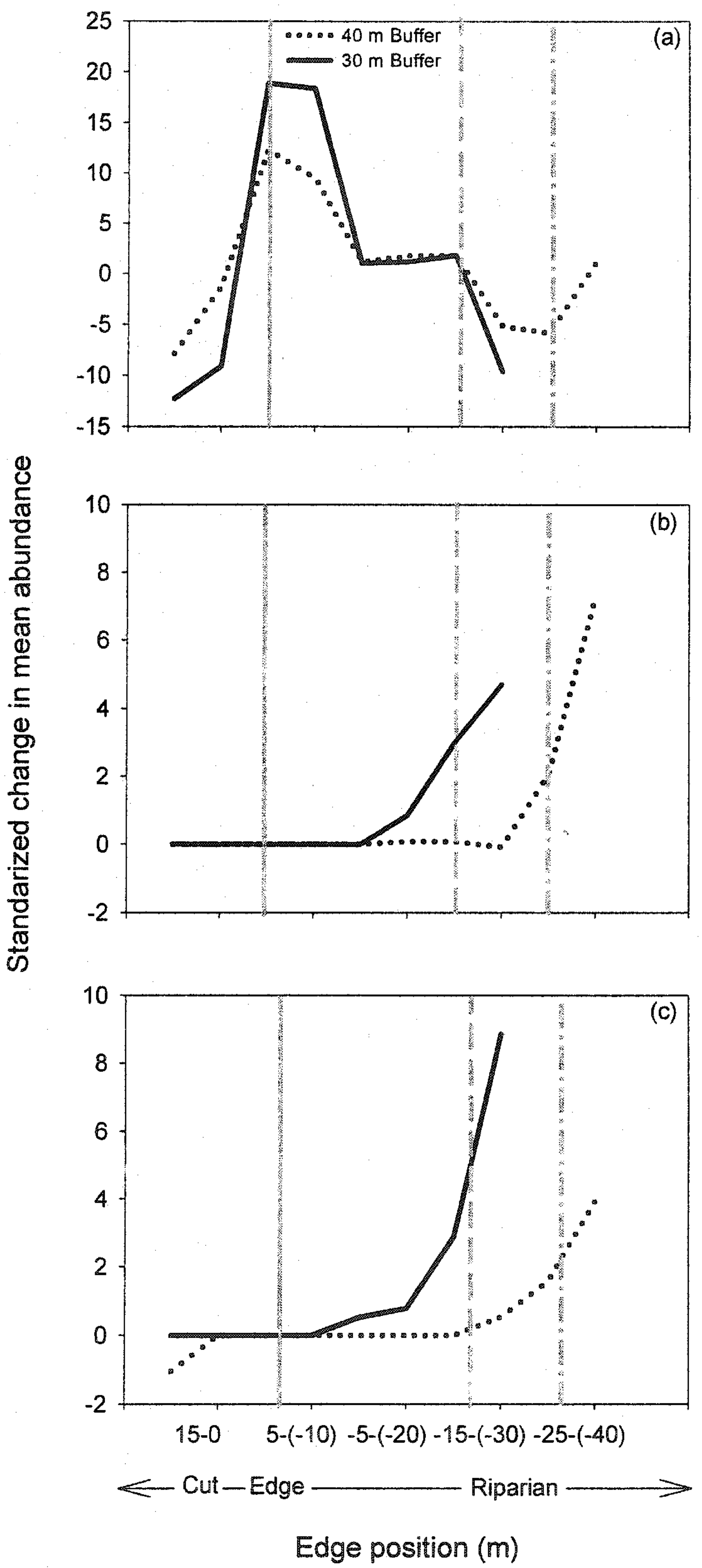


Figure 18. Changes in the mean abundance of *Bromus ciliatus* (a) *Lonicera villosa* (b) and *Aster umbellatus* (c) across wide (40 m) and narrow (30 m) buffers detected in a splitting moving window analysis (16 m window). See Figure 16 for details.

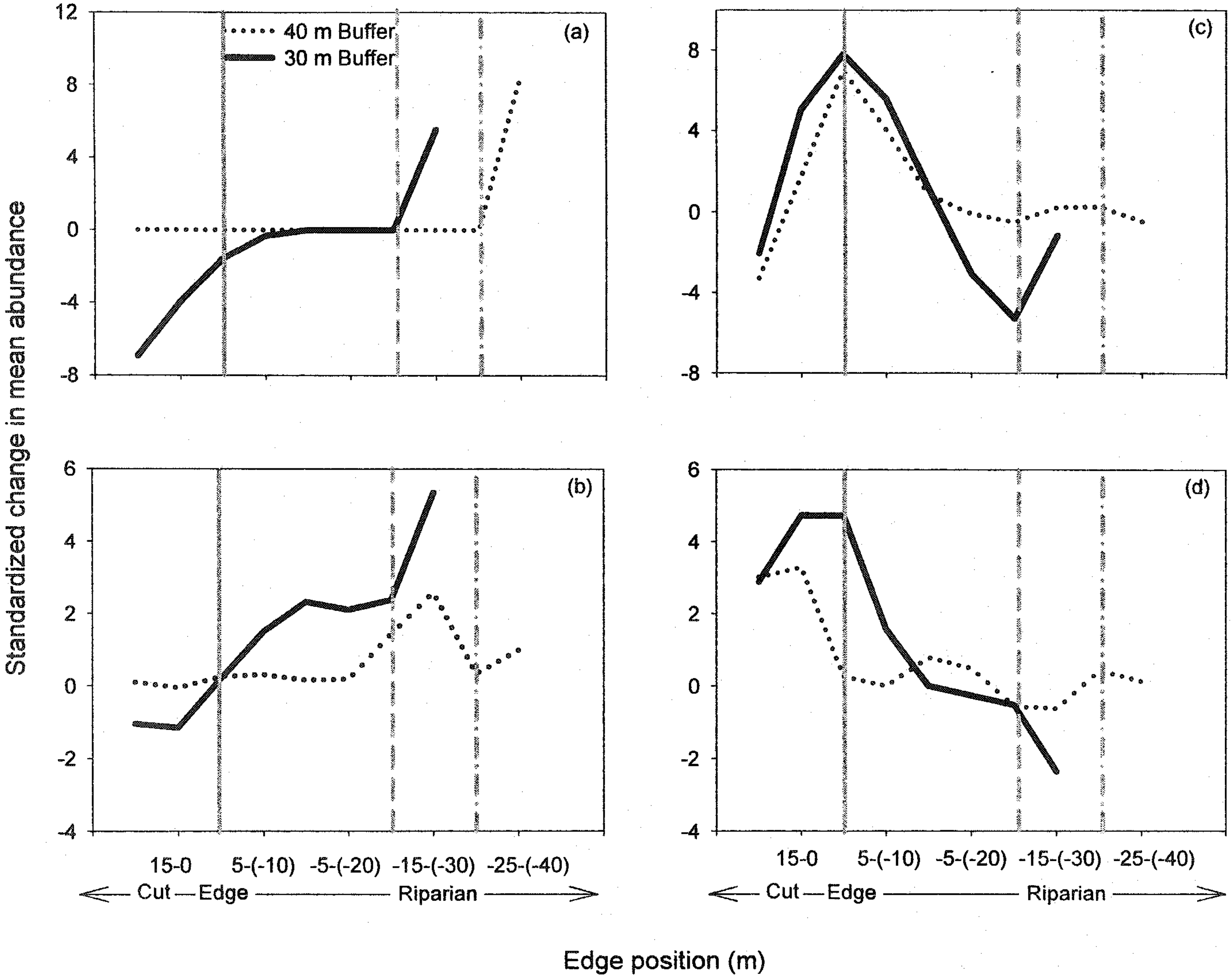


Figure 19. Changes in the mean abundance of *Carex aquatilis* (a), bryophyte spp (b), *Rubus idaeus* (c) and *Taraxacum* spp. (d) across wide (40 m) and narrow (30 m) buffers detected in a splitting moving window analysis (16 m window). See figure 16 for details.

Discussion

The vegetation structure and composition of wide and narrow buffers showed a response to both the clearcut edge and the upland-riparian transition. Narrow buffers had greater structural canopy damage compared to wide buffers. Both wide and narrow buffers were characterized by shifts in understory species composition in the clearcut area and changes in the abundance of riparian species in the riparian area compared to the undisturbed condition. Several weedy shade-intolerant species occurred only at buffer sites. Narrow buffers had a larger number of "foreign" species and more species with a significantly higher abundance than wide buffers. A number of species that had a significant DEI were also identified as ecotonal indicators through the SMW analysis. Changes were detected in bryophyte spp., *Carex aquatilis*, *Rubus idaeus* and *Taraxacum* spp. at both the clearcut edge and the upland-riparian transition in narrow buffers, but only at the clearcut edge of wide buffers.

Characterizing buffer edges

Canopy structure and composition

Differences in canopy structure and composition between wide and narrow buffers are crucial in determining the microclimatic conditions at stream edges and the understory species composition in buffers. Compared to the undisturbed condition, this study found lower canopy cover, a greater number of fallen trees and larger snags at the clearcut edge and up to 20 m past the edge, which is similar to the findings of other studies (Chen *et al.,* 1992; Burton, 2002; Harper & Macdonald, 2002). In narrow buffers, the DEI for these structural variables occurred across the entire buffer. Removal of trees increases solar radiation and air turbulence, which elevates temperature and wind speed and decreases relative humidity (Geiger, 1965; Brosofske *et al.,* 1997). Therefore, greater structural damage at narrow buffers likely results in warmer, drier and windier conditions, which may account for the greater number of understory species with a DEI across the entire buffer width.

High canopy openness may play an important role in the long-term dynamics of riparian buffers. Windthrow and increased rates of tree senescence may lead to the rapid development of shrub-dominated communities, which in turn may suppress future tree regeneration (Hibbs & Giordano, 1996). In this study, compared to undisturbed stream edges, wide buffers had a lower abundance of *P. mariana* and *A. balsamea* saplings indicating restricted tree regeneration.

Site-to-site variation most likely accounts for the higher canopy cover from 15-20 m past the edge, the higher stem density from 0-20 m and the higher dbh of *P. mariana* across the entire width of large buffers. A number of compositional changes may also be related to site differences. The compositional differences in *P. balsamifera* and *P. glauca*, however, are more likely due to a high rate of growth and recruitment in the more open environment across narrow buffers. Under the relatively closed canopy condition at wide buffers these processes are limited to the clearcut edge or 20 m past the clearcut edge.

Understory species response

Compared to wide buffers, narrow buffers had higher richness and total cover, which is most likely due to site differences. A larger number of the wide buffer edges were less than five years old, so lower richness and cover may be expected due to less time for regeneration at these sites.

Understory species with a significant DEI at the clearcut edge of wide and narrow buffers were similar to species with a significant DEI at conifer clearcut edges reported in Chapter 1. Compared to the upland conditions at undisturbed stream edges, a higher abundance of deciduous saplings (e.g. *Populus* spp.), tall shrubs (e.g. *Prunus pensylvanica*), low-growing shrubs (e.g. *Rubus idaeus*), grasses (e.g. *Bromus ciliatus* and *Oryzopsis asperifolia*) and shade-intolerant herbs (eg. *Hieracium caespitosum, Anaphalis margaritacea,* and *Taraxacum* spp.) occurred in the clearcut area of both wide and narrow buffers. Adaptation to disturbance allows these species to rapidly colonize and persist in the clearcut. Perhaps more importantly, at narrow buffers some shade-intolerant shrubs (eg.. *R. idaeus*) and herbs (e.g. *Taraxacum* spp. and *Vicia americana*) were able to persist across the entire width of the buffer, which may indicate disturbed conditions across the buffer.

Compared to the undisturbed condition, mosses, such as *Dicranum* spp. (both buffer widths), *Pluerozium schreberi* (narrow buffers) and *Ptilium crista-castrensis* (narrow buffers) had a lower abundance across the entire buffer, which may be indicative of low relative humidity and increased light in the buffers. Mosses that rely on humid air are especially sensitive to microclimatic change (Dong *et al.,* 1998; Hylander, 2002). A lower abundance in shade-tolerant herbs, such as *Coptis trifolia* (narrow buffers) and *Trientalis borealis* (wide buffers), across the entire buffer further supports high light conditions.

Shrubs, such as *Salix* spp., *Viburnum edule* and *Rhamnus alnifolia*, had a higher abundance in the riparian area of buffers than in undisturbed riparian areas. Increased light, temperature and moisture may initiate increased growth and suckering at the riparian edge. Most of the species that had a significant DEI at riparian edges were characteristic of the riparian community (e.g. *Thalictrum dasycarpum, Lyocopus uniflora, Circaea alpina, Sagittaria cuneata*) suggesting that species abundance rather than species composition was altered in the riparian area of buffers. Lamb *et al.,* (2003) also found riparian species, such as *Aster puniceus*, *Eupatorium maculatum*, *Gallium triflorum*, *Lycopus uniflora* and *Scutellaria galericulata* had a higher abundance near streams.

Upland-riparian dynamics

The use of multiple reference data sets not only ensured that buffer data were compared with a representative undisturbed condition, but also provided insight into the upland-riparian dynamics across buffers.

Of the species with a significant DEI, more than 80% were significantly different than reference values that included both upland and riparian areas and reference values for those areas alone. The high percentage of species with a significant DEI, therefore, is not an artifact of the manner in which reference data were divided.

Comparison of the critical values allowed for detection of changes in both species composition and abundance. Floristic composition and dominance (abundance) changes provide complementary information on the vegetation dynamics at ecotones (Delcourt & Delcourt, 1992; Fortin, 1997). The presence or absence of species can be used to indicate a transition zone marked by the co-occurrence of species physiological limits, while changes in abundance correspond more to an ecotone where species are responding to microclimatic change (Fortin, 1997). There were 25 "foreign" species that were found only at buffer sites, more than 60% of which were found in the clearcut area. Hibbs & Giordano (1996) had similar results with 52 herbaceous species found on undisturbed sites and 97 on buffer sites, 22 of which were unique to buffer sites. The high percentage of foreign species in the clearcut area at narrow (30%) and wide (18%) buffers is indicative of a compositional shift in the disturbed upland areas. The riparian area of narrow and wide buffers, however, appears to be better characterized by shifts in species abundance. The microclimatic changes at clearcut edges may be much more extreme, exceeding the tolerance ranges of some species, whereas changes in the riparian area may be a more subtle response to microclimatic gradients.

Riparian communities are often disproportionately species rich in comparison to upland communities (Naiman *et al.,* 1993; Naiman & Decamps 1997; Hylander, 2002). In this study, the riparian reference values for understory species richness and total cover were higher than upland reference values. In addition, 52% of the critical values for individual understory species were twice as high in the riparian area as in the upland area. Other studies have also found cutbank edges and riparian forests to be more complex and compositionally different from interior forest (Kupfer & Malanson, 1993; Harper & Macdonald, 2001). High complexity and diversity associated with riparian communities is a reflection of the coincidence of multiple disturbance histories. Species are distributed as a result of fluvial disturbance regimes including periodic flooding, river currents, ice scouring, hillslope failure, and nonfluvial disturbance regimes including fire, wind, plant disease and insect outbreak (Holt et al, 1995; Gregory et al, 1991; Pabst & Spies, 1998).

Distribution of riparian species is further complicated by their relative tolerance to continuously saturated soils, competition for germination sites and shade tolerance (Pabst & Spies, 1998).

The peak in diversity observed at 15 and 20 m past the edge in narrow and wide buffers respectively is most likely characteristic of the upland-riparian ecotone. The dominant species (> 3%) at these locations commonly occur in the upland understory, for example, *Cornus canadensis, Maianthemum canadense, Ledum groenlandicum* and *Pleurozium schreberi*. A number of riparian species (e.g. *Alnus incana, Aster umbellatus, Lonicera villosa*) were also found 15 to 20 m past the edge. Inherent edges may support higher richness than adjacent communities (Leopold, 1933; Petts, 1990); however, induced edges may be better explained by richness being more similar to one of the adjacent community (Lloyd *et al.*, 2000).

The increase in diversity and the number of species with a significant DEI at the riparian edge was not a result of invasive species from the clearcut colonizing the riparian zone, but was primarily due an increased abundance of riparian species themselves. Rapid decline in the percentage of species with a significant DEI at the clearcut edges suggests invasive species may be limited in their ability to penetrate buffer strips.

Riparian edges resembled earlier successional habitats with riparian species adapted to frequent disturbance (Kupfer & Malanson, 1993). The inherent highly competitive nature of riparian plants may limit the potential invasion of upland species associated with the clearcut. For example, open habitats, such as floodplains, have been suggested as one of the original habitats of weedy plants prior to anthropogenic modification of the forest landscape in North America (Marks, 1983). In addition, riparian habitats commonly include species associated with both the upland and hydric soils and may be a major source of most plant colonists throughout the landscape (Gregory *et al.*, 1991).

Brosofske *et al.*, (1997) suggested that the amount of solar radiation in the riparian zone is primarily affected by overstory canopy, however, narrower buffer widths may provide an additional inlet, increasing light levels near the stream. As buffers widen, the amount of solar radiation able to penetrate the canopy would decrease. In this study higher light levels in the riparian area are likely due to the greater potential for light penetration at narrower buffers coupled with the structural canopy damage. The interacting processes of facilitation and tolerance in the riparian zone may account for the higher richness and abundance in buffers (Figure 19). Increased light may allow different species to prosper (facilitation), while existing species are able to continue growth after the initial microclimatic change (tolerance) (Finegan, 1984; Kuper & Malanson, 1993).

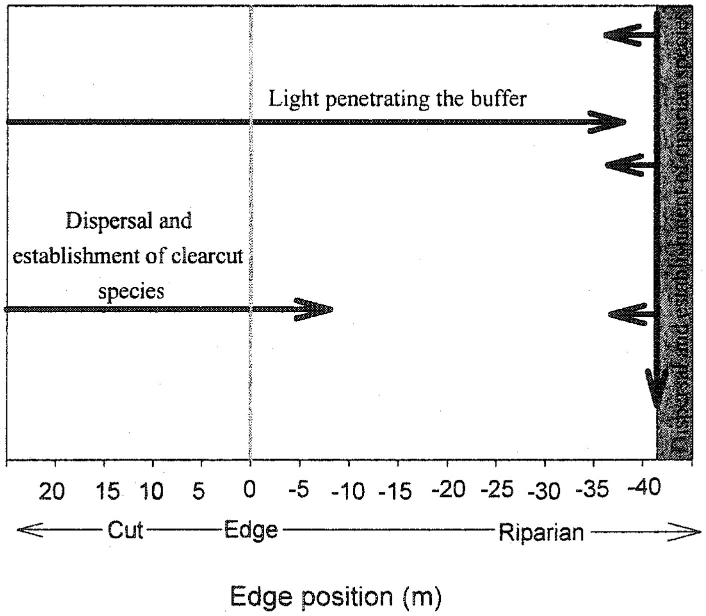


Figure 20. Increased abundance of riparian species in the riparian zone at buffer sites due to higher light conditions and dispersal and establishment of clearcut species at the upland buffer edge (solid grey line).

Ecotonal indicators

Species with a significant DEI at both buffer widths are perhaps most useful in describing the boundary dynamics. Underlying processes at edges including the interactions between boundaries can be investigated through the coincidence or discrepancies in the location of boundaries delineated by different species (Forman & Godron, 1986; Holland *et al.,* 1991; Fortin, 1997; Fortin 1999). In this study, the similarities and differences in the response of species at the different buffer widths was used to investigate how buffer width may be affecting the clearcut edge and upland-riparian ecotone dynamics.

Cornelius and Reynolds, (1991) suggested that split moving window analysis (SMW) will detect discontinuities even within random data at both large and small scales. Therefore, additional objective methods are necessary for determining statistical significance. Only species with a significant DEI at both buffer widths were used in the SMW, which allowed for a comparison of the two methods and ensured that the changes detected in the SMW were verified by an objective statistical test (i.e. the critical values approach).

Ecotones are observed at multiple scales; therefore the comparison of boundaries detected at different spatial scales is necessary in determining ecotone dynamics (Gosz, 1993; Fortin, 1999). Comparison of the 6 and 16 m windows used in this study revealed a similar pattern. Due to a higher level of noise in the 6 m window, however, the 16 m window was predominately used to investigate edge dynamics.

The area of maximum change for *Epilobium angustifolium* occurred in the upland for both buffer widths and coincides with the area where a significant DEI was detected.

The SWM provides more detailed information regarding the edge dynamics; for example, the edge is located 5 m further past the clearcut edge at narrow buffers. The different delineation of edge may be related to the greater amount of structural damage and associated microclimatic changes at narrow buffers. In addition, the SMW indicates a second edge in narrow buffers, which is likely related to the upland-riparian transition. This second edge may not have been detected through the critical values approach because it was not abnormal in comparison to the ecotonal conditions found at undisturbed upland-riparian ecotones. *Bromus ciliatus* primarily responded to the clearcut edge, but also indicated a response to the upland-riparian transition at both buffer widths. *B. ciliatus* had a significant DEI in both the upland and riparian area at narrow and wide buffers. Therefore, the response detected in the SMW likely indicates higher abundance under disturbed conditions due to migration from the clearcut to the riparian area.

Most species with a significant DEI only at the upland-riparian ecotone are absent or have a very low abundance in both the upland and riparian areas of the buffer. In the SMW, therefore, very little change occurred across the buffer until the upland-riparian transition is reached, where a dramatic change occurred. High light and/or temperature conditions at the riparian ecotone may account for the increased growth and recruitment of riparian species, such as *Lonicera villosa* and *Aster umbellatus*.

Species that have a bi-directional DEI response (i.e. higher and lower abundance) indicate how the upland and riparian edges differ. At narrow buffers the lower abundance of bryophytes at the clearcut edge was most likely due to reduced relative humidity, and high light and temperature conditions. Higher abundance of bryophytes at the riparian ecotone may not only be the result of optimal growing conditions with increased light but also the maintenance of high soil moisture and relative humidity.

Compared to narrow buffers, wide buffers had a larger number of species with a bi-directional response. The hotter and drier microclimate of the clearcut edge may not penetrate the entire width of wide buffers, leading to more variable conditions and a stronger expression of the riparian ecotone. In addition, there were a number of species with a significant DEI across the entire width of narrow buffers, but in wide buffers these species showed a significant response only in the upland or riparian areas.

Bryophytes and *Carex aquatilis* had a significant DEI and a high rate of change across the entire width of narrow buffers, whereas these parameters were only met in the riparian area at wide buffers. The high canopy density and low structural damage at wide buffers may maintain conditions more suitable for bryophytes and discourage the dispersal of riparian plants beyond the riparian-upland transition.

Rubus idaeus and *Taraxacum* spp. had similar DEI and SMW response at the clearcut edge of both buffer widths. At narrow buffers, however, high rates of change and significantly higher abundance were also found in riparian areas. Wide buffers may more effectively ameliorate clearcut microclimatic conditions in the buffer, whereas narrow buffers may be less able to ameliorate clearcut conditions before gradients are further influenced by the microclimatic conditions of the riparian area. Edge effects appear to be compounded in narrow buffers due to stronger interactions between the clearcut edge and riparian ecotone.

Management recommendations

Management strategies have tended to focus on specific habitats rather than the boundaries between habitats; therefore, the development of management strategies that directly address boundary dynamics is a relatively new challenge (Risser, 1990). As suggested by Brosofske *et al.,* (1997) multiple factors must be considered when determining the appropriate buffer width.

The high level of inherent variation in riparian habitats makes the detection of significant changes difficult. In addition, site-to-site variation appears to play a significant role in species response to harvesting in the upland. For example, sites with a higher canopy density may not require the same width of buffer as sites with a more sparse canopy.

Small-scale changes across buffers must be viewed in the context of watershed level disturbance. Broader perspectives that incorporate the relative importance of large-scale disturbance and give precedence to maintaining hydrological connectivity and viable riparian corridors are necessary (Naiman *et al.,* 1993).

The function of riparian buffers must be considered when determining the appropriate width. This study suggests that 30 m buffers may allow for the maintenance of understory composition representative of undisturbed riparian areas, but may not effectively mitigate microclimatic change leading to changes in riparian species abundance at the stream edge. A distance of > 40 m may be required for the amelioration of microclimatic gradients penetrating the buffer from the clearcut edge. Riparian species do not appear to be threatened by harvesting in the upland, however, undisturbed upland forest conditions were not maintained in narrower buffers. If buffers are to maintain undisturbed upland forest, the current minimum buffer width needs to be increased.

Buffers may play an important role in the protection of fish habitats and stream water quality, however, there is no natural analogue for riparian buffers. The boundaries of fire disturbance are related to soil moisture and landscape topography rather than a given distance from the stream. Therefore, in the context of forest management practices that aim to emulate natural disturbance patterns, buffers may not be justified (Macdonald *et al.*, 2004). Undisturbed upland forest may be more effectively preserved in adequately sized retention patches that are placed on the landscape in a manner that emulates natural fire behaviour.

Chapter 3

Habitat conditions across small stream buffers in northwestern Ontario as indicated by bryophyte response to microclimatic change

Abstract

Edge effects in riparian buffers are complex due to the presence of microclimatic gradients in response to the upland clearcut edge and the stream edge. Buffers are an important aspect of forest management in the boreal forest, although little is known about the habitat conditions within buffers. The objective of this study was to determine the influence of edge effects on the maintenance of undisturbed conditions in 40 m buffers with respect to microclimatic conditions and the biological response of two bryophyte species (*Hylocomium splendens* and *Polytrichum commune*). Both bryophyte species were transplanted into pots and placed at 10 m intervals along 60 m transects perpendicular to the stream across buffers and at undisturbed stream edges. Stem growth, cover and vitality were measured over a three month period in the summer 2003. Microclimate, shrub cover and understory cover were also assessed along each transect.

Bryophyte growth near the stream was similar at both buffers and undisturbed stream edges. However, differences in moss growth and vitality were detected in buffers up to 20 m past the clearcut edge. Relative humidity was the most important factor for *H. splendens* growth, whereas, soil moisture was the most important factor for *P. commune* growth. This study suggests that management guidelines need to incorporate edge effects if they aim to maintain a given amount of undisturbed forest along shorelines. Interior species that are sensitive to edge effects can be used as phytometers to monitor edge effects and biodiversity recovery following forest harvesting.

Introduction

Riparian areas (communities occurring between the open water and the upland forest) play a key role in many environmental processes and are a source of high species diversity. Effective riparian management therefore, is of great importance and encompasses many ecological issues relating to environmental quality and land use (Naiman *et al.,* 1993). Current guidelines regarding forest harvesting near streams in Ontario focus on the protection of aquatic ecosystems that support fish populations (Ministry of Natural Resources, 1988). The effect and function of strips of uncut forest that are maintained adjacent to open water (riparian buffers) to limit the impact of upland harvesting on water quality are poorly understood. Habitat conditions in riparian buffers must be assessed to develop management strategies that will ensure long-term protection of key ecological processes and species diversity (Hylander *et al.,* 2002).

In assessing the structure and dynamics of riparian forests there tends to be a bias towards vascular plants (Jonsson, 1997). Nonvascular species such as bryophytes, are an important component of the plant community in many forest ecosystems (Cooper, 1912; Longton, 1984, 1990; Jonsson, 1997). Most boreal landscapes have an abundance of well-developed moss communities in organic and inorganic soils with dominant conifer canopies (Weetman & Timmer, 1967; Longton, 1984; Vitt, 1990). Bryophytes enhance species diversity, add to forest biomass and production (Longton, 1990), and provide habitat and food for invertebrate and vertebrate species (Glime, 1978; Gerson, 1982; Jonsson, 1997). Due to the insulating properties of bryophytes, well-developed communities have a major impact on soil temperature and moisture. Bryophytes also influence nutrient cycling through nutrient interception and the subsequent release of nutrients to vascular plant roots via decomposition (Vitt, 1990; Bates, 1992). Bryophytes not only play a critical role within boreal forests, but also provide model organisms in studying community organization following disturbance (Grime *et al.,* 1990; Slack, 1990; Jonsson, 1997).

Bryophytes are often indicators of habitat conditions due to their unique life history strategies, physiological characteristics and strong response to microclimatic gradients. Using bryophytes as indicators, Hylander *et al.,* (2002) found that the current buffer strip width (10-15 m) in the boreal forest of Sweden can keep plants alive, but is insufficient to maintain natural growth conditions for riparian forest plants. However, Hylander *et al.,* (2002) did not examine fine-scale changes in bryophyte response associated with clearcut edges and the upland-riparian ecotone. Measuring of bryophyte growth response in relation to microclimatic conditions at intervals across the buffer width can provide in-depth information regarding edge effects and the habitat conditions in buffers. The environmental characteristics of ecotones are poorly understood and little is known about how these environmental characteristics affect the growth rates and habitat limits of many understory species including bryophytes (Busby *et al.,* 1978; Hylander *et al.,* 2002).

The main objective of this study was to determine the influence of edge effects on the maintenance of undisturbed conditions in 40 m buffers with respect to microclimatic conditions and the growth and vitality of two bryophyte species. Further objectives included i) examining how microclimatic factors and life strategies of bryophytes interact to influential bryophyte growth and vitality and ii) developing management suggestions for maintaining undisturbed habitat conditions and species diversity within riparian buffers.

Methods

Site selection

Four study sites were selected including two buffer sites and two undisturbed stream edges. All four sites were located in the southwest corner of the study area within approximately 10 km of each other. The two buffer sites were located in the Current river watershed and the two undisturbed sites were located in the Mackenzie river watershed (Figure 1). The study sites (EW1, EWC1, Hooks Rd. and Hooks Friend) were a sub-set of the buffer and undisturbed stream edge sites used in Chapter 1 (see Appendix I for exact site locations).

Between sites species composition, edge orientation and general site characteristics were similar (see Chapter 1 for study area description). All sites were in coniferous stands with a dominant *Picea mariana* canopy and had south-facing (± 45^{o}) clearcut edges and/or riparian-upland ecotones. The size of the riparian area (i.e. the area between the upland-riparian ecotone and the stream) was similar between sites (approximately 10 m) and all streams had a watershed area of approximately 1 km^2. Both Hooks Rd and Hooks Friend were clearcut during the winter of 2002.

The canopy at buffer sites consisted of dense *P. mariana* with scattered *Pinus banksiana* throughout. Undisturbed sites had more canopy openness with more *Abies balsamea* and a higher shrub cover in the riparian area. Continuous carpets of pleurocarpous mosses and common understory herbs, such as, *Cornus canadensis, Maianthemum canadense, Ledum groenlandicum* and *Clintonia borealis* were present in the upland understory of all sites. All of the study sites had a low-lying riparian area containing *Alnus incana, Lycopus uniflora*, *Carex* spp., *Equisetum sylvaticum* and

Sphagnum spp.. *Hylocomium splendens* and *Polytrichum commune* were also found growing naturally at the sites.

Study species

H. splendens and *P. commune* are widespread throughout Ontario and occur frequently within the study area (Ireland & Ley, 1992). During (1979), identified a number of bryophyte life strategies, two of which can be applied to the study species. *H. splendens* has a perennial stayer life strategy, due to a long life span and reduced reproductive effort. The perennial stayer strategy often occurs in later successional stages where the environment is relatively constant with regular fluctuations that are within the species tolerance range. *H. splendens* is a pleurocarpous upland boreal bryophyte and thrives under shaded habitat conditions, where canopy trees provide high humidity, low temperatures and an over-head source of nutrients (Tamm, 1953; Busby *et al.,* 1978).

P. commune has a colonist life strategy due to a moderately short life span and high reproductive effort. The colonist strategy often occurs in environments that are initially unpredictable, but likely to be maintained for a few generations. The underground stem with rhizoids, internal water conducting tissues and water loss resistant leaves allow *P. commune* to photosynthesize and grow in dry exposed conditions (Bayfield, 1973; Callaghan *et al.,* 1978). These strategies also facilitate the ability of *P. commune* to grow as individual shoots rather than in a dense carpet.

A number of studies have explored the response of *H. splendens* and *P. commune* to different environmental conditions (Weetman & Timmer, 1967; Bayfield, 1973; Busby *et al.,* 1978; Callaghan *et al.,* 1978; Vitt, 1990). In addition, the mean cover of *H.*

splendens and *Polytrichum* spp. (including *P. commune* and *P. juniperinum*) across all buffer sites in Chapter 1 were compared (Figure 21). *Polytrichum* spp. had a high abundance in the clearcut, whereas *H. splendens* had a high abundance in the buffer. Both exhibited similar cover and abundance near the stream edge. Selection of species with different strategies promotes an in-depth understanding of species response to disturbance conditions (i.e. microclimatic alterations) in buffers.

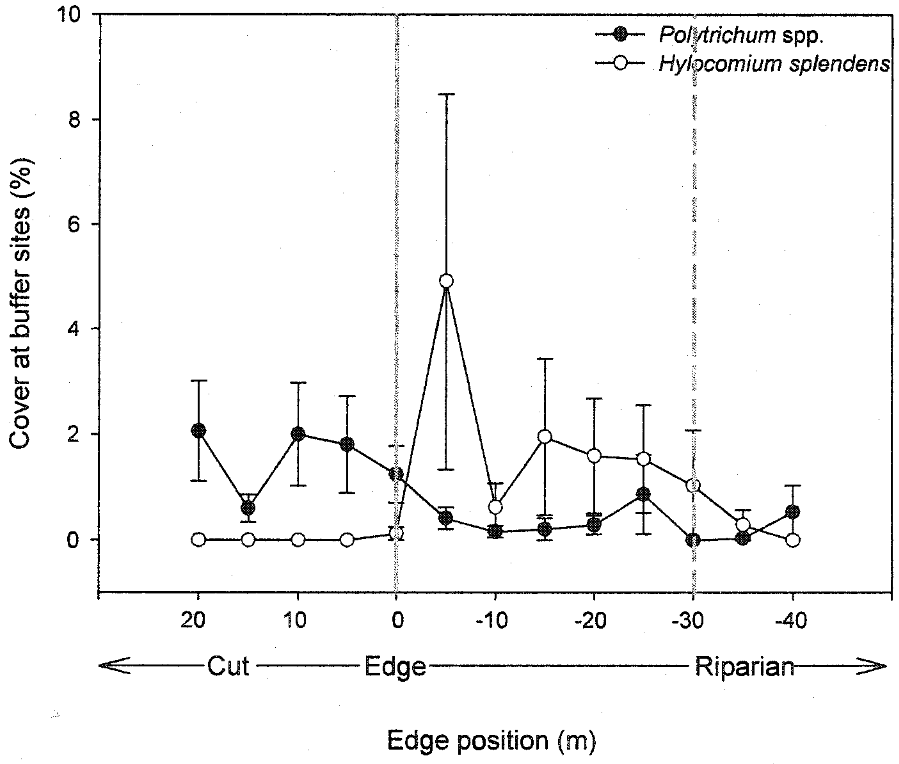


Figure 21. Mean cover of *H. splendens* and *Polytrichum* spp. across 24 buffer transects. The solid grey line represents the upland buffer edge and grey dashed line represents the riparian-upland transition. Bars represent mean ±1 SE

Experimental design

In this study there were two experimental treatments each with two sites: a disturbed riparian buffer condition and an undisturbed shoreline condition (Figure 22).

At each site three 60 m transects were located approximately 40 m apart, for a total of six transects per treatment. Transects were laid perpendicular to the buffer and/or stream edge. At the undisturbed sites, transects crossed 10 m into the riparian area and 50 m into the undisturbed upland forest. At disturbed buffer sites, the transects crossed 40 m into the buffers including the 10 m in the riparian area and 20 m into the clearcut.

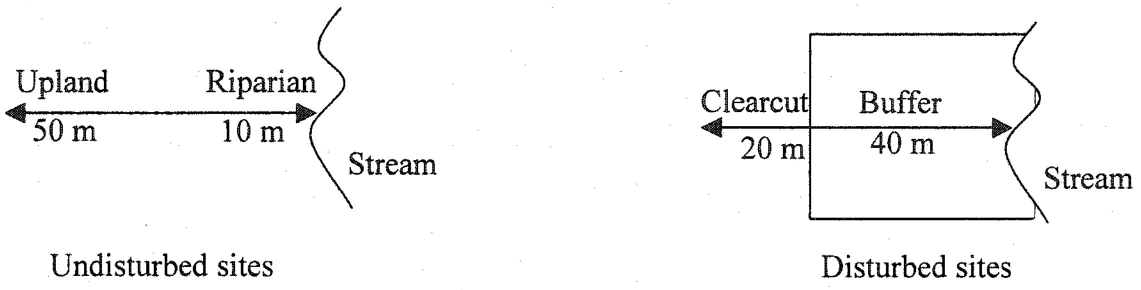


Figure 22. Transect location at undisturbed stream sites and disturbed buffer sites.

Two pots, one with five stems of *H. splendens* and one with five stems *P. commune* were placed at 10 m intervals along each transect (Figure 23).

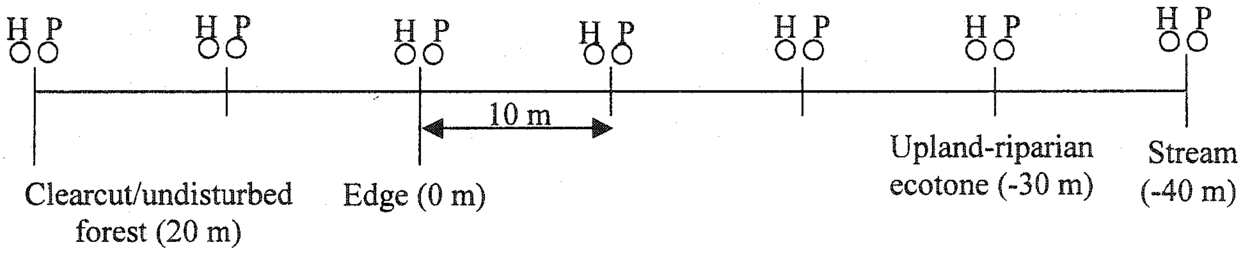


Figure 23. Transect located perpendicular to all edges with pots placed at 10 m intervals containing five stems of *H. splendens* (H) and five stems of *P. commune* (P) in each pot.

Pot preparation and bryophyte transplantation

Terrestrial bryophytes have a strong response to edaphic gradients with many bryophytes restricted to particular soil types in terms of texture, chemistry and the amount of organic matter (Slack, 1990). Therefore, soil conditions were kept similar among all of the pots. Following a protocol similar to Hylander (2002), dark green plastic pots 12 cm in diameter and containing an equal amount of a fertilized peat composed of sphagnum peat moss (75-85% by volume), perlite, vermiculite and time release fertilizer with an N-P-K ratio of 0.7, 0.2, 0.3 (Premier Horticulture Ltd, Quebec) were used in this experiment.

Bryophytes were collected, settled in pots and transferred to the transect locations between 3-7 June 2003. *H. splendens* and *P. commune* were collected from two coniferous stands within the study area, located at 340500E 5377700N and 347300E 5391850N (Zone 16, NAD27), respectively. The bryophyte samples were collected from a single colony of either *H. splendens* or *P. commune*. To help prevent transplant related mortality handling and potting of bryophytes was done at the collection sites.

Five *H. splendens* stems and five *P. commune* stems were separated from their larger colonies and placed in each pot. The decaying stem bases and attached humus of *H. splendens* was planted below the soil surface with all green stems occurring 3 to 5 cm above the surface. Stems of *P. commune* with rhizoids were extracted from the soil, measured and cut to length of 5 cm. Stems containing rhizoids were planted below the soil surface with aboveground shoots extending 3 to 5 cm above the surface. The mat structure of *H. splendens* is its functional unit, which helps retain water; therefore, to simulate natural conditions the five *H. splendens* stems were planted in a cluster in the center of the pot. *P. commune* has individual stems that grow separately, therefore, the five stems were planted apart with equal distance in between (Figure 24). In each pot one of five differently coloured pieces of thread were tied around each of the stems for shoot identification.

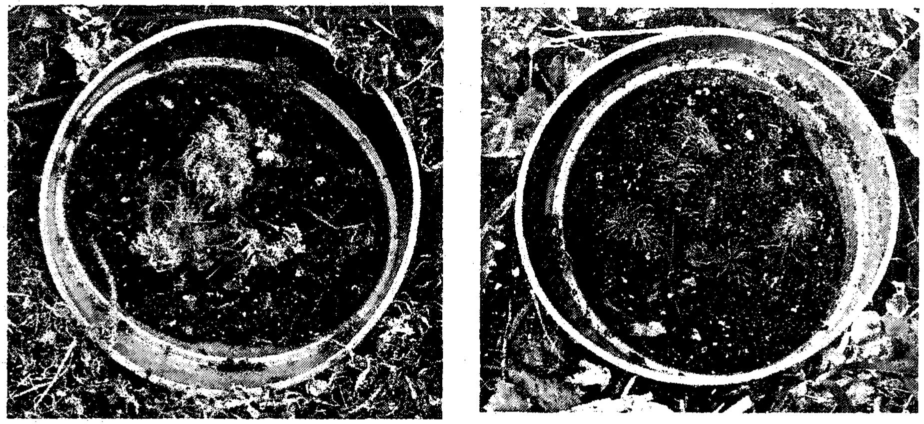


Figure 24. Placement of *H. splendens* and *P. commune* in pots. *H. splendens* stems were planted in a group within pots to simulate mat structure and *P. commune* stems were planted separately with equal space to simulate natural growing conditions.

Growth and vitality measurements

Length and width measurements of bryophyte segments were taken immediately after transplanting (June 3–7, 2003) and at the final sampling period (September 4-7, 2003). Annual cyclic fluctuations provide a simple method for measuring growth rate in *H. splendens* and *P. commune* (Clymo, 1970). In early spring new growth on *H. splendens* is produced laterally from the previous season's growth providing a clear innate marking of seasonal growth (Callaghan *et al.*, 1978). Similarly, *P. commune* shoots have a segmented appearance due to the production of small leaves at the beginning and end of the season with larger leaves produced in between (Figure 25). The annual dry mass accumulation of segments has a highly significant correlation with annual segment length (Vitt, 1990).

The length and width of the two youngest segments (year 0 and year 1) were measured on each moss stem. The year 0 segment refers to the current year's growth, whereas, year 1 segment refers to the previous year's growth (Figure 25). An accurate measurement of growth can be determined from the two youngest segments for both bryophytes. Most accumulation of dry weight in *H. splendens* occurs only in the three youngest segments (Callaghan *et al.*, 1978). *P. commune* shoots do not usually grow past three years.

Growth of the underground system in *P. commune* was also considered. Rhizoids (initially cut to 5 cm) were measured again during the final sampling period in September. Rhizoid growth over the summer was then calculated by subtracting initial growth from the final growth. Any new shoots found on the stems were counted during the September sampling period. Percent cover of the bryophyte species was also estimated by eye to the nearest percent by two separate individuals after potting the bryophytes, during a mid-summer monitoring period (28 July to 5 August 2003) and during the final sampling period (September 4-7, 2003). Final percent cover values were the average of the two separate estimates.

Bryophyte stems with green apices have the fastest elongation rates followed by a decline, as apices become yellow and brown. Water content is correlated with stem colour and bryophyte health (Busby *et al.*, 1978). Assessment of stem colour (*H.*

splendens) and leaf arrangement (*P. commune*), therefore, provides an estimate of the health and relative water content of stems.

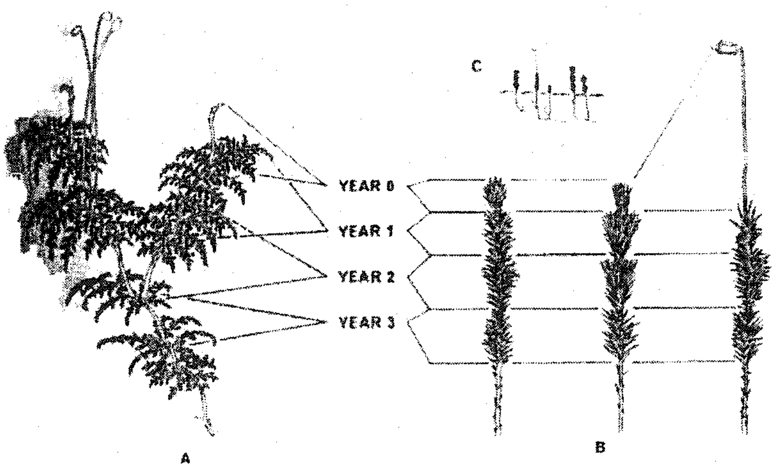


Figure 25. The growth forms of *Hylocomium splendens* (A) and *Polytrichum commune* (B) showing innate markers of annual growth. The relationship between above and below ground shoots of *P. commune* (C) (Callaghan *et al.*, 1978, p. 75).

Vitality was assessed immediately after the bryophytes were transplanted into pots, during the mid-summer monitoring and at the termination of the experiment in September. Vitality of *H. splendens* was assessed by using a modified vitality classification developed by Hylander *et al.*, (2002): (1) all shoots dead; (2) some leaves green on some shoots (no entire shoots green); (3) less than half of shoots are green; (4) half of the shoots are green (alive); (5) more than half of the shoots green (alive); (6) all of the shoots green (alive) but affected; (7) all of the shoots green, fresh and growing. One of the above vitality classes was assigned to each pot.

Distinct leaf arrangements related to water content were used as an indicator of vitality for *P. commune* stems (Bayfield, 1973) (Figure 26). Hydration values were scaled between 9, indicating the highest level of hydration, and 1, indicating the lowest level of hydration. After long periods of heavy rain inter-lamellar spaces are filled with water, and leaves appear slightly recurved (9). The normal turgid leaf arrangement (8), changes with loss of turgidity and leaves become laterally incurved and eventually appressed to the stem (4). Further drying leads to twisting and flattening of leaves in a vertical plane (2). When stems are almost air dry they become regularly and tightly flattened on a vertical plane (1). A leaf arrangement value was assigned to each stem and the average of each pot determined during sampling periods.

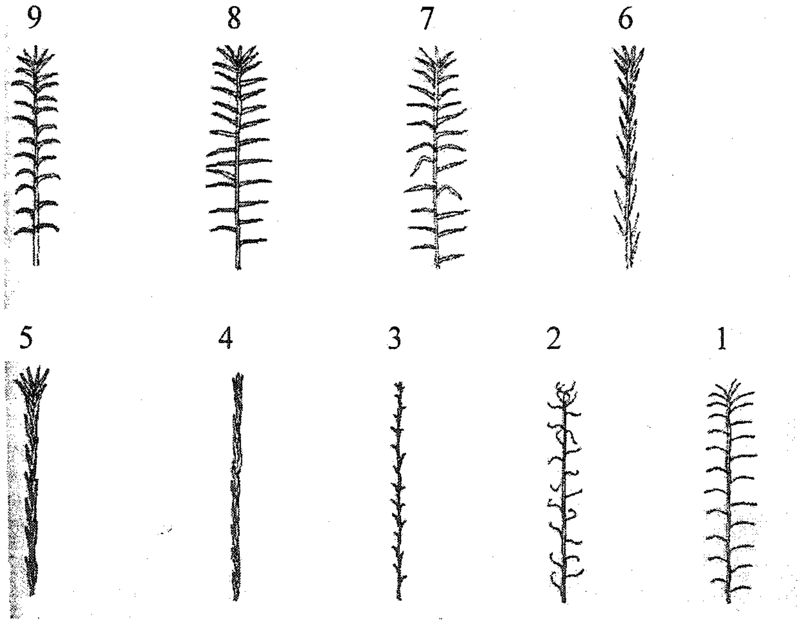


Figure 26. Leaf arrangements with progressive desiccation used to present vitality. 9 represents the highest level of hydration and bryophyte health, whereas 1 represents the lowest level of hydration and health (Bayfield, 1973, p. 609).

Field set-up and monitoring

Pots of transplanted bryophytes were transported to the experimental study locations. The bottom of each pot was cut off and the pots were sunk into the ground keeping the top rim of each pot approximately 4 cm above the soil surface (Figure 27).

Figure 27. Transect sampling location with one pot of each moss species sunk into the ground and a rainfall collector.

Canopy and understory species cover

At each pot location canopy openness was visually estimated as a discrete variable with 0 indicating the absence of canopy and 1 indicating the presence of canopy (see Chapter 1 for details). Shrub and herb cover define the habitat and play an important role in light and water relations, often ameliorating harsh microclimatic conditions in the disturbed areas. Therefore, percent cover of all understory species within 1 x 1 m quadrats was visually estimated at each pot location.

Microclimate

Near ground microclimatic parameters were measured three times during the experiment: 1) 18-21 June 2003, 2) 28 July to 5 August 2003 and 3) 4-7 September 2003. Five microclimatic parameters were measured at each pot location: photosynthetically active radiation (PAR) ($\mu mol^{-1}m^{-2}$), air temperature (^{o}C), relative humidity (%), soil moisture ($m^3.m^{-3}$) and rainfall (ml) (measured every 2 weeks). All microclimatic measurements were made on days with similar clear and sunny weather conditions. Air temperature and relative humidity measurement were taken between 9:30 am and 12:00 pm and all PAR measure were taken between 12:00-1:30 pm.

PAR values were determined using a LI-190SA, LI-COR Quantum Sensor (LI-COR inc, NE, USA) and a portable Decagon Sunfleck Ceptometer (Decagon Devices, WA, USA). Eight instantaneous readings were taken simultaneously at each pot location with the ceptometer and in the open (no canopy trees present) with the quantum sensor. The eight readings for each location were then averaged. Measurements at the pot locations were taken at approximately 1 m above the ground in all four major compass directions to determine the incident radiation below the canopy. The percentage of light transmittance was calculated as the ratio of incident radiation below the canopy to that in the open (Jose *et al.,* 1996).

Air temperature and relative humidity were measured with a traceable hygrometer at 5 cm above the soil surface. The average of four measurements at each pot location was used.

Instantaneous soil moisture was measured using the ML2x Theta Probe (Delta-T Devices, Cambridge, England). All soil moisture measurements were taken at a depth of

5 cm. Four measurements were taken in four different directions approximately 10 cm from each pot location. The average of the four measurements at each pot location was used.

Rain gauges consisting of white plastic cups with funnels (9 cm in diameter) attached to the top were placed at each pot location. Rainfall was collected and measured every two weeks. A small amount (10 mL) of vegetable oil was placed in each cup to prevent evaporation between measurement periods (Matlack, 1993).

Data analysis

The width of the buffer from the clearcut edge to the stream was 40 m at Hooks Rd. and 60 m at Hooks Friend. Interior buffer values where the minimum amount of change was detected were averaged for the Hooks Friend site making both buffers 40 m in width. Having buffers of the same width was necessary for comparing between locations on the transect.

Growth measurements (length and width) of the year 0 and year 1 segments taken at the end of the experiment were subtracted from the initial growth measurements. Total stem growth was the sum of both the width and length of the year 0 and year 1 segments. The average growth of each pot was determined by dividing the total stem growth of all stems within a pot by the number of stems in each pot. A square root transformation was performed on the growth data to approximate normal distribution and equal variance, which were confirmed for all variables with Kolmogorov-Smirnov and Levene tests respectively ($p = 0.05$). Analysis of covariance (ANCOVA) was performed to test for differences in moss stem growth and cover between the disturbed and undisturbed treatments with location on the transect as a covariate. All analyses in this study were performed in SPSS version 9.0 (SPSS, 1999).

Data that had a non-linear response or were categorical, such as rhizoid growth, new shoot growth, shrub cover, total understory cover and vitality were analyzed using Kruskal-Wallis tests. Hylander (2002) also used a combination of ANOVA models and Kruskal-Wallis tests to examine differences in growth and vitality. Correlations between the biological parameters were tested by using Spearman's rank-order correlation.

Multiple regression can be used to examine the response of species to groups of simultaneously operating environmental factors (Bates, 1982). Both Callaghan, (1978) and Hylander, (2002) used multiple regression to explore how differences in moss growth were related to different environmental parameters. In this study a principal components analysis (PCA) and a linear backward stepwise regression were used to examine the relationship between microclimatic variables (light, air temperature, relative humidity, soil moisture and rainfall), understory cover (shrub and total understory) and moss growth (*H. splendens* growth and *P. commune* cover). For details regarding the use of *P. commune* cover rather than growth see discussion p. 125. Since the buffer edges had the largest variation in both microclimatic conditions and moss growth, relationships between microclimatic conditions and growth were only explored with reference to buffer sites.

A PCA was performed on the environmental parameters to identify those variables that had the maximum discriminatory power between buffer locations. Initially all seven environmental parameters were included and 42 samples were used. Variables that were highly significantly correlated or had low factor loadings were eliminated.

Subsequent PCA were performed to obtain the optimal solution with the highest percent of variation explained and a minimum number of variables.

The environmental parameters identified in the PCA were then used in a linear backward stepwise regression to explore their relative effect on the growth of each bryophyte species. Normality, linear relationships and equal variation of growth data with respect any environmental parameter values were confirmed through residual plots. The regression model that explained the largest variation in bryophyte growth was selected for further discussion.

Several bryophyte stems were disturbed after the initial transect placement. Disturbed stems were excluded from the dataset and the average of remaining stems or pots were used in the analysis. Similarly, several disturbed rain gauges were also excluded from the dataset.

Results

Bryophyte response

Growth

The total seasonal stem growth of *H. splendens* was variable at undisturbed stream edges. However, more growth occurred near the stream edge than in the upland (Figure 28a). *H. splendens* growth near the stream edge in buffers, was similar to growth near the stream edge at undisturbed sites (-20 m to –40 m). However, at buffer sites, a rapid decrease in growth occurred from 10 m past the clearcut edge into the clearcut.

The percent cover of *H. splendens* did not have a clear trend across the riparian-upland gradient at undisturbed stream edges, although cover was somewhat similar to the pattern of total stem growth (Figure 28b). Across buffers, cover had a similar pattern to growth with a rapid decease in cover from 10 m past clearcut edge into the clearcut.

P. commune had a relatively consistent amount of total seasonal stem growth across the entire riparian-upland gradient at undisturbed stream edges (Figure 28c). Buffers had a pattern of reduced growth from the stream edge to the clearcut edge, but a slight increase in growth in the clearcut (20 to 10 m).

Undisturbed stream edges had a similar pattern of *P. commune* cover and growth, although cover had a slight increase towards the upland area (Figure 28d). Cover of *P. commune* across buffers also exhibited a similar pattern compared to total stem growth, however, reduced cover did not occur until 20 m from the stream edge.

Differences in total stem growth of *H. splendens* and *P. commune* were significant between the disturbance treatments, when location on the transect was included as a covariate (Appendix XI). Between the disturbance treatments, cover of *P. commune* showed a greater distinction than that of *H. splendens* (Figure 28b and d). Cover was not significantly different between the undisturbed stream edges and buffers for *H. splendens*, but was significantly different for *P. commune* (Appendix XI). Percent cover was significantly correlated with the growth of both *H. splendens* and *P. commune* (Appendix XII).

The current year's growth segment (year 0) and the previous year's growth (year 1) segments of *H. splendens* responded differently across buffers and undisturbed stream edges (Figure 29a). More growth was observed for year 0 segments at both disturbance treatments. Year 0 growth was variable across the undisturbed stream edges, with a slight reduction in growth in the upland (20 to 10 m).

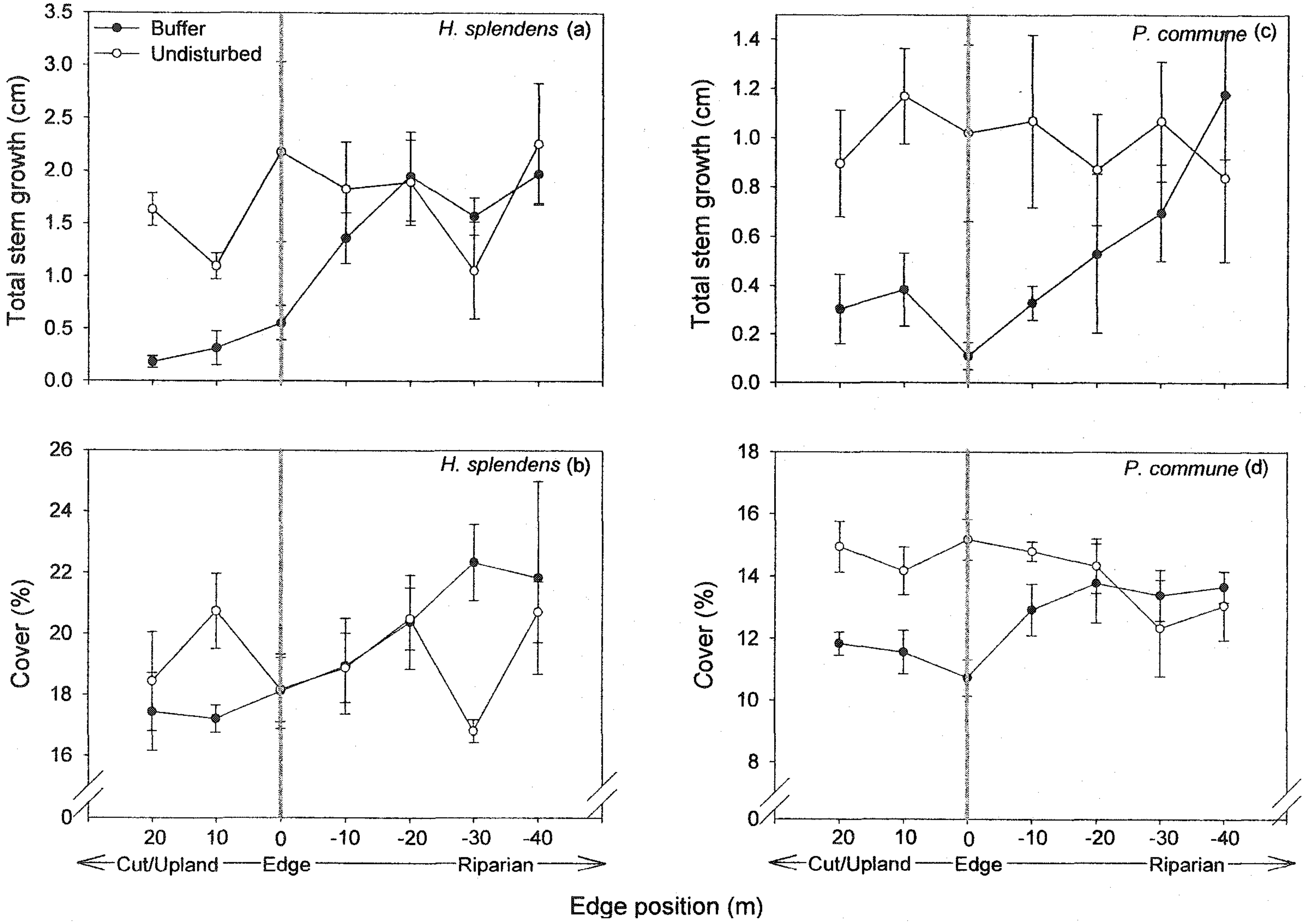


Figure 28. Mean total seasonal stem growth and mean cover of *H. splendens* (a & b) and *P. commune* (c & d) across buffers and undisturbed stream edges. Bars represent mean ±1 standard error. Solid grey line represents the upland buffer edge.

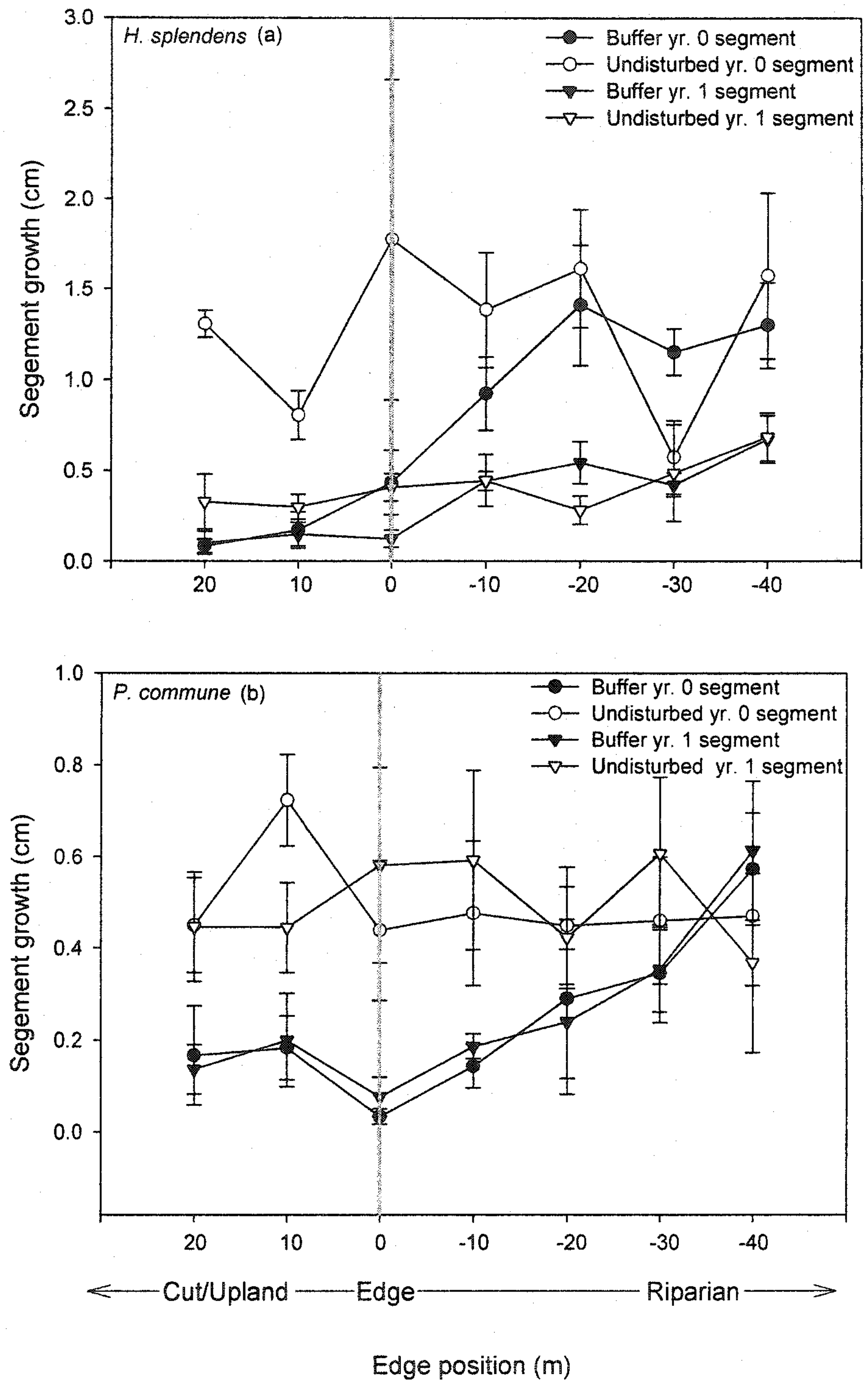


Figure 29. *H. splendens* (a) and *P. commune* (b) mean year 0 and year 1 segment growth across buffers and undisturbed stream edges. Bars represent mean ±1 standard error. Solid grey line represents the upland buffer edge.

At buffers year 0 growth was highest near the stream and rapidly declined from 20 m past the clearcut edge into the clearcut. Year 1 growth was similar across the riparian-upland gradient at buffer and undisturbed sites, although, slightly less growth was observed from the clearcut edge into the clearcut at buffer sites. Comparison of the current and previous year's segment growth with total stem growth indicates that the response of *H. splendens* was primarily driven by the response of the current year's (year 0) segment (Figure 28 and 29a).

The growth segments of *P. commune* had a different response than that of *H. splendens*. Year 0 and year 1 segments had a relatively consistent pattern of growth across the riparian-upland gradient at undisturbed stream edges (Figure 29b). At buffer sites both segments had declining growth from the stream to the clearcut edge and a slight increase in growth in the clearcut. Both the current and previous years segments responded in a similar manner at either the buffer or undisturbed stream edge, corresponding with the pattern of total stem growth (Figure 28 and 29b).

There was no significant difference in rhizoid growth (*P. commune*) or the number of new shoots (*P. commune* and *H. splendens*) between buffers and undisturbed steam edges, or between different locations on the transect (Kruskal-Wallis, $p<0.05$). However, the number of new shoots on *H. splendens*, showed a significant correlation with total stem growth (Appendix XII). In addition, new shoot initiation responded to the upland buffer edge. Compared to the upland at undisturbed stream edges, the number of new shoots rapidly declining from 10 m past the clearcut edge into the clearcut at buffers (Figure 30).

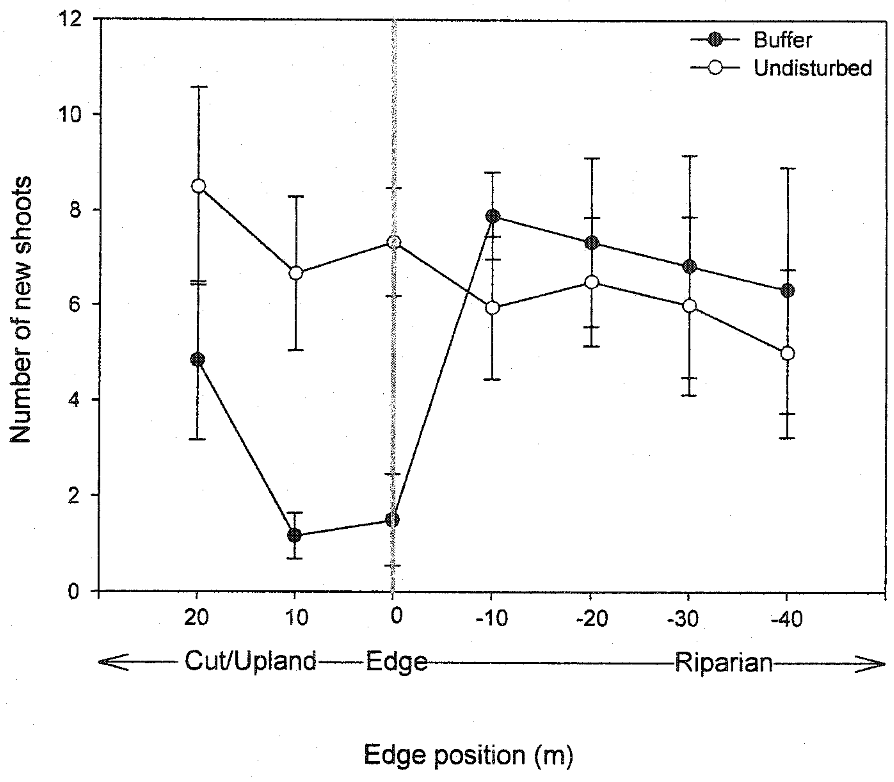


Figure 30. Mean number of new shoots on *H. splendens*. Bars represent mean ±1 standard error. Solid grey line represents the upland buffer edge.

Vitality

Vitality for both *H. splendens* and *P. commune* was relatively constant across the riparian-upland gradient at undisturbed sites (Figure 31). At buffer sites vitality of both bryophytes declined rapidly from 10 m past the clearcut edge into the clearcut. Vitality was significantly different between both disturbance treatment and location on the transect (Appendix XIII). Bryophyte vitality was significantly correlated with total stem growth and percent cover of both *H. splendens* and *P. commune*, and with shrub and total understory cover (Appendix XII).

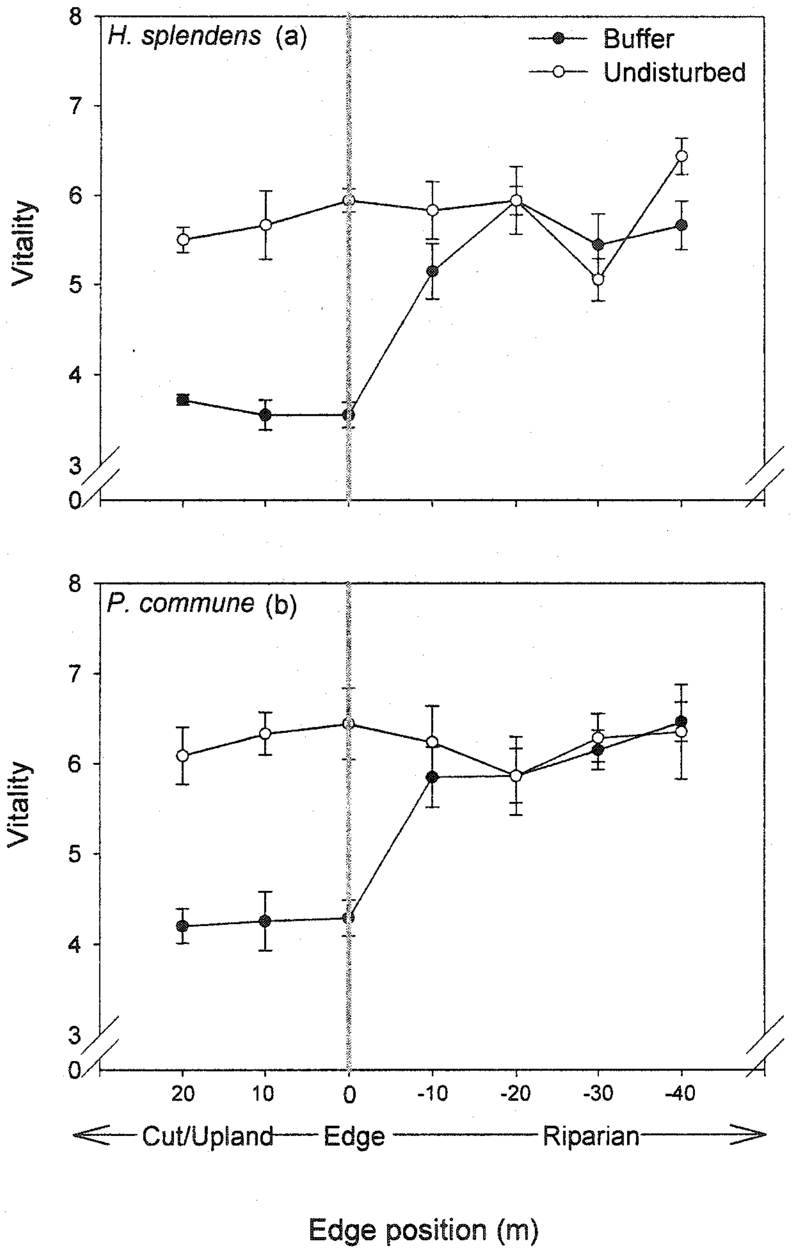


Figure 31. Mean vitality of *H. splendens* (a) and *P. commune* (b) across buffer and undisturbed stream edges. Vitality was assessed on a scale where 7 and 9 represent the highest values and 1 the lowest for *H. splendens* and *P. commune* respectively. Bars represent mean ±1 standard error. Solid grey line represents the upland buffer edge.

Canopy and understory species cover

Canopy cover was similar between buffers and undisturbed stream edges from the stream up to 20 m into the upland (Figure 32). Canopy cover peaked 30 m from the stream in buffers, but then rapidly declined at the clearcut edge. Undisturbed stream edges had more variation in canopy cover, but maintained higher cover in the upland area compared to the clearcut area of buffers. Differences in canopy cover were not significant with respect to disturbance treatment, but were significantly different with respect to location on the transect (Appendix XIV).

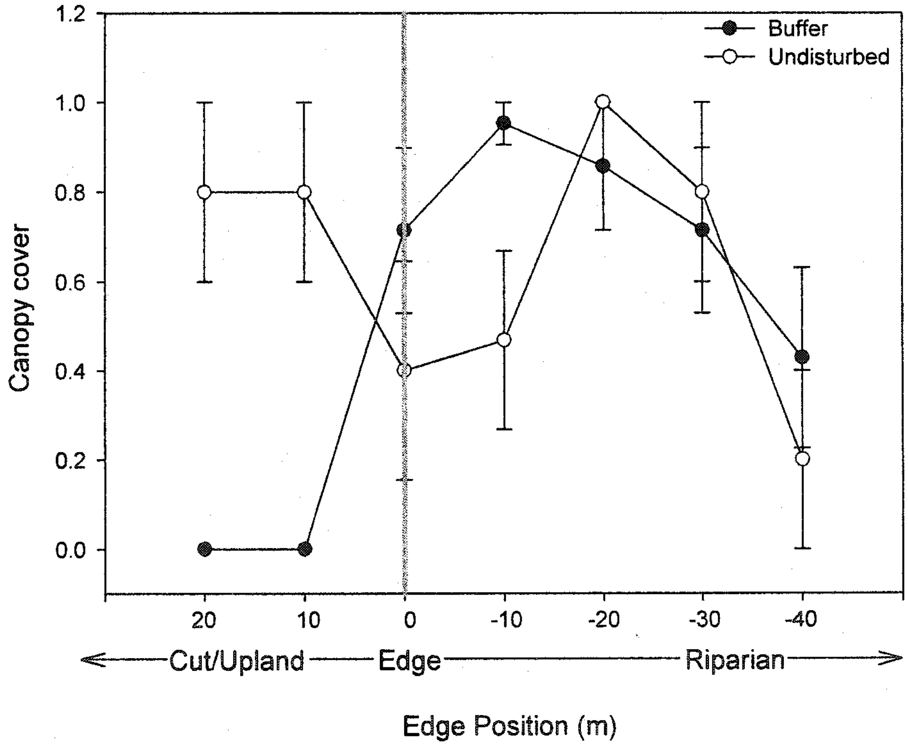


Figure 32. Mean canopy cover across buffers and undisturbed stream edges. Canopy cover was visually assessed, 0= open, 1= cover. Bars represent mean ±1 standard error. Solid grey line represents the upland buffer edge.

Total shrub cover and total understory cover had a different response at buffer and undisturbed stream edges than canopy cover (Figure 33). Shrub cover was highest at the stream edge and declined rapidly towards the upland area in buffers and undisturbed sites. Undisturbed stream edges, however, maintained a higher shrub cover at the riparian-upland transition (-30 m) and in the upland area. Total understory cover had a similar pattern with the highest abundance occurring at the stream edge. Compared to buffers, undisturbed sites maintained a higher understory cover across the entire riparian-upland gradient. Total understory cover at buffers was similar to the response of shrub cover with the exception of a rapid decrease at the clearcut edge. Shrub cover and understory cover were significantly different both with respect to disturbance treatment and location on the transect (Appendix XV). In addition, both shrub and understory cover were significantly correlated with the total stem growth of both mosses (Appendix XII).

Microclimate

Most microclimatic variables had strong response patterns relating to both distance from the stream and disturbance treatment (Figure 34). At undisturbed sites, light transmittance was relatively constant from the stream edge into the upland, however, slight increases in air temperature and slight decreases in relative humidity were detected with distance from the stream. At buffer sites light transmittance and air temperature showed a large increase and relative humidity a large decrease between the clearcut edge and 10 m past the clearcut edge. Light transmittance was most stable in the riparian area with only a slight increase at the stream edge. Air temperature appeared to stabilize approximately 20 m past the clearcut edge and relative humidity continued to increase up to the stream (Figure 34c).

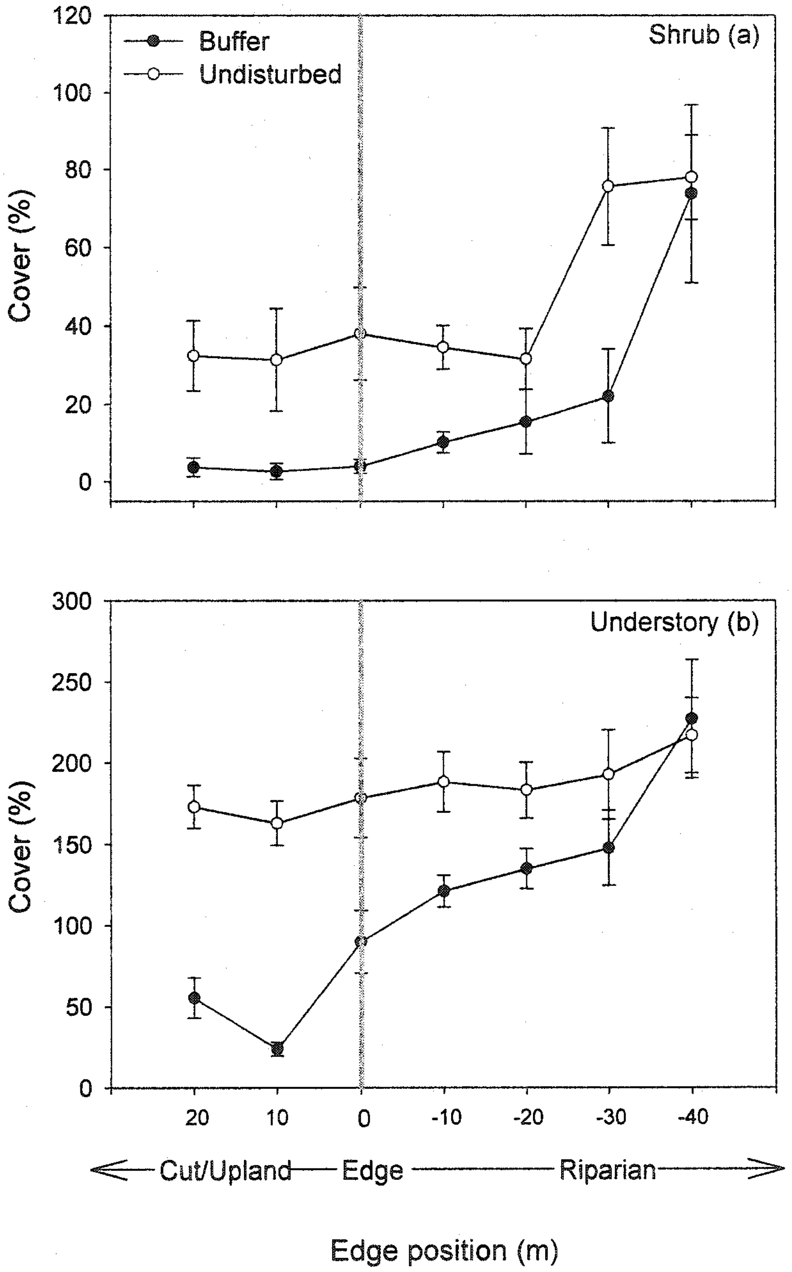


Figure 33. Mean total shrub cover (a) and understory cover (b) across buffer edges and undisturbed stream edges. Bars represent mean ±1 standard error. Solid grey line represents the upland buffer edge.

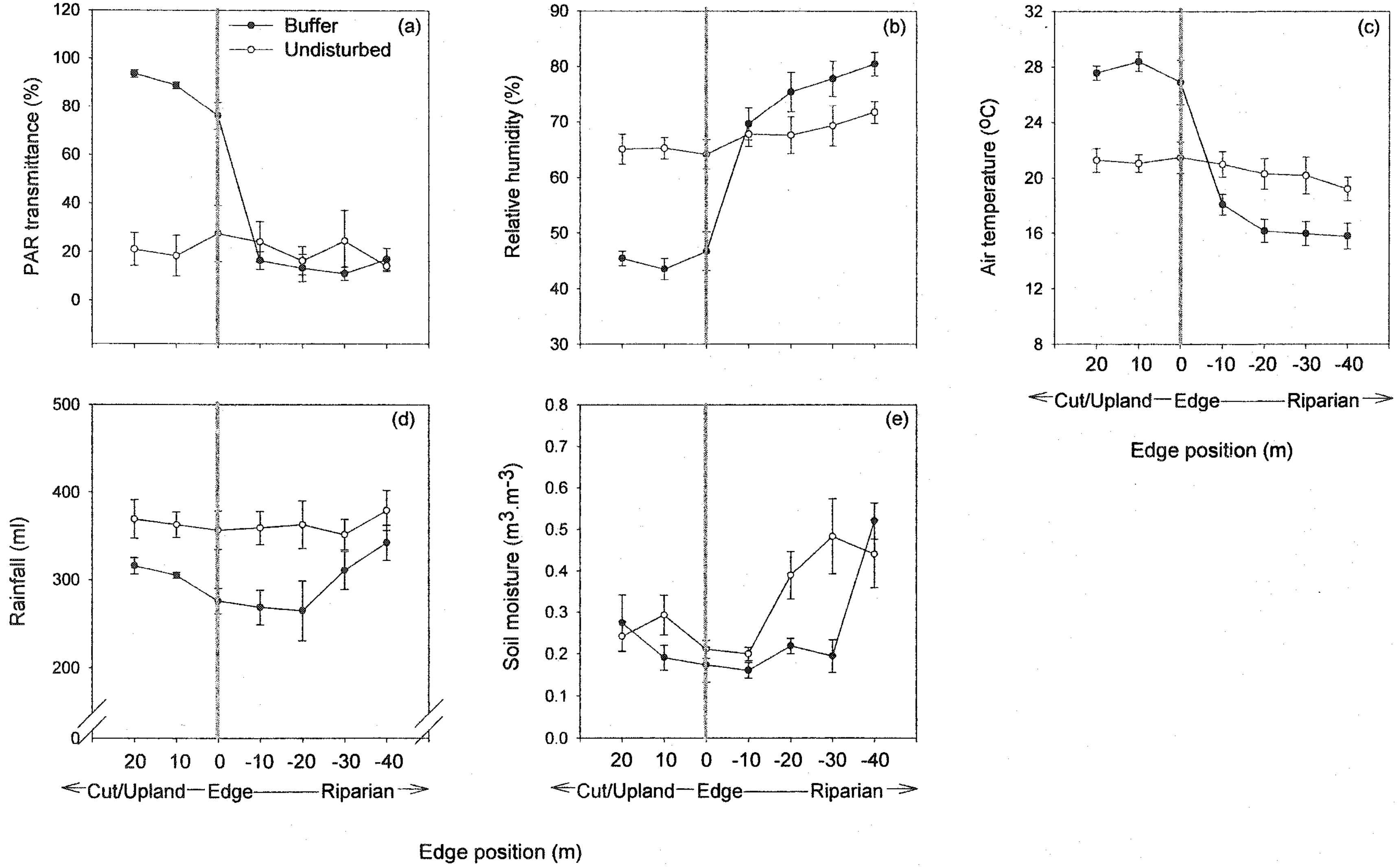


Figure 34. Microclimatic response of PAR transmittance (a), relative humidity (b), air temperature (c), rainfall (d) and soil moisture (e) across undisturbed stream edges and buffers. Bars represent mean ±1 standard error. Solid grey line represents upland buffer edge.

The amount of rainfall was similar from the stream edge into the upland at both undisturbed and buffer sites, however, a slight decrease in rainfall occurred under the closed canopy in the buffer from 0 to -20 m (Figure 34d).

Soil moisture had the strongest riparian-upland gradient at undisturbed sites with moisture decreasing with distance from the stream (Figure 34e). A similar response was found in buffers, however, there was a more dramatic drop in moisture between the stream edge and 10 m towards the upland.

PCA and multiple regression

The initial PCA included all environmental parameters and extracted three components with the first component explaining 51.18% of the variance in locations on the buffer transects. PAR transmittance, air temperature and relative humidity were highly colinear (>0.9) and shrub cover and total understory cover were highly colinear (>0.8). Relative humidity and total understory cover had the highest factor loadings and were selected for further analysis. The PCA with relative humidity, soil moisture, rainfall and total understory cover extracted one component explaining 47.37% of the variance in locations on buffer transects. Rainfall had the lowest factor loading (.258) and was removed from the final PCA.

The final PCA included relative humidity, soil moisture and total understory cover, which were significantly correlated, but not highly colinear (Appendix XVI). The PCA extracted one component with an eigenvalue of 1.759 and explained 58.63% of the variation in locations on the buffer transects. Factor loadings for all three variables were quite high with total understory cover (.833) having the greatest influence on the component followed by relative humidity (.821) and soil moisture (.626). Factor scores for component one were plotted against *H. splendens* growth and *P. commune* cover (see p. 125 for details regarding the use of cover as a growth measure) (Figure. 35). *H. splendens* growth had a stronger relationship with component one, however, growth measures for both mosses had a linear response.

A backward stepwise regression was performed to determine which of the environmental parameters contributing to component 1 were most important in predicting the bryophyte growth. Two significant models were created for both bryophyte species. The second model had the highest adjusted R^2, explaining 50.1% and 20.4% of the variation in *H. splendens* and *P. commune* growth respectively (Table 14). Model 2 for *H. splendens* had two significant environmental parameters: relative humidity and total understory cover (Table 15). Relative humidity had a slightly larger coefficient. Model 2 for *P. commune* also had two significant environmental parameters: soil moisture and total understory cover (Table 15). Soil moisture had a much larger coefficient.

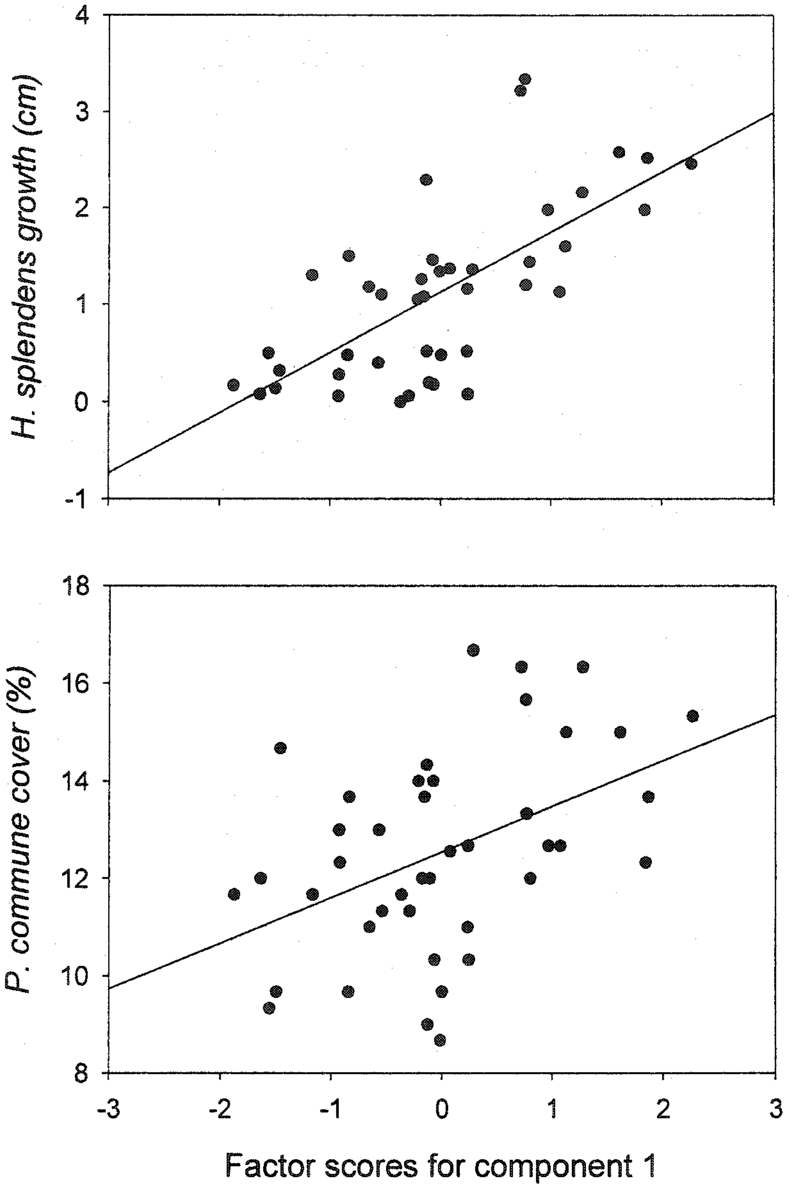


Figure 35. *H. splendens* growth and *P. commune* cover plotted against the factor scores for component 1.

Table 14. Summary of the significant models with the highest adjusted R^2 value. a Predictors: (Constant), understory cover, relative humidity. b Predictors: (Constant), understory cover, soil moisture. The dependent variable was growth and cover respectively.

Moss species	Model	N	df	Adjusted R Square	F	Sig. (<0.05)
H. splendens	2a	42	2	.501	21.604	.000
P. commune	2b	42	2	.204	6.238	.004

Table 15. Coefficients for the growth model of *H. splendens* and *P. commune*. The dependent variable is *H. splendens* growth and *P. commune* cover.

Moss species	Model	Unstandardized coefficients		Standardized coefficients	t	Sig. (<0.05)
		B	Std. Error	Beta		
H. splendens	2 (Constant)	-.799	.518		-1.543	.131
	Relative humidity	1.867E-02	.009	.272	2.071	.045
	Understory cover	6.354E-03	.002	.541	4.122	.000
P. commune	2 (Constant)	10.296	.716		14.382	.000
	Soil moisture	4.047	1.968	.300	2.056	.047
	Understory cover	8.408E-03	.004	.310	2.123	.040

Discussion

Both *H. splendens* and *P. commune* had less growth and reduced vitality in the clearcut and up to 20 m past the clearcut edge compared to undisturbed stream edges. Both the current year's segment (year 0) and the previous year's segment (year 1) showed a growth response for *P. commune*, whereas the growth response of *H. splendens* was primarily due to the current year's segment. The near ground microclimatic conditions were different between the buffers and undisturbed stream edges. The clearcut and clearcut edge had higher light transmittance and air temperature and lower relative humidity and soil moisture. The growth response of *H. splendens* appeared to be most effected by relative humidity and understory cover. Due to the presence of an underground rhizoid system and internal water conduction, *P. commune* growth was more effected by soil moisture and may be better able to occupy recently disturbed environments.

Bryophyte response

Growth and vitality of both *H. splendens* and *P. commune* were significantly different between the buffer and undisturbed sites. At undisturbed stream edges bryophyte growth was highly variable, but vitality remained relatively unchanged with no clear pattern relating to distance from the stream. The transplanted bryophytes were not strongly influence by the more subtle environmental changes associated with riparian-upland gradient within the duration of the study. Longer-term studies may be required for biological expression of the more subtle gradients perpendicular to stream edges.

Growth and vitality of the bryophytes had a strong negative response across upland buffer edges, indicating that the alteration of microclimatic gradients due to harvesting in the upland is more influential than the riparian-upland gradient. The growth response of bryophytes across the clearcut edge followed a similar pattern to the alteration of microclimatic gradients. Differences in microclimatic conditions tend to amplify growth response of plants across edges (Ranney *et al.,* 1981).

H. splendens had less growth and reduced vitality from 20 m past the clearcut edge into the clearcut with the most drastic drop at the outer edge (10 m past the clearcut edge, see p. 129). *H. splendens* also produced fewer new shoots at the outer edge. Although, the number of new shoots was not significantly different between the buffers and undisturbed stream edges, the number of new shoots was significantly correlated with growth, suggesting that a certain level of growth and vitality are required for shoot formation. Callaghan *et al.,* (1978) suggested that sporophyte development of *H. splendens* over the spring and autumn appear to be synchronous with vegetative growth and environmental factors. The bud of the following year's growth in *H. splendens* is initiated at the same time as lateral branches of the current year's growth, and the bud does not elongate until the previous years segment has completed its growth (Busby *et al.,* 1978). There may be some hormonal balance involved in the reproductive process of *H. splendens,* where the segments must reach a certain size before the bud growth inhibition is released and the next year's growth commences (Tamm, 1953; Busby *et al.,* 1978). Microclimatic factors such as light, temperature and soil moisture may play a part in regulating the growth and development process. Desiccation of the bryophyte caused by canopy removal during forest harvesting may delay growth of the current year's segment, which in turn may delay development of the next year's bud. This study shows that harvesting seems to reduce the ability of *H. splendens* to grow and reproduce.

P. commune had a more gradual decrease in growth from the stream edge to the clearcut edge. Percent cover and vitality, however, declined sharply at the outer edge (10 m past the clearcut edge). The number of new shoots was not significantly different between buffers and undisturbed stream edges, or significantly correlated with growth. Changes in microclimate, such as summer drought do not appear to interrupt the reproductive cycle of *P. commune* (Callaghan *et al.,* 1978).

Assessment of growth through percent cover estimation led to different results for the two species. Percent cover of *H. splendens* was not significantly different between buffers and undisturbed stream edges, however, percent cover was correlated with growth and vitality. *H. splendens* was transplanted into central clusters in the pots and tended to grow vertically with overlapping leaves, therefore, percent cover may not be as accurate a growth measure for this species.

. Percent cover of *P. commune* was significantly different between buffers and undisturbed stream edges and was significantly correlated with growth and vitality of the bryophyte. In addition, *P. commune* cover had higher correlation coefficient with vitality than *H. splendens.* Vitality of *P. commune* was a reflection of leaf arrangements relating to hydration. Stems that are more hydrated are not only healthier, but also have a larger percent cover because the leaves have a more horizontal orientation. Percent cover of *P. commune*, therefore is a combined measure of both growth and vitality. Growth of *P. commune* was highly variable and the total seasonal stem growth was minimal, making detection of significant differences between disturbance treatments difficult. In short term studies, such as this study, percent cover may be a preferable growth measure for *P. commune*.

The growth response of the current (year 0) and previous (year 1) years' segments were different for *H. splendens* and *P. commune.* Growth response of *H. splendens* to disturbance was predominately driven by the year 0 segment, whereas in *P. commune* the entire stem responded to disturbance. The year 1 segment of *H. splendens* had a much lower growth rate than the year 0 segment and did not have a strong response to the alteration of microclimatic conditions. The limited response of the year 1 segment is likely due to the physiological independence of individual segments. Callaghan *et al.*, (1978) found that the rate of photosynthesis in *H. splendens* decreased with segment age. Segments three years or older had a negligible rate of photosynthesis or the rate of photosynthesis in these segments was exceeded by respiration loss. In higher order plants reduced ability of older segments to photosynthesize can be compensated for by translocation of photosynthate from the younger segments, but such translocation does not take place in *H. splendens* (Tamm, 1953; Callaghan *et al.*, 1978). The absence of an active transport system limited the survival and growth of *H. splendens* in areas disturbed by clearcutting. Any damage to the youngest segment of *H. splendens* results in death of the entire shoot making *H. splendens* very susceptible to any form of disturbance (Callaghan *et al.*, 1978).

In *P. commune* growth of the current year's segment steadily increases to match the weight of the preceding segment. New shoots are initiated when an apex dies and arise as an innovation from the below ground system (Callaghan *et al.*, 1978). The presence of translocation and internal water conduction in *P. commune* most likely accounts for the whole stem response to disturbance. In addition , the maintenance of an underground system provides a mechanism for survival following disturbance (Callaghan *et al.*, 1978).

Growth and vitality of both mosses were significantly correlated with shrub cover and total understory cover, but not with canopy cover. The realized niche of a species is a function of both the physiological tolerances of the species and the kinds of co-occurring species nearby (Watson, 1981). Due to the minute statue of *H. splendens* and *P. commune*, total shrub and understory cover may play a more important role in creating a suitable microclimate for the bryophytes than the forest canopy cover. Development of a shrub canopy following harvesting may allow some moss species, such as *H. splendens* to persist in the clearcut (Busby *et al.,* 1978).

Microclimatic response

Strong near ground microclimatic changes due to harvesting were evident in this study. PAR transmittance, air temperature and relative humidity had different response patterns at buffers and undisturbed sites and they were all highly correlated. Matlack (1993) also observed high correlation between relative humidity, temperature and light across forest edges. Relative humidity varies greatly depending on the presence of canopy, the proximity to water, temperature and solar insolation (Busby *et al.,* 1978; Vitt, 1990). In comparison to buffer edges, light transmittance, air temperature and relative humidity were relatively unchanged from the stream edge into the upland at undisturbed stream edges. However, an increase in air temperature and decrease in relative humidity occurred with distance from the stream at undisturbed sites. Brosofske *et al.,* (1997) also found riparian-upland gradients at undisturbed stream edges for air temperature and relative humidity. Temperature at undisturbed streams was approximately 2-4°C lower than in the interior forest (Brosofske *et al.*; Dong *et al.,* 1998); similar results were found in this study with temperature in the upland 2-4°C higher than at the stream edge. Proximity to the stream most likely led to higher relative humidity.

Proximity to the stream also had the strongest influence on soil moisture at both buffers and undisturbed stream edges. The response of soil moisture at the clearcut edge of buffer sites was similar to the response detected by Cadenasso *et al.,* (1997): soil moisture levels remained constant across the boundary with a slight increase (not significant) in soil moisture in the clearcut.

Matlack, (1993) found that rainfall was not significantly related to distance from the edge with values varying by only ~100 ml. Rainfall in this study also was relatively consistent (varying by ~100 ml) across both disturbance treatments with a slight increase at the stream and in the clearcut where canopy cover was absent. Rainfall values can vary greatly depending on the duration and intensity of the precipitation event and rainfall of 1 mm or less can be entirely intercepted by a *P. mariana* canopy (Geiger, 1966). Missing samples due to rain collector disturbance limit the explanatory power of rainfall in this study.

The shape of microclimatic responses across buffers appears to be related to the expression of two different environments. The riparian environment is characterized by lower PAR transmittance and air temperature and higher relative humidity, while the clearcut environment had opposing trends. Several other studies have found similar patterns in microclimatic response across clearcut or pasture edges (Raynor, 1971; Williams-Linera, 1990; Young & Mitchell, 1991; Jose *et al.,* 1996; Matlack, 1993; Cadenasso *et al.,* 1997).

Young & Mitchell (1991) identified three general microclimatic zones, which correspond to the microclimatic responses detected in this study: 1) a 10 m outer edge zone where the most drastic changes in light, temperature and humidity occurred; 2) beyond this was an inner edge zone that extended up to 50 m into the forest where temperature and humidity continued to decrease; 3) an interior zone, where light, temperature and humidity were relatively constant. The presence of a hydrological feature leads to slightly more complex patterns in this study. The most drastic changes, however, were confined to a 10 m outer edge zone, located in the buffer 10 m past the clearcut edge. An inner edge zone was also detected further into the buffer for temperature and humidity. In this study, the interior zone is best characterized by the undisturbed stream edges.

While harvesting altered the microclimatic gradients across the width of the buffer for most variables, near-stream microclimate showed little difference from the undisturbed condition. Differences in site conditions can have controlling effects on microclimatic change near the stream. The buffer sites in this study had greater canopy closure within the buffer, which likely accounts for lower PAR transmittance and air temperature and higher relative humidity near the stream edge. An intact canopy changes the spectral composition of light, limits temperature change, and maintains a zone of higher humidity (Geiger, 1966; Hutchison & Matt, 1977; Matlck, 1993).

Comparison of life strategies

The response of species to edge may differ due to the different life strategies employed by species. Although, *H. splendens* and *P. commune*, had similar edge related responses there were a number of differences due to their life strategies.

The PCA found total understory cover, relative humidity and soil moisture accounted for most of the variation among locations on the buffer transects. *H. splendens* had a stronger linear relationship with these three factors than *P. commune*. Therefore, *H. splendens* is more sensitive to environmental changes across edges and perhaps a more effective edge indicator. Identification of species that are sensitive to edges can lead to more effective monitoring of edge effects. The rate of recovery of these phytometers has implications for biodiversity protection in forest management.

Multiple regression analysis identified relative humidity and total understory cover as the most important factors for *H. splendens* growth, whereas, soil moisture and total understory cover were the most important factors for *P. commune* growth. Both bryophytes had a marked decrease in growth in the clearcut. In areas disturbed by the removal of tree and shrub canopies a decrease in growth rate occurs and growth may be delayed for approximately one month (Busby *et al.,* 1978). Understory cover is not only crucial in providing more favourable microclimatic conditions, but it is also an indicator of aboveground disturbance in this study.

Numerous studies have shown a strong relationship between precipitation, growth and the length of time bryophytes remain wet (Busby *et al.,* 1978; Vitt, 1989; Vitt; 1990; Proctor, 1990). Hylander *et al.,* (2002) suggested that while all bryophyte species have poorer vitality and growth in logged areas than in buffers, the response of buffer strips varies depending on ground moisture and the bryophyte species. Shaded and moist environments, such as those under the canopy, can limit evaporation extending the post precipitation wet time substantially (Busby *et al.,* 1978; Hylander, 2002). *H. splendens* is dependent on the downward movement of rainwater and tree leachates for its supply of water and nutrients (Tamm, 1953; Callaghan *et al.,* 1978). The formation of dense moss carpets preserves water and creates a water pool within the carpet, which active segments on the surface may draw upon ectohydrically. However, water losses may not be recouped due to the absence of an underground system with rhizoids, no internal water conducting system and simple leaves that are only one cell thick and lack cuticule ornamentation (Callaghan *et al.,* 1978). In this study, the limited growth and poor vitality of *H. splendens* in the clearcut, emphasizes the dependence of *H. splendens* on relative humidity. Species that are dependent on high humidity are strong indicators of edge effects, because they are unable to compensate by drawing on underground resources when the canopy is removed.

P. commune may have some inhibition related to low water content, however, in the *Polytrichum* genus an internal water conduction system transports water from below the soil surface to the stem apex (Callaghan *et al.,* 1978; Vitt, 1990). *P. commune* is endohydric due to the fact that it is cuticularized and has a well-developed central strand of conducting tissue (Bayfield, 1973). Both external and internal water conduction occur in *P. commune* and water transportation can occur via either pathway under low water stress conditions. Under high evaporative stress, internal conduction is often more effective, because external conduction pathways may dry up (Bayfield, 1973). *P. commune* was likely under higher water stress conditions in the buffers and especially in the clearcut. Internal water conduction, therefore, was emphasized causing soil moisture to be of greater importance for vitality and growth of this bryophyte.

Unlike *H. splendens*, *P. commune* utilizes higher energy environments in mid-summer (Callaghan *et al.,* 1978). Under high temperature and irradiance *P. commune* has higher rates of photosynthesis in comparison to *H. splendens,* and much of the increased efficiency provides energy for maintenance of the non-photosynthetic underground system (Callaghan *et al.,* 1978). The slight increase in *P. commune* growth in the clearcut compared to the clearcut edge is most likely a reflection of the ability of *P. commune* to utilize the high temperature and light conditions experienced in the clearcut.

The differential ability of *P. commune* and *H. splendens* to occupy disturbed microhabitats may result in shifts in the abundance and frequency of these bryophytes in managed landscape. As landscapes become increasingly disturbed, the frequency of microhabitats representative of the disturbed condition will also increase. Colonist species, such as *P. commune*, appear to be effected by edge creation, but they also have some ability to utilize disturbed habitats. On the other hand, interior species, such as *H. splendens*, are limited by disturbed habitats and may become increasingly scarce in managed landscapes. The creation of forest edges and the resulting alteration of abiotic and biotic conditions may be particularly disadvantageous for organisms adapted to interior conditions (Renhorn *et al.,* 1997).

Management recommendations

The alteration of microclimate due to harvesting of *P. mariana* forest is most pronounced within a 10 m outer edge zone occurring 10 m past the clearcut. Further studies are needed to determine if gradual change in air temperature and relative humidity in buffers are significantly different from the riparian-upland trends at undisturbed stream edges.

Bryophyte growth near the stream was similar at both buffers and undisturbed stream edges. However, differences in growth were detected up to 20 m past the clearcut edge at the buffer sites. Forty meter wide buffers with a high canopy density and little or no structural damage have only 10-20 m of forest conditions that are similar to undisturbed stream edges. Management guidelines, therefore, need to incorporate edge effects if they aim to maintain a given amount of undisturbed forest along shorelines.

Site conditions appear to play an important role in the response of plant species following disturbance. When applying forest management guidelines, therefore individual site conditions need to be considered. Sites with more open canopy conditions or extensive structural damage may not maintain undisturbed forest conditions within a 40 m buffer (see Chapter 2).

Comparison of the different life strategies of *H. splendens* and *P. commune* provides an example of the significance of species life history attributes in response to edge. Interior species that are sensitive to edge effects can be used as phytometers to monitor edge effects and biodiversity recovery following forest harvesting.

Chapter 4

Stand and landscape-level changes following forest disturbance: A multi-scale approach

Abstract

The structure and function of edges vary depending on the scale of investigation. A more comprehensive understanding of the impacts of edge effects within a landscape can be gained by integrating many scales. A multi-scale approach was used to examine both the structural legacy left by clearcutting and fire and to determine the potential disturbance value of these two disturbances. A 1997 Forest Resource Inventory map and a remotely sensed image of the 1999 Nipigon10 burn were used to represent the landscape. Six 1000 ha sampling windows were randomly placed on the landscape, three in clearcut areas and three in burnt areas. Within each 1000 ha sampling window, two 250 ha windows were also randomly selected. The amount of residual patch area, core area, near edge (20 m bordering disturbed area) and far edge (20 m beyond near edge) were determined in each window. A Disturbance Index was derived from a separate stand-level study and applied to the landscape. Burnt areas had the single largest residual patch and a larger number of small residual patches than clearcut areas. Clearcutting disturbance had a higher disturbance value, as a result of high Disturbance Index values associated with the cut area. Many current forest management practices aim to emulate natural disturbance. Increasing the number of retention patches in clearcut areas would help to mimic the larger number of small patches left on the landscape by fire and provide refuge habitat for interior species potentially reducing the disturbance value of clearcuts.

Introduction

Currently there is a growing interest in the structural and functional heterogeneity of ecological systems resulting from disturbance (Pickett & White, 1985; Holland & Risser, 1991; Gosz, 1991; Wiens, 1992). Ecological disturbance can have a variety of attributes, including spatial distribution, frequency, return interval, rotation period, predictability, area, intensity, severity and synergism (Turner, 1989). Forest patterns reflect the effects of prior disturbances and constitute context variables in the study of species patterns (Perera & Baldwin, 2000).

Much of the heterogeneity in the landscape is a direct or indirect result of both anthropogenic and natural disturbance. Humans modify landscape patterns either through direct landuse conversion or indirect alteration of the frequency, extent and magnitude of natural disturbance processes (Tang *et al.,* 1997; Carleton, 2000; Perera & Baldwin, 2000). Many management plans currently aim to emulate patterns of natural disturbance, however, very little is known about natural disturbance patterns and the effects they have on ecosystem processes. The emulation of natural disturbance in forest management relies on our ability to understand and mimic the complexities and characteristics of natural landscapes within anthropogenically modified landscapes (Mladendoff *et al.,* 1993).

Disturbances, such as clearcutting and fire may cause fragmentation, a process by which the landscape becomes segmented into smaller, widely spread, and unevenly spaced patches resulting in both physical and biogeographical changes (Saunders *et al.,* 1991; Forman, 1995). High levels of fragmentation often occur in landscapes heavily modified by anthropogenic activities (Turner, 1989; Saunders *et al.,* 1991; Mladendoff *et* *al.,* 1993; Zipperer, 1993). Habitat fragmentation is considered a serious threat to biological diversity and is the primary cause of the present species extinction crisis (Wilcox & Murphy, 1985; Lovejoy *et al.,* 1986, Wilcove *et al.,* 1986; Zipperer, 1993). Noss and Harris, (1986) identified two major problems associated with the fragmentation of habitat into small isolated patches: 1) the loss of generalist or ecologically specialized species that cannot be "contained within" remaining patches of inadequate size, and 2) the progressive domination of remaining fragments by opportunistic and invasive species that are characteristic of highly disturbed landscapes. Proper landscape design may reduce fragmentation, help maintain biodiversity and ensure the preservation of habitat quality (Noss, 1983; Franklin & Forman, 1987; Ripple *et al.,* 1991).

Several theoretical models exist about the ecological consequences of fragmentation patterns. However, few studies have quantitatively investigated fragmentation on a true landscape (Ripple *et al.,* 1991; Spies *et al.,* 1994). To ensure that theoretical models are ecologically meaningful and applicable for management planning, they must be examined within the constraints of the current landscape (Ripple *et al.,* 1991; Spies *et al.,* 1994). Quantitative measurement of spatial structure is a prerequisite for assessing the effects of fragmentation and for the development and implementation of landscape-level management (Baskent & Jordan, 1995). Quantitative methods allow for a comparison of spatial and temporal changes in landscape pattern, which is needed in order to understand relationships between landscape pattern and ecological function (Turner, 1989).

Some landscape indices focus upon patch size, shape, abundance and distribution, while others consider the spatial relationships between patches. Measurements at the patch-level are confined to characterizing the spatial properties of individual patches (Baskent & Jordan, 1995). Patch-level measurements can be arithmetically combined into a single indirect landscape-level measurement. For example, the core area determined for individual patches can be summed to acquire total core area. Direct landscape-level indices, such as, average proximity, dispersion and contagion are calculated simultaneously for the entire landscape (Baskent & Jordan, 1995). Landscape indices provide a means to assess landscape pattern, however, further techniques are necessary if the ecological consequences of landscape pattern are to be understood.

Multi-scale approach

Due to the broad spatial-temporal scales involved, experimentation and hypothesis testing become more challenging at the landscape-level. Results from studies conducted at relatively fine scales, therefore, may need to be extrapolated to broader scales to obtain insights about pattern-process relationships (Turner, 1989; Weins *et al.,* 1993). A more comprehensive approach to landscape ecology integrates many biological levels and spatial scales (Weins *et al.,* 1993). Efforts to understand disturbance induced spatial patterns occurring in Ontario forests have just begun, and there is a limited knowledge about how these spatial patterns relate to stand-level dynamics (Perera & Baldwin, 2000). Currently, we can only suggest some trends regarding the consequences of different forest disturbances that give rise to particular landscape patterns. If stand-level studies can be correlated with landscape alteration, then large shifts in species composition, biomass allocation, habitat quantity and quality can be assessed on a scale that is more appropriate for land management and large-scale preservation of biodiversity (Noss, 1983).

The structure, function and dynamics of landscapes are scale-dependent. The appropriate scale of investigation depends on the research question, organisms of interest and temporal parameters (Wiens, 1989; Wiens *et al.,* 1993). Anthropogenic disturbance can increase or decrease the heterogeneity of the landscape depending on the parameter and the spatial scale examined (Krummel *et al.,* 1987; Mladenoff *et al.,* 1993). At a coarse-grained scale (1:250 000 to 1: 10^6) human activities may reduce heterogeneity in mixed agricultural/forest landscapes, particularly with reference to patch shape (Krummel *et al.,* 1987; O'Neil *et al.,* 1988; Mladenoff *et al.,* 1993). However, at finer scales within entirely forested landscapes, natural and anthropogenic disturbances tend to create more complex and heterogeneous landscape patterns (Pastor & Broschart, 1990, Mladenoff *et al.,* 1993).

A multi-scale approach requires a number of methods for measuring both pattern and process at different scales. Many methods have been developed for quantifying landscape structure (i.e. landscape indices) and predicting the effects of landscape patterns (i.e. models). Remote sensing provides is an effective tool for the application of conceptual models within true landscapes. Improvements in the acquisition and processing of remotely sensed data, as well as an increasing focus on interdisciplinary approaches is enhancing the use of spatial analysis tools in a Geographic Information Systems (GIS) for ecological studies (Turner & Gardner, 1991; Fortin & Edwards, 2001).

The boundaries between heterogeneous patches provide a focal point for investigating stand-level changes in composition and distribution at a landscape-scale.

Larger amounts of cut edge may lead to a significant increase in species that favour edge and open-canopy conditions (Ranney *et al.,* 1981; Matlack, 1994; Murica, 1995; Perera & Baldwin, 2000). An increase in edge density indicates that habitat conditions for interior species have most likely declined. However, the degree to which the decline affects interior species within a study area is difficult to assess (Ripple *et al.,* 1991). Stand-level studies can provide the necessary information to assess the manner and degree to which interior species will be affected by such changes. Edge effects depend at least in part on the landscape context, suggesting that results obtained from locally conducted studies should to be evaluated in light of landscape-scale forest conditions (Donovan, 1997).

The aim of this study was to examine if a better ecological understanding of landscape pattern can be gained by incorporating stand-level data regarding species composition and distribution across edges into a landscape-level analysis of patch, core and edge area. This was approached by: i) comparing the structural legacy left by clearcutting and fire disturbance on a 1000 ha scale and a 250 ha scale and ii) providing ecological meaning associated with the spatial attributes of cutting and fire, by including disturbance index values derived from stand-level research. The methodological challenges associated with using input data from multiple scales and the significance of this approach in developing land management strategies that emulate natural disturbance patterns are discussed.

Methods

Study area and data sources

Located in the Black Sturgeon and Poshkokagan river watersheds (370000E 5458000N (NAD 27)), the study area was approximately 1750 km^2 and the landscape had been modification by both fire (Nipigon 10 burn) and clearcutting (Figure 36). The study area selected for the landscape-level analysis was a part of the study area used in the stand-level study in Chapter 1 (Figure 1).

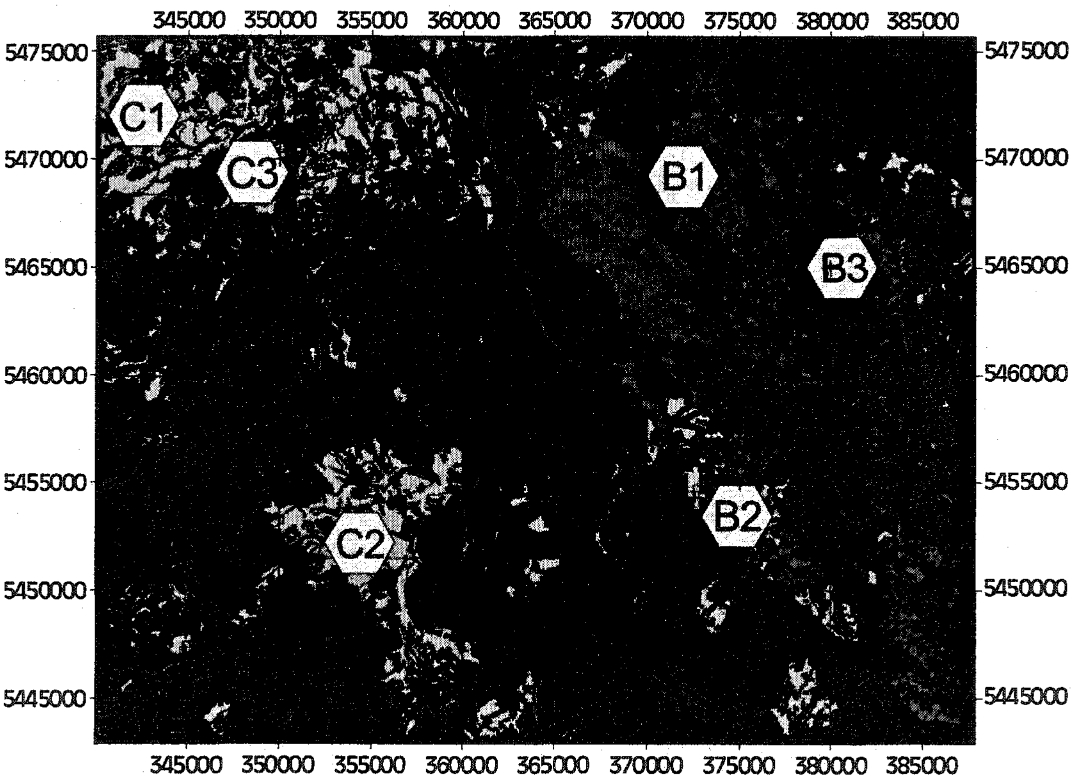


Figure 36. Study area with landscape sampling hexagons in clearcut and burnt areas. The light green area represents 1997 clearcuts, red area 1999 fire, dark green area forested land and blue area lakes. Datum: NAD27. Projection: UTM, Zone: 16.

Two disturbance types, clearcutting and fire were considered in this study. The temporal scale was confined to a single year for each disturbance type. Using the most recent data available, only 1997 clearcuts and a 1999 fire event were considered. The two data sources were: a 1997 Forest Resource Inventory (FRI) created from air photographs (Bowater Inc., Thunder Bay) and a 2002 burn intensity map created from the classification of 1999 Landsat TM images (Freeburn, 2002). Although, the burn intensity map included three burn intensity classes, only a single burn class (i.e. all burn intensities) was considered in this study. Classification accuracy of the burn map was high, with a user's accuracy of 90.5% and a Kappa Coefficient of 88.9% (Freeburn, 2002). User's accuracy refers to errors of commission, which is the probability that a class shown on a map actually represents that class on the ground. The Kappa coefficient includes both errors of commission and errors of omission and excludes agreements that occur by chance (Treitz & Howarth, 2000).

Dataset creation

Using ArcView GIS software (version 3.2) the datum of the Forest Resource Inventory (FRI) was converted from NAD83 to NAD27 to match that of the burn map. All 1997 clearcuts were identified and a clearcut layer was created. The burn map was imported into ArcView and a fire layer was created. The fire layer and the FRI data were intersected so that the fire layer included stand composition information from before the fire event. Hexagons 1000 ha and 250 ha were created and intersected with both the clearcut layer and the fire layer. Three1000 ha hexagons were randomly selected in the 1997 clearcut area and three 1000 ha hexagons were randomly selected within the 1999 burnt area (Figure 36). Hexagon selection was random with the exception that all water features were avoided. Within each of the six 1000 ha hexagons, two smaller 250 ha hexagons were also randomly selected.

Data analysis

Residual patch area, core area and edge

Patch Analyst provides a tool for quantifying landscape structure (Elkie *et al.*, 1999) and was used within the GIS to determine residual patch area, core area and edge. Residual patch area was determined within each hexagon by removing the 1997 clearcut and 1999 burnt patches. The core area of the residual patches within each hexagon window was also found. To determine core area a buffer distance must be selected. The buffer distance, therefore, must either be an arbitrary value or predetermined from stand-level studies. A 40 m buffer distance was used, which corresponds with the distance to which edge effects were measured in the stand-level study (Chapter 1). Two different edge depths were considered in this study. A 40 m buffer was created around the clearcut or burnt area. The first 20 m bordering the disturbed area was considered near edge, and the second 20 m beyond the near edge was considered far edge.

Disturbance index

The disturbance index was based upon the percentage of species showing a significant depth of edge influence (DEI) detected in Chapter 1. Values across conifer clearcut edges were used to derive clearcut disturbance index and values across conifer fire edges were used to derive the fire disturbance index. Both mixedwood and deciduous stands were present in the landscape, although conifer-dominated stands (primarily dominated by *Picea mariana*) were most abundant within the hexagon windows. The stand-level study (Chapter 1) only assessed the DEI at conifer fire edges and the DEI at conifer and deciduous clearcut edges was similar.

Between conifer clearcut and conifer fire edges, the highest percentage of species with a significant DEI was 26.71%, which occurred in the cut area. The disturbance index was standardized by dividing all values by the highest percentage, therefore, values in the disturbance index were between 1, where the greatest edge influence was detected and 0 where no edge influence was detected.

The percentage of species with a significant DEI was determined at 5 m intervals in the stand-level study. In this landscape-level study, the cut area, the near edge and the far edge were each assigned a unique disturbance value based upon the average standardized disturbance value detected from 20 to 5 m, -5 to –20 m and –25 to –40 m, respectively (Table 16). The disturbance index value was then determined by multiplying the total area detected for each edge location within the 1000ha and 250ha windows by the respective disturbance values.

Table 16. Disturbance index for disturbed areas across clearcut and fire edges.

Disturbance type	Edge location	Disturbance value
Clearcut	Cut	0.8642
	Near edge	0.0928
	Far edge	0.0714
Fire	Burn	0.6262
	Near edge	0.2578
	Far edge	0.1105

Statistical analysis

Frequency histograms were used to explore patterns in the size distribution of residual patches and core areas. Patch size distributions were non-normal and largely effected by infrequent but extreme values, requiring nonparametric tests. The Mann-Whitney U test available in SPSS version 9.0 (SPSS, 1999) was used for comparisons between disturbance type and disturbance size classes. The Mann-Whitney U test is similar to a t-test, but can be used when extreme values are leading to skewed distributions (Dytham, 1999). In a Mann-Whitney U test raw data is converted to ranks before the test is carried out.

The area and disturbance index value of patches, core areas and edges within clearcut and fire windows (1000 ha and 250 ha) were compared. In addition, comparisons were made between the amount of edge belonging to disturbance patches of different size. Disturbance patches of different size within 1000 ha and 250 ha windows were divided into two equal groups based on the median value.

Results

Residual patch area, core area and edge

Both clearcut and fire disturbance had similar a distribution of residual patch size and core area size within 1000 ha windows, with a high frequency of small patches/cores and only one or two larger patches/cores (Figure 37). Total core area within 1000 ha windows was 40 % less than total residual patch area for clearcut disturbance and 59% less than total residual patch area for fire disturbance. Absolute values were lower within 250 ha windows. However, the frequency distributions of residual patch and core area size were found to be similar to the 1000 ha windows (Figure 38).

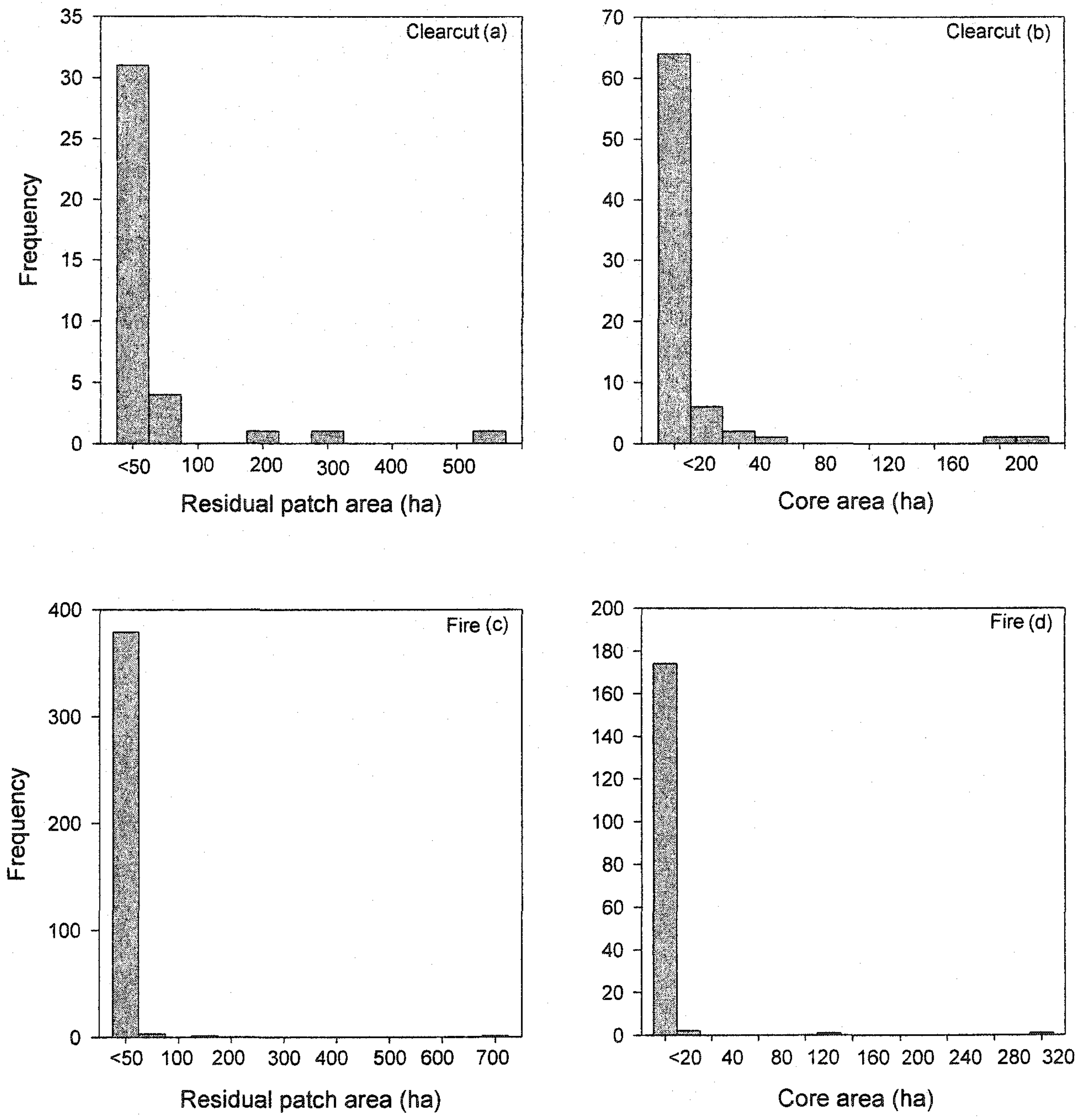


Figure 37. Residual patch area and core area in three 1000 ha windows in areas disturbed by clearcutting (a & b) and fire (c & d). Note the axes scales are different

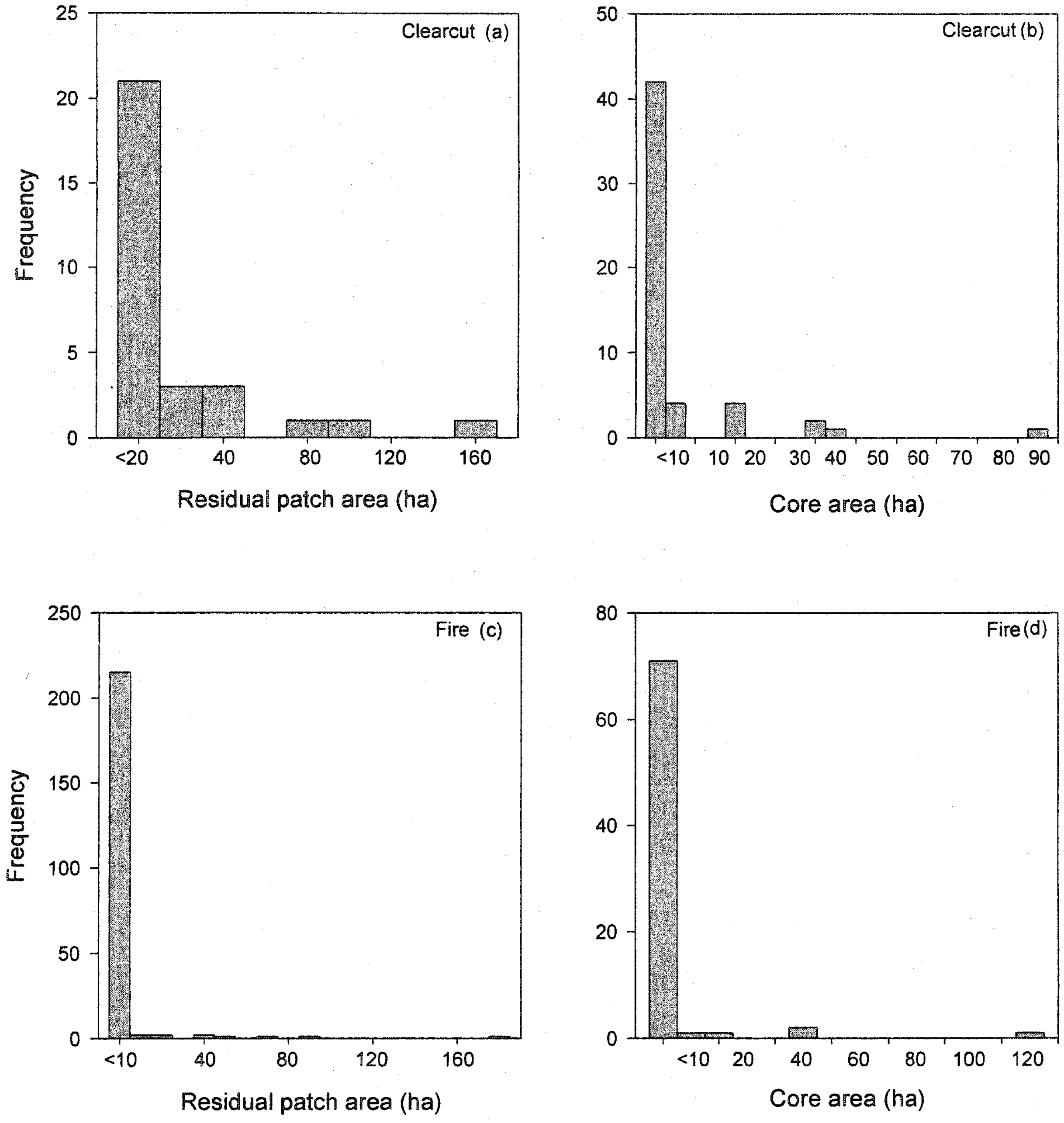


Figure 38. Residual patch area and core area in six 250 ha windows in areas disturbed by clearcutting (a & b) and fire (c & d). Note the axes scales are different

Although residual patch area and core area were not significantly different between the disturbance types (Mann-Whitney U, $p<0.05$), there were differences in both the number and the maximum size of patches. Burnt areas had a larger number of residual patches (384) and core areas (178) than clearcuts (38 and 75), most of which were < 50 and < 20 ha respectively (Table 17). The single largest residual patch and core area were found in the burnt area windows. Compared to the burnt area, the clearcut area had a lower total residual patch area, but a higher total core area. The mean of both residual patches and core areas was higher in clearcut than in fire disturbance windows (Table 17). The total area and mean area of residual patches and core areas followed a similar trend in 250 ha windows (Table 17).

Among the three 1000 ha windows in the clearcut area hexagon C2 and C3 had the largest and smallest cut area respectively (Figure 39). Similarly, in the three 1000 ha windows in the fire disturbance hexagon B1 and B2 had the largest and smallest burnt area (Figure 40). The 250 ha windows within each 1000 ha window had a similar amount of residual patch area and core area, varying only by approximately 20 ha (Table 18).

Compared to clearcut hexagon C2 , hexagon C3 had less cut area and more core area. Hexagon C3, however, had a greater amount of near and far edge (Table 18). Burnt area hexagon B2 had much less burnt area and more of core area compared to hexagon B1 (Table 18). The amount of near edge was similar between the two burnt area hexagons, but hexagon B1 had a slightly larger amount of near edge.

When the amount of edge as a function of disturbed area was compared using all hexagons the results were similar to the visual assessment of Figures 39 and 40.

Table 17. Number, minimum and maximum size, total area (sum), mean area and standard deviation of residual patches and core area in three 1000 ha and six 250 ha clearcut and fire windows.

Hexagon area	Habitat type	Disturbance	N	Minimum (ha)	Maximum (ha)	Sum (ha)	Mean (ha)	Standard Deviation
1000 ha	Residual patch	Clearcut	38	0.0007	549.6189	1378.073	36.2650	101.4825
		Fire	384	0.0003	695.9982	1437.9422	3.7446	36.7407
	Core area	Clearcut	75	0.0007	226.4189	832.3769	11.0983	35.2001
		Fire	178	0.0002	317.4183	593.6216	3.3349	26.0262
250 ha	Residual patch	Clearcut	30	0.0002	162.5921	652.6057	21.7535	37.4326
		Fire	225	0.0002	182.0613	700.9558	3.1153	15.3868
	Core area	Clearcut	54	0.0007	95.8913	362.4599	6.7122	16.1864
		Fire	76	0.0002	130.3718	299.2897	3.9380	17.0680

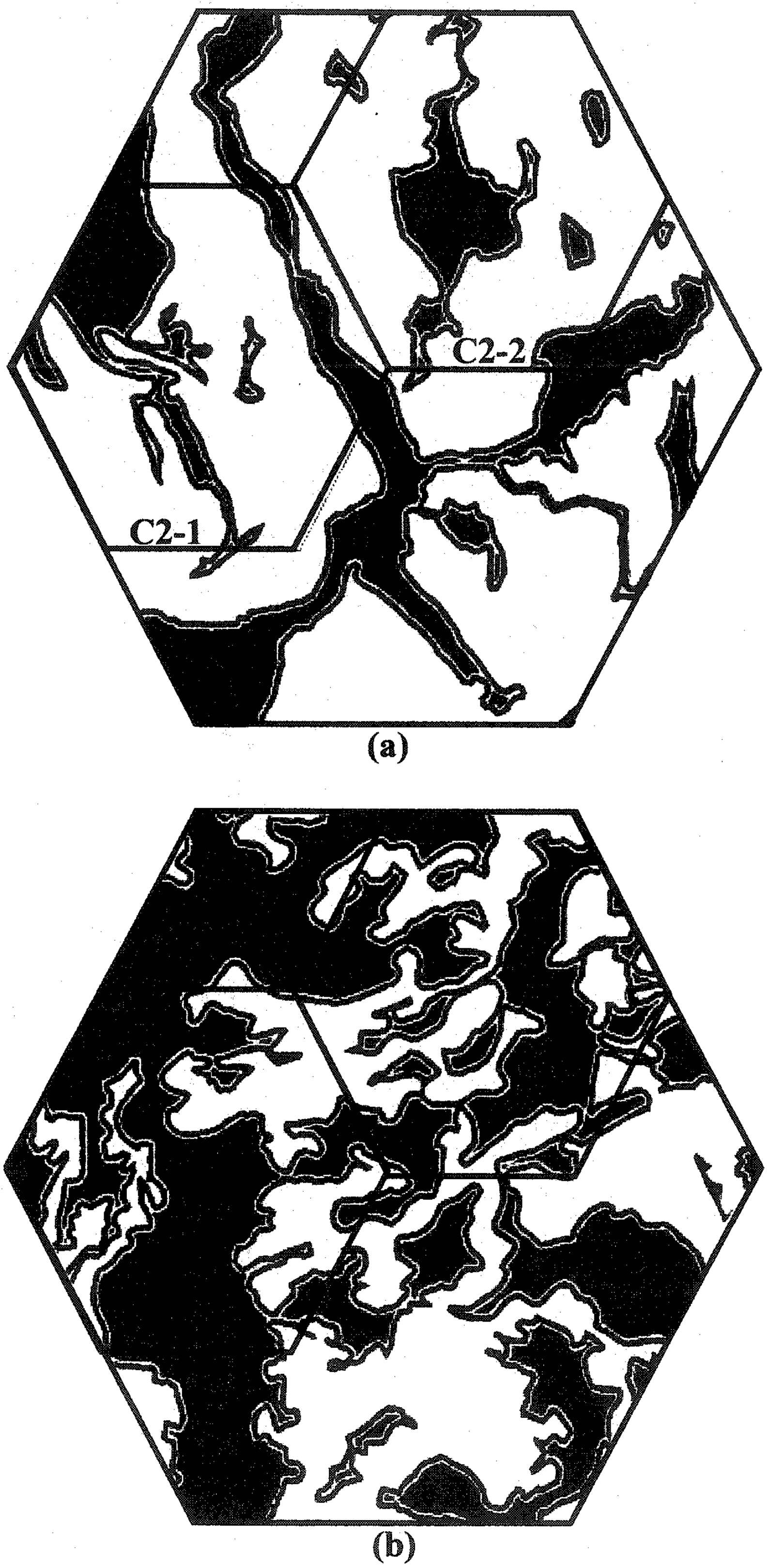
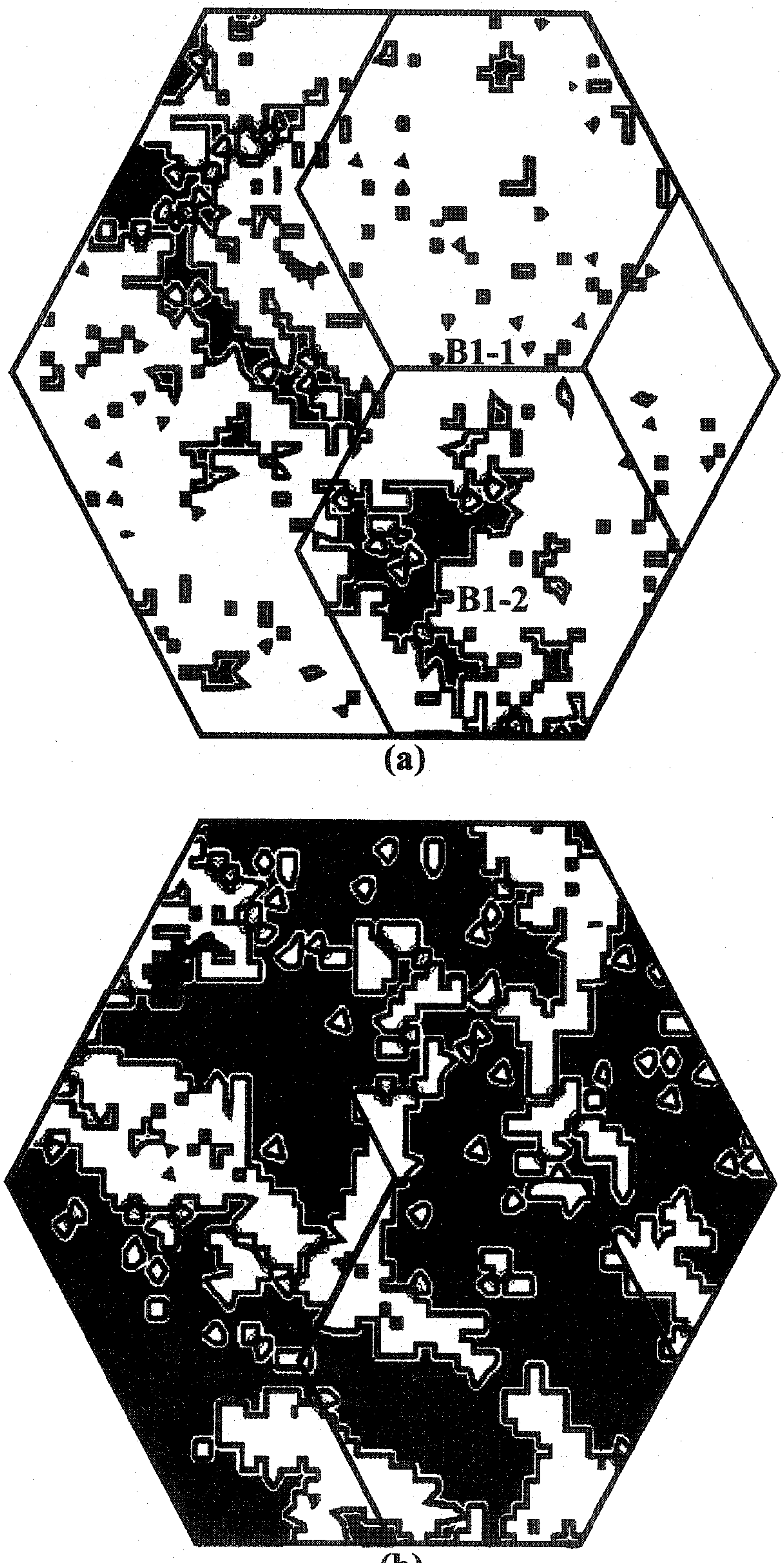


Figure 39. Two 1000 ha hexagons C2 (a) and C3 (b) of Figure 41 each containing two 250 ha windows (C2-1, C2-2; C3-1, C3-2). The white area represents the clearcut, green area residual patch, and red and yellow near and far edge respectively.



(a)

(b)

Figure 40. Two 1000 ha hexagons B1 (a) and B2 (b) of Figure 41 each containing two 250 ha windows (B1-1, B1-2; B2-1, B2-2). The white area represents the burn, green area residual patch, and red and yellow near and far edge respectively.

Table 18. Percentage of disturbed area, residual patch area, core area (beyond 40 m buffer), near edge (20 m width) and far edge (20 m width) for 1000 ha hexagons C2, C3, B1, and B2 and 250 ha hexagons C2-1, C2-2; C3-1, C3-2; B4-1, B4-2; B5-1, and B5-2.

Hexagon		Disturbed area (%)	Residual area (%)	Core area (%)	Near edge area (%)	Far edge area (%)
Number	Area					
C2	1000 ha	68.9010	31.0989	15.9429	9.6198	8.3102
C2-1	250 ha	68.1288	31.8831	14.4010	12.5059	10.6784
C2-2	250 ha	76.2404	23.7558	11.5682	10.5578	9.8947
C3	1000 ha	38.3022	61.7023	37.6101	13.1189	11.8401
C3-1	250 ha	30.9726	69.0260	41.9435	14.0309	12.6871
C3-2	250 ha	37.3566	62.6415	31.1931	17.4792	16.3323
B1	1000 ha	77.7347	22.3702	4.1307	14.0064	8.7336
B1-1	250 ha	91.0251	8.97365	0.2955	11.5758	6.6281
B1-2	250 ha	66.8814	33.1106	8.8663	19.2036	14.8417
B2	1000 ha	28.0690	72.0411	45.9134	13.8175	13.0434
B2-1	250 ha	25.2679	74.7241	52.2422	13.0029	12.8702
B2-2	250 ha	30.4149	69.6930	41.5455	13.8798	12.4542

The burnt area had a slightly higher amount of edge in both the 1000 ha and 250 ha windows compared to the clearcut area; when the total edge area was calculated as a proportion of the total cut or burnt area (Figure 41).

The proportion of edge (i.e. amount of edge/disturbed area) was also higher for smaller disturbance patches within both 1000 ha and 250 ha windows. Within 1000 ha windows disturbance patches below the 450 ha median had more edge and within 250 ha windows disturbance patches below the 150 ha median had more edge. The proportion of edge was significantly different between disturbance patch sizes only at the 250 ha scale (Appendix XVII).

Disturbance Index

Disturbance index values for cut/burn areas, near edge and far edge had a slightly different pattern than area in both 1000 ha and 250 ha windows (Figure 42).

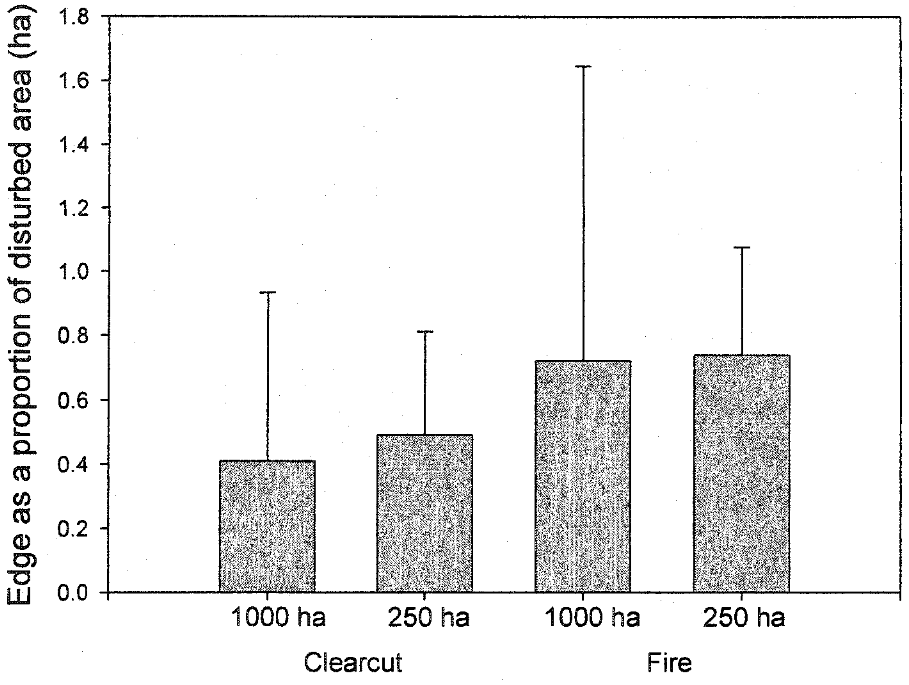


Figure 41. Mean total edge as a proportion of cut/burnt area in 1000 ha and 250 ha clearcut and fire windows. Bars represent mean with 95% confidence interval.

Clearcut areas had a higher disturbance value than burnt areas. Fire disturbance had significantly higher disturbance values associated with and the near edge and far edge within 250 ha windows (Appendix XVIII).

The total area disturbed including the cut/burnt area, the near edge and far edge was slightly higher in both 1000 ha and 250 ha fire windows than in clearcut windows (Figure 43). The total Disturbance Index value, however, was higher for both window sizes in clearcut areas. Total disturbed area was not significantly different between the disturbance types in either window size (Mann-Whitney U, $p< 0.05$). However, in 250 ha windows the total Disturbance Index value as a proportion of the total disturbed area was significantly higher for clearcut disturbance (Appendix XIX).

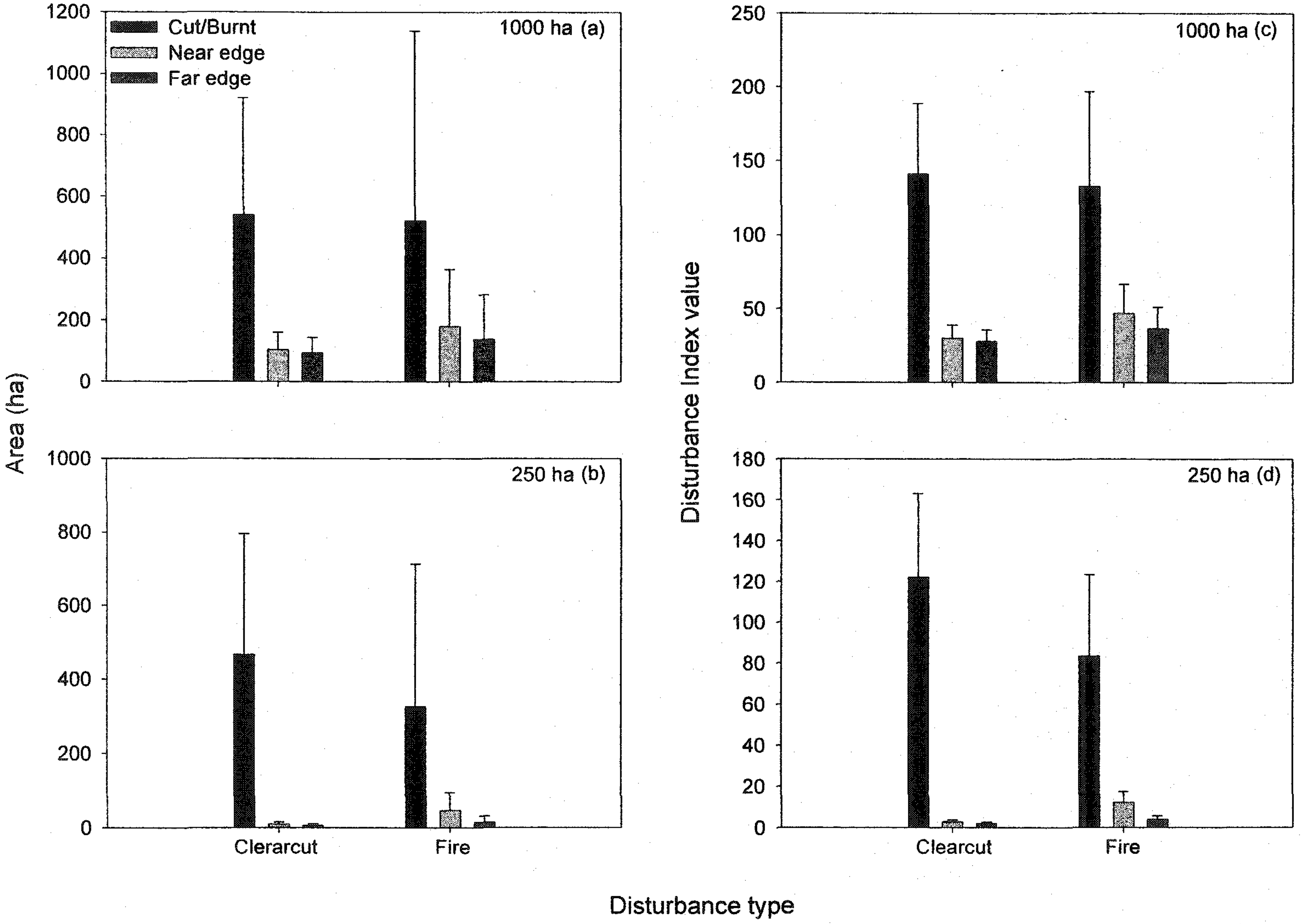


Figure 42. Mean area and Disturbance Index values of cut/burnt, near edge (0-20 m) and far edge (20-40 m) within 1000 ha (a & c) and 250 ha windows (b & d) respectively. Bars represent mean with 95% confidence interval.

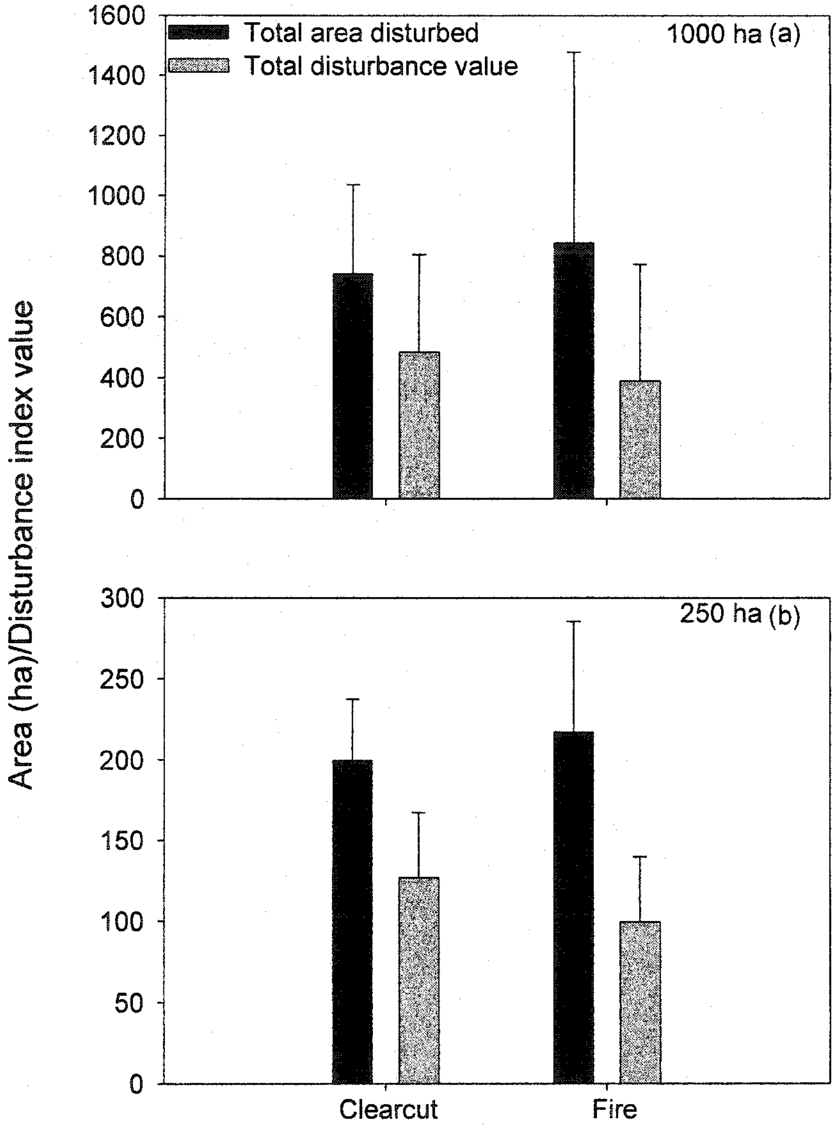


Figure 43. Mean total area and total Disturbance Index values within 1000 ha (a) and 250 ha (b) windows. Bars represent mean with 95% confidence interval.

Discussion

The incorporation of stand-level data into the landscape-level analysis provided insight into the ecological consequences of landscape patterns resulting from clearcutting and fire. The two different scales used in this study did not affect the trends detected. However, similar techniques need to be tested at a larger scale to gain a more comprehensive understanding of landscape structure and the implications of incorporating stand-level data. In addition, a more diverse array of landscape indices needs to be incorporated into this type of analysis to ensure landscape patterns and the resulting ecological consequences are fully understood. This study reveals many of the methodological challenges that must be overcome to accurately characterize spatial patterns at the landscape-scale. Even though burnt areas had a larger amount of edge, the high Disturbance Index value associated with clearcut areas, resulted in clearcut disturbance having a higher overall disturbance value.

Scale

The two different scales used in this study did not affect the major trends detected in landscape structure and disturbance. Demonstration of the effect of scale may require windows with a greater difference in size. Due to the scale of investigation and the input data used in this study, burnt areas were found to have more edge, which is somewhat contradictory to the current understanding of the amount of edge associated with clearcutting and fire. In a larger landscape context fires tend to be more clustered creating less edge, while harvesting is dispersed across the landscape creating more edge (Perera & Baldwin, 2000). In this study, however, equal amounts of burnt and clearcut land were compared, which is not representative of the proportion of burnt and clearcut land on a larger scale. The detection of more edge associated with fire disturbance most likely reflects this skewed proportion of burnt to cut land and differences in the properties and scale of the data sources used (see p. 158).

Difference in sample size between the 1000 ha and 250 ha scale influenced the detection of statistically significant results. Results were not significantly different at the 1000 ha scale, which had only three samples per disturbance type. However, at the 250 ha scale, which had six samples per disturbance type, a number of landscape variables, such as the proportion of edge belonging to different disturbance patch sizes, and Disturbance Index values due to clearcutting and fire were significantly different. An increase in the sample size of 1000 ha windows, would likely lead to statistically significant results for some landscape variables. Other techniques, such as spatial convolution filtering, may give a more accurate assessment of the average condition of a larger area (Jensen, 1996). A convolution mask composed of several 250 or 1000 ha windows could be passed over a landscape with both fire and clearcutting disturbance. The average patch, core and edge area calculated within the convolution mask for each of the disturbance types could then be compared.

Only a single fire event and two clearcut areas in close proximity were included in this study. In order to develop a more comprehensive understanding of the spatial patterns associated with clearcutting and fire, a number of burns and clearcuts across the landscape need to be included. Stand-level data would also need to be collected in a number of different burns to gain a more accurate estimate of the average disturbance value across edges. New approaches to sampling must be taken into consideration when scaling up from spatially restricted samples to the entire landscape (Botkin & Simpson, 1990; Caldwell *et al.,* 1993; Clark *et al.,* 1996).

Residual patch area, core area and edge

The similarity of residual patch size and core area size distribution, suggests that knowledge of residual patch size distribution may help forest managers in estimating the remaining core area distributions in the landscape. Total core area, however, may not follow the same trend as the total residual patch area. Forest interior will disappear much more rapidly in landscapes with wide edges or a large depth of edge (Franklin & Forman 1987). For example, in a landscape with 10 ha patches and an edge width of 160 m, there would be no forest interior remaining after 50 % of the landscape has been cut. Assessing the core area is perhaps the most valuable means for determining interior habitat availability (Haines-Young & Chopping, 1996). The remaining interior habitat within a landscape may be more ecologically significant in terms of plant species dynamics than changes in other patch dynamics (Ripple *et al.,* 1991).

Clearcut and fire disturbance had similar residual patch size distribution, with many small patches of undisturbed forest scattered across the landscape and rare occurrences of large patches. In the clearcut and burnt area windows the single largest patch accounted for approximately 40 % and 48 % of the total residual patch area respectively. While large residual patches may be rare in landscapes disturbed by both fire and clearcutting, their major contribution to residual forest lends them special attention. Large patches with low edge to area ratios tend to have more interior habitat (Forman & Godron, 1981; Zipperer, 1993).

In this study burnt areas had a larger number of small residual patches and had the single largest residual patch exceeding the largest clearcut residual patch by approximately 145 ha. Similarly, Spies *et al.,* (1994) found clearcut patch size was similar to fire patch size, however clearcut patch sizes had a narrower size distribution. Hall *et al.,* (1991) found larger patch sizes following logging disturbance and suggested that fire suppression may be responsible for the lack of large patches.

Burnt areas in this study had a larger total residual patch area, but less total core area compared to clearcutting. In addition, compared to clearcut areas, burnt areas had a larger amount of edge and higher proportion of edge to disturbed area (cut or burn). The large amount of edge in burnt areas and specifically in hexagon B1 was due to a large number of small residual patches that were often composed entirely of edge. Small fragments are more strongly influenced by external factors than internal factors, primarily due to edge effects (Harris, 1988; Yahner, 1988; Saunders *et al.,* 1991).

This study revealed a number of methodological challenges that must be overcome when employing multi-scale techniques. Since two different types of input data were used in this study, the inherent properties of the data sources must be considered. Patch boundaries for the burnt area were determined through a classification procedure of a remotely sensed image. Remotely sensed images are composed of a two dimensional array of pixels and a pixel is the smallest nondivisible two-dimensional picture element (Jensen, 1996). The smallest patch size in the burnt area was pre-determined based upon the size of a single pixel (30 x 30 m), whereas the minimum patch size in the clearcut area was based upon the smallest polygon (7.5 ha) in the FRI. The delineation of clearcut boundaries was the result of digitized air photographs (1: 20,000);

therefore landscape features were more generalized and clearcut areas had a much larger minimum patch size. The larger number of small patches found in the burnt area is most likely an artifact of the different minimum patch sizes of the input data. In addition, a few very small residual patches were created where the boundary of the hexagon included only a sliver of an adjoining patch. To eliminate these slivers and standardize the minimum patch size of the input data a modal filter could be applied.

Another important consideration is the shape of fire and clearcut patches. Shape is a major determinant of the amount of edge created within the landscape and irregular patch shapes can enhance edge effects (Ranney *et al.,* 1981; Laurence & Yensen, 1991). Long thin remnants have proportionally more edge than square or round remnants (Diamond, 1975; Saunder *et al.,* 1991). Shape becomes increasingly important in smaller forest fragments, because it can greatly influence the edge to interior ratio. The larger amount of edge detected in the burnt areas was not only due to a smaller minimum patch size, but was also an artifact of comparing raster and vector data. Patches associated with fire disturbance were limited in their shape to squares (i.e. pixels), which affected the amount of edge detected due to the stair-case effect. This study not only illustrates the sensitivity of landscape indices to shape, especially indices related to edge, but also emphasizes the importance of ensuring input data has the same currency. Conversion of the clearcut data (FRI) to a raster format (i.e. pixels) and then back to vectors would allow for accurate direct comparisons to be made between the two disturbances. In this study, the detection of spatial patterns that accurately reflect patterns associated with fire and clearcutting were limited due to the use of input data with different scales and spatial properties. Regardless of the inaccuracies in detecting spatial patterns, the technique used to incorporate stand-level data did provide insight into the ecological consequences of these patterns.

Disturbance Index

The application of the Disturbance Index not only provided a connection between the stand-level study (Chapter 1) and the landscape-level study, but also helped in assessing ecological values associated with structural characteristics of the landscape. Changes in species composition and abundance across edges can provide insight into the interactions between internal and external patch processes, which are likely to be of critical importance (Saunders *et al.,* 1991). Species composition will differ depending on the amount of interior habitat present, which is a function of the minimum patch size and width of edge conditions (Forman & Franklin, 1987). The dispersal and patch choice of different species is dependent upon how each individual species responds to an ecotone or patch (Gosz, 1991; Weins *et al.,* 1993). If the theory of island biogeography is extended to include relative habitat area, a community is predicted to be most rich in species adapted to growth and establishment in the spatially most common patch types (MacArthur & Wilson, 1967; Denslow, 1980). Laurence & Yensen, (1991) suggested that interior species that are sensitive to edge should have a strong positive correlation with core area. Species that depend on primary habitat but are not edge sensitive should have a positive correlation with total area and edge specialists should have a positive correlation with the total length of fragment edges.

In this study total area disturbed by clearcutting and fire was very similar, however, the total disturbance value was higher in clearcut than burnt areas. The disturbance value was highest in the cut, which was due to a large number of shade-intolerant weedy species that had a significant DEI (Chapter 1, Figure 6). Burnt areas had a lower disturbance value indicating that four to five years after the fire event, burnt areas were more similar to interior conditions (Chapter 1, Figure 5). The species composition and abundance of clearcut areas may have more drastic differences from interior conditions resulting in greater disturbance. Spies *et al.*, (1994) found that clearcuts cumulatively contribute more early successional forest patches to the landscape. Consideration of not only species numbers, but also their functional types is essential in the development of stand and landscape-level practices that maintain biodiversity.

Compared to clearcut disturbance, fire had slightly more near and far edge and higher disturbance values for near and far edge. The higher disturbance value of fire edges was not only the result of greater edge area, but also due to the application of higher Disturbance Index values (see Table 16). Compared to clearcut edges, fire edges had a higher number of species with a significant DEI past the edge (Chapter 1, Figure 5). High moisture at fire edges led to distinct shifts in the understory community (Chapter 1, Figure 10). Significantly higher disturbance values for near and far edge, therefore, do not necessarily indicate that fire edges present a greater landscape barrier, but suggest that fire edges are more heterogeneous than clearcut edges. Therefore, in comparison to clearcut edges, burnt edges appear to be more structurally heterogeneous on a landscape-level scale, and compositionally their edges display more heterogeneity on a stand-level scale. Tilman (1994) suggested that spatial heterogeneity may lead to the maintenance of more species within an area. The spatial heterogeneity associated with fire edges most likely contributes to higher richness values observed at fire edges in Chapter 1.

Although the burnt area had more edge area and had higher disturbance values associated with edge, overall the burnt area had a lower disturbance index value than the clearcut area. The high Disturbance Index value associated with the cut area at clearcut edges resulted in clearcuts having a significantly higher disturbance value (as a proportion of disturbed area). At a landscape-scale larger than the one used in this study, more clearcut area than burnt area would be expected. Therefore, application of a similar Disturbance Index would result in an even higher disturbance value associated with clearcutting. Establishment of non-native species seems to be enhanced by some forms of disturbance, although invasion of remnants may be restricted to the edge if disturbance factors decline with distance from the edge (Cale & Hobbs, 1991; Panetta & Hopkins, 1991; Saunders *et al.,* 1991). Boundary permeability or the degree to which a boundary deflects the movement of abiotic and biotic vectors is an important edge characteristic and has important consequences on a landscape-scale. Edge effects in the boreal forest appear to be mitigated relatively rapidly by post-disturbance regeneration and management may need to focus on reducing the disturbance value within the clearcut itself.

Management recommendations

Anthropocentric disturbance regimes often increase microsite availability for invasive species (Hobbs & Huenneke, 1992; Peltzer *et al.,* 2000). The use of retention patches provides one such solution, by providing refuge habitat for interior species and structural diversity. Increasing the number of retention patches would also help to mimic the larger number of small patches left on the landscape by fire. Current forest management guidelines in Ontario suggest 2 to 8% of planned disturbance area, depending on forest cover type, be left as insular residual patches (OMNR, 2001). Although, forest managers must consider this guideline, it is not mandatory and open for interpretation. Findings from this study suggest that in order to emulate the structural legacy of fire disturbance, residual patch requirements must not only become mandatory, but also a larger percentage of the disturbed area must be left as small residual patches. Current standards (mandatory) in Ontario regarding insular residual patches left within cutovers, state that patches must be well distributed, emulate fire residual patch distribution and are unavailable for subsequent harvest (OMNR, 2001).

Rich and productive patches of high species diversity cannot be expected to maintain long-term native diversity when they exist as isolated fragments (Noss & Harris, 1986). Providing landscape connectivity by linking patches with habitat corridors is one possible way to reduce the problems associated with small fragments and patch isolation. In addition, widening existing corridors to allow for edge effects may facilitate the flow of species, individuals, genes and energy across the landscape (Noss & Harris, 1986).

Fire, the natural disturbance regime in the boreal forest, tends to leave large disturbed areas; therefore, boreal forest species may be more adapted to recolonization associated with large-scale fire disturbance. Increasing clearcut size, however, may be detrimental due to the higher disturbance value associated with clearcuts. Interior species that are sensitive to disturbance and have a limited dispersal range may be unable to fully recolonize larger areas in the time between two successive disturbance events. Burnet & Oheimb (1998) suggested that it may take as long as 70 years for an area 30-35 m into recently disturbed temperate forest to attain the species richness of adjacent undisturbed forest. If natural disturbance regimes are to be emulated through increasing clearcut size, forest management practices many need to include longer rotations in order to maintain understory species diversity (Halpern & Spies, 1995; Burnet & Oheimb, 1998). At historic rates of disturbance, the patterns of mortality and generation of establishment sites should be most favourable for the largest number of species (Denslow, 1980). Emulating natural disturbance regimes, therefore, may assist in maintenance of the highest total species diversity.

Conservation efforts have often been very narrow in space and time, focusing on individual management areas or parks, instead of whole landscapes, and providing protection for local populations instead of the larger systems in which they interact (Noss & Harris, 1986). Landscape-level research may ignore the processes and patterns occurring at finer scales due to filtering or averaging effects. Conversely, focusing entirely on fine-scale effects may overlook broader scale implications (Gosz, 1991). Therefore a comprehensive multi-scale approach may be the only acceptable alternative to the current form of forest management.

General Discussion

Much of the past research on edge effects has been conducted in tropical or temperate environments (e.g. Wales, 1972; Ranney *et al.,* 1981; Kapos, 1989; Pallik & Murphy, 1990; Williams-Linera 1990a & b; Matlack, 1993 & 1994; Jose *et al.,* 1996; Cadenasso *et al.,* 1997; Mesquita *et al.,* 1999; Gascon *et al.,* 2000). Both the abiotic and the biotic responses in clearcut and fire edges depend upon the type of forest ecosystem (Chen *et al.,* 1992). In addition, most studies of edge vegetation have focused on woody species; therefore, little is known about the impact of edge creation on understory species, or the flora as a whole (Matlack, 1994). The understory layer is very important when considering the preservation of biodiversity because the understory supports much of the diversity both directly and indirectly. This thesis on edge effects in the boreal forest not only provides information regarding edge characteristics and the depth of edge influence, but also gives insight into the presence or absence of ecotonal features that other studies have suggested to be inherent.

Differential response of species to changes in the physical environment across edges may result in localized shifts in species composition (Murica, 1995). Several studies have found that species composition is altered along gradients from the edge to the interior, often with an increase in ruderal, exotic species better adapted to drier and warmer climates closer to the edge (Ranney *et al.,* 1981; Matlack, 1994; Halpern & Spies, 1995). In this thesis, clearcut areas adjacent to conifer and deciduous edges and upland conifer buffer edges were all characterized by a large number of weedy shade-intolerant herbs that were not found in the interior or at undisturbed stream edges. The depth of edge influence (DEI), however, was greatly decreased for most response variables 10 m past the clearcut edge, with the exception of a significant DEI for some response variables at 40 m. Fewer weedy shade-intolerant herbs were found in burnt areas or penetrating burnt edges. High moisture conditions at fire edges appeared to buffer edge effects. The number of species with a significant DEI was higher beyond fire edges than clearcut edges, which was due to distinctive shifts in community composition in response to higher soil moisture at burnt edges. Changes in plant physiognomy were found at all edges; however, the presence of distinctive communities across the edge was only found at fire edges and across the upland-riparian ecotone in buffers.

Boreal forests occur at high latitudes where low solar angles should result in light penetrating further into the interior; therefore, canopy cover may play a very important role in the depth of edge influence (Harper & Macdonald, 2002). Similar to many studies, this thesis found the DEI for understory variables was greater than for overstory variables (Palik & Murphy, 1990; Williams-Linera 1990a; Chen *et al.,* 1992; Malcolm, 1994; Harper & Macdonald, 2001; Harper & Macdonald, 2002). The importance of an intact canopy in maintaining undisturbed conditions beyond the edge was best exemplified by the response of species across riparian buffers (see Chapter 2). The penetration of species from the upland clearcut edge was limited at wide buffers (40 m or greater), however, a larger number of species were found to have a significant DEI across the entire width of narrow buffers (30 m or less). Narrow buffers did not appear to be as effective at ameliorating the high light conditions of the clearcut. Narrow buffers and buffers with structural canopy damage likely resulted in higher light levels in the riparian area, which in turn resulted in a high diversity and abundance of riparian species near the stream. There was some evidence (see Chapter 1) of the initial development of a side canopy due to increases in tall shrubs. Shortly after logging, fast-growing shrubs (e.g. *Alnus* sp., *Rubus* sp., and *Salix* sp.) can invade the clearcut and inner edge of adjacent forest stands, taking advantage of increased light availability and may act to rapidly decrease light "sealing" newly formed edges (Wales, 1972; Matlack, 1994; Mallik *et al.*, 1997; Mesquita *et al.,* 1999; Burton, 2002).

Early recovery of understory diversity following logging and burning has been described as following two sequential successional processes: rapid colonization by ruderal, non-forest species and the gradual reestablishment of characteristic understory species (Halpern & Spies, 1995). The community composition of regenerating clearcuts is changed considerably from that of areas disturbed by fire; for example, understory of juvenile forests may persist much longer in clearcut stands than in burnt stands (Carleton, 2000). Disturbance Index values derived from the percentage of species with a significant DEI in Chapter 1 reflect the larger number of early successional species that were present in clearcut areas. The application of the Disturbance Index to a landscape-scale in Chapter 4 resulted in a higher disturbance value associated with clearcuts even when less edge area was present.

Anthropogenic ecotones are very recent in evolutionary time; therefore, it can be assumed that native ecotonal species occur by pre-adaptation (Llyod *et al.,* 2000). No species were found exclusively at the edge, however, a number of boreal forest species appear to be able to occupy the edge. In this thesis, a number of shade-tolerant generalist herbs and shrubs were found across the entire edge, surviving both in the clearcut and taking advantage of the more shaded area under the canopy. Survival of generalists in the clearcut was likely influenced by adaptation to above ground disturbance.

The species that appeared to have the most negative response to edges were bryophytes. Both pleurocarpous and sphagnum mosses had a lower abundance in the clearcut area compared to the interior conditions. In Chapter 3 *P. commune* and *H. splendens* had significantly less growth and poorer vitality in the clearcut and up to approximately 10 m past the cut edge towards the stream. As landscapes become increasingly disturbed, the frequency of microhabitats representative of the disturbed condition will also increase. Interior species, such as *H. splendens*, however, are limited by disturbed habitats and may become increasingly scarce in managed landscapes. The creation of forest edges and the resulting alteration of abiotic and biotic conditions may be particularly disadvantageous for organisms adapted to interior conditions (Renhorn *et al.,* 1997).

The impact of edge effects are not limited to plant species response and multiple processes including species interactions may be altered (Fagan *et al.,* 1999). For example, seed predation by rodents at the edge can affect plant population dynamics (Kollomann & Buschor, 2002; Tallmon *et al.,* 2003). Edge effects may reduce the probability of species dispersal between fragments or into clearcut areas. The dispersal of flying insects or potential pollinators is significantly influenced by wind speed, temperature, humidity and solar radiation (Johnson, 1969), all of which can be altered due to edge creation.

Wildlife managers have traditionally considered edges as a positive landscape feature, because species diversity often increases near habitat edges (Yahner, 1988). A number of studies, however, have suggested that edges may act as barriers for various fauna. Some small mammals, such as deer mice (*Peromysucs maniculatus*) and voles

(*Clethrionomys* spp.) have shown an aversion to edges (Shlaepfer & Gavin, 2001; Sekgororoane & Dilworth, 1995). Seasonal edge effects have been observed in both lizards (*Norops* spp.) and frogs (*Eleutherodactylus* spp.), with a higher abundance of species found in the interior than near the edge after the onset of the wet season (Shlaepfer & Gavin, 2001). Several studies have found an edge response in bird species with significantly greater nest predation and parasitism in edge habitats and highly fragmented landscapes (Paton, 1994; Major & Kendal, 1996; Donovan *et al.,* 1997). Forest-dependent bird species in riparian buffers appear to decline with decreasing buffer width (Hannon *et al.,* 2002). In addition, higher bird species diversity has been observed during post-fire succession as compared to clearcut areas due to the presence of burnt trees, which provide nesting habitat (Per-Anders *et al.,* 1992).

Management recommendations

Management strategies have tended to focus on specific habitats rather than the boundaries between habitats; therefore, the development of management strategies that directly address boundary dynamics is a relatively new challenge (Risser, 1990). In this thesis many management recommendations regarding the emulation of natural disturbance were made based on the comparison of edges created by both fire and clearcutting at the stand-level and landscape-level.

At the stand-level, edges in the boreal forest of northwestern Ontario appear to be relatively effective at buffering edge effects. The number of response variables with a significant DEI greatly decreased 10 m past the clearcut edge, with the exception of some compositional changes occurring up to 40 m, which was the furthest distance measured in this study.

Residual patches or peninsulas left on the landscape to emulate natural fire disturbance must allow for at least 40 m of edge habitat on their southern border if they are to maintain interior conditions. To emulate the structural legacy left by fires, discourage weedy species invasion and provide faunal habitat, more stems should be left, especially near edges. From the stand-level observations made in this study it appears that the presence of higher ground moisture at clearcut edges may be paramount to emulating natural fire disturbance.

On the landscape-scale, increasing clearcut size to emulate large fire events may be detrimental due to the higher disturbance value associated with clearcuts. As discussed in Chapter 4, clearcuts had the highest Disturbance Index value, therefore regardless of the distribution of clearcuts, more cut area will result in higher disturbance values. If natural disturbance regimes are to be emulated through increasing clearcut size, forest management practices many need to include longer rotations in order to maintain understory species diversity (Halpern & Spies, 1995; Burnet & Oheimb, 1998). The use of retention patches in clearcut areas would help to mimic the larger number of small patches left on the landscape by fire and reduce the disturbance value of clearcuts by providing structural diversity and refuge habitat for interior species. Current forest management guidelines regarding the use of retention patches are not mandatory. Findings from this study suggest that in order to emulate the structural legacy of fire disturbance, residual patch requirements must not only become mandatory, but also a larger percentage of the disturbed area must be left as small residual patches. In addition, a multi-scale approach that incorporates both landscape-scale processes and patterns with fine-scale responses is necessary for a comprehensive approach to forest management.

A number of management recommendations regarding riparian buffers were also developed in this thesis. The high level of inherent variation in riparian habitats makes the detection of significant changes difficult. In addition, site-to-site variation appears to play a significant role in the response of species to harvesting in the upland. For example, sites with a higher canopy density may not require as wide a buffer as sites with a more sparse canopy. Findings from this thesis suggest that current buffer guidelines may allow for the maintenance of understory composition representative of undisturbed riparian areas, but may not effectively mitigate microclimatic change leading to changes in species abundance at the stream edge. A distance of > 40 m may be required for the amelioration of microclimatic gradients penetrating the buffer from the clearcut edge. In addition, broader perspectives that incorporate the relative importance of large-scale disturbance and give precedence to maintaining hydrological connectivity and viable riparian corridors are necessary (Naiman *et al.*, 1993).

Future research

More research is needed in the boreal forest regarding edge effects. A number of issues not addressed in this thesis require attention:

1) An understanding of changes in edge effects over time, including the rate of canopy closure and understory recovery, is needed to assess the long-term stability of upland residual patches and riparian buffers.

2) Monitoring microclimatic conditions across edges is needed in order to develop a more precise understanding of the response of plants to microclimatic change.

3) Studies comparing both pre- and post-harvest conditions are needed to help determine the effects of pre-harvest conditions on the recovery of disturbed areas and the depth of edge.

4) The ability of retention patches to function as sources of seed and vegetative regeneration in disturbed areas should be determined if retention patches are to be incorporated into forest management practices.

5) Characterization of natural fire boundaries with respect to species composition, soil moisture, slope, topography and standing stem density would help in the development of more realistic forest management guidelines emulating natural disturbance.

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Appendix I

Study sites for each of the edge types. UTM co-ordinates are in NAD27. Orientation of for all transects at each site, and buffer width for all buffer transects are given. Notes refer to important site characteristics or discrepancies.

Edge types	Site	UTM27_X	UTM27_Y	Transect orientation	Notes
Conifer clearcut	Carcass-C1	387 464	5415131	T1-186°, T2-186°	Soil disturbance from logging equipment in cut
	3rd Southline-C2	368912	5439394	T1-207°, T2-207°	Wet and bog-like towards interior, cut planted with Jack pine
	Church Rd. Cut-C3	388650	5436121	T1-143°, T2-143°	Edge uneven, scattered deciduous trees, marshy area on T2
	Death By Bev-C4	366178	5447430	T1-158°, T2-155°	Widely spaced tree, small patches of Alder, beside large blowdown
	Dog's B-fast-C5	364710	5451294	T1-177°, T2-177°	High species variability, blowdown at edge
	JP on Posh-C6	343260	5468097	T1-135°, T2-135°	Scattered Jack pine, interior done in adjacent patch
	Moose Tooth-C7	346716	5395109	T1-200°, T2-215°	Lower lying moist area past edge
	Memory Lane-C8	336628	5440153	T1-190°, T2-190°	Interior had high soil moisture
	Hot n' Sticky-C9	349444	5403541	T1-180°, T2-190°	Canopy widely spaced trees, drier conditions past edge
	Finale-C10	352973	5407347	T1-200°, T2-200°	Canopy scattered Jack pine, continuous moss carpets
Deciduous clearcut	1st Southline-D1	380495	5437579	T1-135°, T2-135°	Small area of blowdown in interior
	Bottom BS-D2	384439	5422943	T1-178°, T2-191°	Cut planted with White spruce, T2 near small path
	Little Crk-D3	383 795	5423692	T1-189°, T2-165°	Edge uneven, dense shrubs at edge, small drier creek past end T1
	Edge Gods-D4	366606	5457870	T1-202°, T2-202°	Extensive blowdown at edge, patch shape very irregular
	Across DN-D5	350890	5388895	T1-220°, T2-220°	On a slight hill, moist area in the cut
	Fog City-D6	345498	5394914	T1-210°, T2-210°	Canopy widely space trees, some conifer patches in interior
	Plan B-D7	350600	5399650	T1-225°, T2-225°	Dense shrub layer and sparse understory on T1
	Hideout-D8	361162	5402112	T1-225°, T2-225°	Some gentle hills towards interior, cut area relatively small
	Momma 3cubs-D9	358012	5396319	T1-165°, T2-155°	Scattered Balsam fir, heavy leaf litter past edge, moisture in cut
	Warm Rasp-D10	378222	5438141	T1-160°, T2-160°	Heavy leaf litter towards interior, dense shrub layer near edge
Fire	1st Burn Church-F1	390592	5442930	T1-180°, T2-180°	Rock exposed in burn, canopy trees clumped with gaps between
	2nd Burn Church-F2	390600	5446000	T1-225°, T2-225°	Large burnt area, small hill and high moisture at edge at T1
	K's Hike-F3	379179	5448567	T1-190°, T2-190°	Smaller patch, Alder thicket towards interior
	Blowdown City-F4	355066	5476952	T1-225°, T2-225°	Very wet bog-like towards interior
	Lab Soup-F5	389341	5448150	T1-220°, T2-200°	Edge very irregular at T2, high soil moisture towards interior
	Mound Lk-F6	386950	5448790	T1-220°, T2-220°	Interior done in adjacent patch, edge wet, snags very charred
	TNA-F7	379842	5451030	T1-145°, T2-140°	High moisture and dense shrub layer at the edge
	Topper-F8	376153	5451196	T1-200°, T2-200°	Scattered cedar in canopy at edge, high species diversity in burn
	Bend in Rd-F9	387205	5453961	T1-150°, T2-135°	Snags very charred, wet edge with dense Alder shrub layer
	Thuja Special-F10	385325	5457902	T1-180°, T2-170°	Scatted cedar in canopy, cedar swamp-like edge

Appendix I continued

Edge type	Site	UTM27_X	UTM27_Y	Transect orientation	Notes/Buffer Width
Riparian buffer (≥ 40m)	Spruce River-B1	366107	5456090	T1-135°, T2-156°	T1-50m, T2-40m, Lots of blowdown, cedar swamp-like patches
	African Safari-B2	347601	5472905	T1-220°, T2-220°	T1-70m, T2-120m, Blowdown, dense shrubs in cut, buffer wet
	Walk 10-B3	351535	5386343	T2-191°	T2-75m, Scattered deciduous near edge, some leaf litter
	DS-B6	350101	5387816	T1-159°	T1-40m, Rip-up trans @ 6m, some insect defoliation
	Hook's Rd-B7	347209	5393885	T1-170°, T2-160°	T1-40m, T2-40m, cut 1 yr. old, Pleurozium dominant understory
	Weed Rd-B8	347535	5392956	T1-153°, T2-180°	T1-40m, T2-40m, Steep slope at T2, wide shallow channel
	Hook's Friend-B12	349608	5397267	T1-170°, T2-170°	T1-60m, T2-60m, Small steep slope at 40m, rip-up trans @ 13m
Riparian buffer (< 40m)	Walk 10-B3	351535	5386343	T1-220°	T1-25m, Scattered deciduous trees, done 30m from road
	M5-B4	363883	5397810	T1-225°, T2-225°	T1-30m, T2-35m, Orientation poor, dry side channel in buffer
	Posh Bridge Out-B5	342900	5469100	T1-174°, T2-174°	T1-30m, T2-35m, cut planted with Jack pine, some rare species
	DS-B6	350101	5387816	T1-135°	T2-20m, Edge uneven, dense shrub cover at stream edge
	Skinny Jay-B9	346450	5395180	T1-210°, T2-180°	T1-30m, T2-35m, Scatter Jack pine trees, some rare species
	Mack L10-B10	368592	5401121	T1-225°, T2-225°	T1-35m, T2-35m, Older cut, steep shoreline, some open areas
	Wet Bum-B11	374410	5448903	T1-145°, T2-180°	T1-30m, T2-25m, cut & buffer high moisture, dense shrub cover
Undisturbed stream	Spruce Twist-S1	365590	5458510	T1-210°, T2-140°	River winding, T1 open area at end
	Mid-Posh-S2	347250	5472190	T1-135°, T2-15°	Rip-up trans. @ 5m, shrubs near shore
	Walk Crown-S3	353158	5384977	T1-135°, T2-140°	Some beaver disturbance near shore, lots of blowdown
	Rocky2-S4	364737	5339680	T1-162°, T2-170°	Steep hill, some open areas with exposed rock, canopy sparse
	Shallownest-S5	361774	5401074	T1-180°, T2-196°	Alder thicket near shore, high species diversity at stream edge
	EW1-S6	353559	5386963	T1-190°, T2-190°	Wet area, some blowdown and canopy gaps
	EWC1-S7	353598	5389027	T1-180°, T2-170°	T1 goes up hill, Alder and sphagnum dominant in rip.
	S. Current-S8	350520	5398995	T1-160°, T2-170°	Rip-up trans on rocky short steep hill
	John Crk-S9	372074	5452171	T1-170°, T2-220°	Creek winding, open area end T2, deciduous canopy beyond T2
	Larson Crk-S10	389308	5436441	T1-140°, T2-140°	Drier upland conditions, homogenous Pleurozium dominant
	Skinny Joe-S11	348115	5401896	T1-190°, T2-190°	Rip-up trans wide, scattered Jack pine, heavy needle litter
	Weed's Friend-S12	335927	5423690	T1-150°, T2-150°	Wide shallow channel, some open areas with blowdown

Appendix II

List of species observed in this study including accession numbers for voucher specimens in the Claude Garton Herbarium at Lakehead University (LKHD). Where species are grouped or only identified to genus is noted.

Family	Species	Herbarium Assession #	Species Groupings
Equisetaceae	*Equisetum arvense* L.	n/a	
	Equisetum pratense Ehrh.	n/a	
	Equisetum scripoides Michx.	n/a	
	Equisetum sylvaticum L.	104334	
Lycopodiaceae	*Lycopodium annotinum* L.	n/a	
	Lycopodium clavatum L.	104278	
	Lycopodium complanatum L.	104270	
	Lycopodium dendroideum Michx.	104274	
Osmundaceae	*Osmunda claytoniana* L.	104281	
Dryopteridaceae	*Athyrium filix-femina* (L.) Roth	n/a	
	Dryopteris carthusiana (Vill.) H.P. Fuchs	n/a	*D. carthusiana* and *D. expansa* = *Dryopteris* spp.
	Dryopteris expansa (C. Presl.) Fraser Jenk & Jeremy	n/a	
	Gymnocarpium dryopteris (L.) Newman	104319	
	Matteuccia struthiopteris (L.) Todara	104273	
	Onoclea sensibilis L.	n/a	
Thelypteridaceae	*Phegopteris connectilis* (Michx.) Watt	n/a	
Pinaceae	*Abies balsamea* (L.) Miller	n/a	
	Larix laricina (Duroi) K.Koch	n/a	
	Picea glauca (Moench) Voss	n/a	
	Picea mariana (Miller) BSP	n/a	
	Pinus banksiana Lambert	n/a	
Cupressaceae	*Thuja occidentalis* L.	n/a	
Alismataceae	*Sagittaria cuneata* E. Sheld.		
Poaceae	*Agrostis scabra* Willd.	104406	
	Bromus ciliatus L.	104279	
	Calamagrostis canadensis (Michx.) P.Beauv	104255	
	Cinna latifolia (Trevir. ex Goepponger) Griseb. in Ledeb.	n/a	
	Glyceria striata (Lam.) A. Hitchc.	n/a	

Appendix II continued

Poaceae	*Glyceria canadensis* (Michx.) Trin.	n/a	
	Oryzopsis asperifolia Michx.	104347	
	Poa palustris L.	n/a	
	Schizachne purpurascens (Torrey) Swallen	n/a	
Cyperaceae	*Carex aenea* Fern.	n/a	Carex group 2
	Carex aquatilis Wahlenb.	n/a	
	Carex arctata Boott	n/a	
	Carex bebbii (L.H. Bailey) Olney ex Fern.	n/a	Carex group 1
	Cares brunnescens (Pers.) Poir. Ex Lam.	n/a	Carex group 1
	Carex canescens L.	104382	Carex group 1
	Carex deflexa Hornem.	104377	Other *Carex* sp. included= *Carex deflexa* group
	Carex deweyana Schwein.	n/a	Carex group 1
	Carex disperma Dewey	104376	Carex group 1
	Carex interior L. Bailey	104416	Carex group 1
	Carex intumescens Rudge	n/a	
	Carex lasiocarpa Ehrh.	n/a	Carex group 2
	Carex leptalea Wahlenb.	104379	Carex group 1
	Carex limosa L.	n/a	Carex group 2
	Carex magellanica Lam.	n/a	Carex group 2
	Carex pauciflora Lightf.	n/a	Carex group 1
	Carex projecta Mack.	n/a	Carex group 2
	Carex rostrata Stokes	104352	
	Carex trisperma Dewey	104415	Carex group 1
	Carex vaginata Tausch	n/a	Carex group 2
	Scirpus cyperinus (L.) Knuth	104261	
	Scirpus microcarpus C. Presl	n/a	
Juncaceae	*Juncus brevicaudatus* (Engelm.) Fern	104390	Other species from genus included = *Juncus* spp.
Liliaceae	*Clintonia borealis* (Aiton) Raf.	104335	
	Maianthemum canadense Desf.	104320	
	Streptopus roseus Michx.	104325	
	Trillium cernuum L.	104331	
Orchidaceae	*Goodyera repens* (L.) R.Br.	n/a	
	Habenaria viridis (L.) R. Br.	n/a	
	Listera cordata (L.) R.Br.	n/a	
Caryophyllaceae	*Stellaria longifolia*	n/a	
Salicaceae	*Populus balsamifera* L.	n/a	
	Populus tremuloides Michx.	n/a	

Appendix II continued

Salicaceae	*Salix* species	n/a	Several species from genus present
Myricaceae	*Myrica gale* L.	104318	
Betulaceae	*Alnus incana* (L.) Monech	104262	
	Alnus viridis (Villars) DC.	104283	
	Betula papyrifera Marshall	n/a	
	Corylus cornuta Marshall	104297	
Santalaceae	*Geocaulon lividum* (Richardson) Fern.	n/a	
Polygonaceae	*Polygonum cilinode* Michx.	n/a	
!Ranunculaceae	*Actaea rubra* (Aiton) Willd.	n/a	
	Anemone quinquefolia L.	104305	
	Aquilegia canadensis L.	104303	
	Caltha palustris L.	104323	
	Coptis trifolia (L.) Salisb.	104321	
	Ranunculus penslyvanicus L.f.	n/a	
	Thalictrum dasycarpum Fischer & Ave-Lall.	104316	
Saxifragaceae	*Mitella nuda* L.	104291	
Grossulariaceae	*Ribes glandulosum* Graur	104287	
	Ribes hirtellum Michx.	104258	
	Ribes triste Pall.	n/a	
	Ribes lacustre (Pers.) Poir.	n/a	
Rosaceae	*Amelanchier* sp. Wiegand	104341	
	Fragaria virginiana Miller	104338	
	Geum species	n/a	Several species from genus likely present
	Potentilla norvegica L.	n/a	
	Potentilla palustris (L.) Scop.	104293	
	Prunus pensylvanica L.f.	104333	
	Prunus virginiana L.	n/a	
	Rosa acicularis Lindl.	104326	
	Rubus idaeus L.	n/a	
	Rubus pubescens Raf.	n/a	
	Sorbus americana Marshall	104414	
	Sorbus decora (Sarg.) C.K. Schneid	n/a	
	Spiraea alba Du Roi	104288	
Leguminosae	*Vicia americana* Muhlenb. ex. Willd	n/a	
Polygalaceae	*Polygala paucifolia* Willd.	104344	
Aceraceae	*Acer spicatum* Lam.	n/a	
Rhamnaceae	*Rhamnus alnifolia* L'Her.	104289	

Appendix II continued

Violaceae	*Viola adunca* Smith	104478	*Viola* spp. group
	Viola cucullata Aiton	104477	*Viola* spp. group
	Viola pubescens Aiton	104290	*Viola* spp. group
	Viola renifolia A. Gray	104484	*Viola* spp. group
Papaveraceae	*Corydalis sempervirens*	n/a	
Hypericaceae	*Hypericum majus* (A. Gray) Britton	n/a	
	Triadenum fraseri (Spach) Gleason	104312	
Urticaceae	*Urtica dioica* L.	n/a	
Geraniaceae	*Geranium bicknellii* Britton	n/a	
Onagraceae	*Circaea alpina* L.	104280	
	Epilobium angustifolium L.	104275	
	Epilobium ciliatum Raf	104355	
	Epilobium palustre L.	n/a	
Araliaceae	*Aralia hispida* Vent.	n/a	
	Aralia nudicaulis L.	104296	
Apiaceae	*Cicuta bulbifera* L.	n/a	
	Heracleum lanatum Michx.	104302	
	Sium sauve Walter	104358	
Cornaceae	*Cornus canadensis* L.	104329	
	Cornus stolonifera Michx.	104328	
Pyrolaceae	*Moneses uniflora* (L.) A. Gray	104314	
	Pyrola elliptica Nutt.	104476	Other species included = *Pyrola* spp.
Ericaceae	*Andromeda polifolia* L.	n/a	
	Chamaedaphne calyculata (L.) Moench	n/a	
	Epigaea repens L.	n/a	
	Gaultheria hispidula (L.)Muhlenb. Ex Bigelow	n/a	
	Kalmia polifolia Wangenh.	n/a	
	Ledum groenlandicum Oeder	104346	
	Vaccinium angustifolium Aiton	104345	
	Vaccinium myrtilloides Michx.	n/a	
	Vaccinium oxycoccos L.	n/a	
	Vaccinium vitis-idaea L.	n/a	
Primulaceae	*Lysimachia thyrsiflora* L.	n/a	
	Trientalis borealis Raf.	104332	
Oleaceae	*Fraxinus nigra* Marshall	n/a	
Scrophulariaceae	*Melampyrum lineare* Desr.		
Gentianaceae	*Gentiana rubricaulis* Schwein	104260	Other species in genus included = *Gentian* spp.
	Halenia deflexa (Sm.) Griseb.	n/a	

Appendix II continued

Menyanthaceae	*Menyanthes trifoliata* L.	n/a
Boraginaceae	*Mertensia paniculata* (Aiton) G. Don	104306 104307
Lamiaceae	*Galeopsis tetrahit* L.	n/a
	Lycopus uniflorus Michx.	104267
	Mentha arvensis L.	104277
	Scutellaria galericulata L.	104254
Apocynaceae	*Apocynum androsaemifolium* L.	n/a
Rubiaceae	*Galium trifidum* L.	104284
	Galium triflorum Michx.	104292
Caprifoliaceae	*Diervilla lonicera* Miller	104317
	Linnaea borealis L.	104330
	Lonicera canadensis Bartram	104299
	Lonicera hirsuta Eaton	104286 104294
	Lonicera involucrata (Richardson) Banks	104343
	Lonicera villosa (Michx.) Roemer & Schultes	104259
	Sambucus canadensis L.	n/a
	Sambucus racemosa L.	n/a
	Viburnum edule (Michx.) Raf.	104342
	Viburnum trilobum Marshall.	n/a
Campanulaceae	*Campanula aparinoides* Pursh	104361
Asteraceae	*Achillea millefolium* L.	n/a
	Anaphalis margaritaceae (L.) Benth & Hook.f. ex C.B. Clarke	104308
	Aster ciliolatus Lindley	104365
	Aster lateriflorus (L.) Britton	n/a
	Aster macrophyllus L.	104359
	Aster puniceus L.	104266
	Aster umbellatus Miller	104268
	Cirsium arvense (L.) Scop.	n/a
	Cirsium muticum Michx.	104269
	Eupatorium maculatum L.	104276
	Hieracium aurantiacum L.	n/a
	Hieracium caespitosum Dumort.	104372
	Hieracium umbellatum	n/a
	Lactuca biennis (Moench) Fern.	104357
	Lactuca canadensis L.	n/a

Appendix II continued

Asteraceae	*Petasites frigidus* (L.) Fr.	n/a	
	Petasites sagittatus (Banks ex Pursh) A. Gray	n/a	
	Prenanthes alba L.	n/a	
	Solidago canadensis L.	104271	
	Solidago uliginosa Nutt.	n/a	
	Sonchus asper (L.) Hill	n/a	
	Taraxacum species	n/a	Several species from genus likely present
Marchantiaceae	*Conocephalum conicum* (L.) Lindb.	n/a	
	Jamesoniella autumnalis (DC.) Steph.	n/a	Other species included = Leafy liverwort
	Marchantia polymorpha L.	n/a	Other species included = Thallose liverworts
Sphagnaceace	*Sphagnum* species	n/a	Several species from genus likely present
Polytrichaceae	*Polytrichum commune* Hedw.	n/a	Other species included = *Polytrichum* spp.
	Polytrichum juniperinum Hedw.	n/a	
Ditrichaceae	*Ceratodon purpureus* (Hedw.) Brid.	n/a	
Dicranaceae	*Dicranum polysetum* Sw.	n/a	Other species included = *Dicranum* spp.
Mniaceae	*Mnium pseudopunctatum* (Bruch & Schimp.) T. Kop.	n/a	
Hypnaceae	*Ptilium crista-castrensis* (Hedw.) De Not.	n/a	
Hylocomiaceae	*Hylocomium splendens* (Hedw.) Schimp. in B.S.G.	n/a	
	Pleurozium schreberi (Bird.) Mitt.	n/a	
Climaceaceae	*Climacium dendroides* (Hedw.) Web. & Mohr	n/a	
Dicranaceae	*Oncophorus wahlenbergii* Brid.	n/a	Other very small low-growing bryophytes included = Bryophyte spp. group
Hypnaceae	*Pylaisiella polyantha* (Hedw.) Grout	n/a	
Aulacomniaceae	*Aulacomium palustre* (Hedw.) Schwaegr.	n/a	
Amblystegiaceae	*Cratoneuron filicinum*(Hedw.) Spruce	n/a	
Cladoniaceae	*Cladina stellaris* (Opiz) Brodo	n/a	Other species included = *Cladina* spp.
	Cladina rangiferina (L.) Nyl.	n/a	
Typhaceae	*Typha latifolia* L.	n/a	
Sarraceniaceae	*Sarracenia purpurea* L.	n/a	
Droseraceae	*Drosera rotundifolia* L.	n/a	

Appendix III

Indicator species at different edge locations (1= cut/burn 20 to 5 m, 2= near edge 0 to –15 m, 3= far edge –20 to –35 m, 4= interior ≥100 m) for each edge type. Relative frequency and abundance of each species within each edge type is summarized by the observed indictor value. The mean randomized indicator value is determined through 1000 Monte Carlo runs with randomized data. The p-value is the proportion of randomized trails with an indicator value equal or exceeding the observed indicator value (sig. ≤0.05).

Edge type	Indicator species	Edge location (Max grp)	Observed indicator value (IV)	Mean randomized indicator value	p-value (sig.≤ 0.05)
Conifer clearcut	*Aster ciliolatus*	1	30.0	12.0	0.0500
	Betula papyifera	1	47.9	27.2	0.0190
	Bromus ciliatus	1	41.4	22.7	0.0300
	Carex deflexa group	1	74.7	23.6	0.0010
	Carex group 2	1	27.3	15.6	0.0500
	Epilobium angustifolium	1	44.4	15.0	0.0070
	Gaultheria hispidula	3	51.0	31.0	0.0040
	Hieracium caespitosum	1	30.0	10.9	0.0470
	Pinus banksiana	1	50.0	13.5	0.0030
	Polygonum cilinode	1	40.0	12.5	0.0100
	Ribes glandulosum	1	28.9	15.2	0.0470
	Rubus idaeus	1	86.0	22.4	0.0010
	Sphagnum spp.	3	41.1	28.0	0.0390
	Taraxacum spp.	1	59.5	16.7	0.0010
	Viola spp.	1	43.8	23.9	0.0140
	Aralia hispida	1	47.8	13.6	0.0040
Deciduous clearcut	*Athyrium felix-femina*	4	41.3	24.0	0.0380
	Betula papyifera	1	42.2	24.6	0.0210
	Bromus ciliatus	1	60.3	33.0	0.0010
	Calamagrostis canadensis	1	79.0	28.0	0.0010
	Epilobium angustifolium	1	55.1	19.8	0.0010
	Hieracium caespitosum	1	30.0	10.9	0.0420
	Picea glauca	1	27.7	11.7	0.0400
	Polygonum cilinode	1	36.5	19.3	0.0540
	Polytrichum sp.	1	63.1	22.4	0.0040
	Prunus pensylvanica	1	40.0	18.2	0.0130
	Rubus idaeus	1	81.9	31.1	0.0010
	Salix spp.	1	33.8	17.6	0.0380
	Taraxacum spp.	1	46.5	19.9	0.0060
	Agrostis scabra	1	30.0	12.2	0.0420
	Anaphalis margaritacea	1	30.0	11.2	0.0540
	Scirpus cyperinus	1	30.0	10.5	0.0450

Appendix III continued

Edge type	Indicator species	Edge location (Max grp)	Observed indicator value (IV)	Mean randomized indicator value	p-value (sig.≤ 0.05)
Fire	*Dicranum* spp.	4	47.1	33.5	0.0080
	Epilobium angustifolium	1	88.5	19.7	0.0010
	Ceratodon purpureus	1	94.3	22.2	0.0010
	Pleurozium schreberi	4	48.3	34.2	0.0170
	Polytrichum spp.	1	81.3	31.6	0.0010
	Prunus pensylvanica	1	30.0	11.8	0.0500
	Rubus idaeus	1	66.2	27.5	0.0010
	Salix spp.	1	46.7	22.8	0.0110
	Sphagnum spp.	3	36.6	30.3	0.0330
	Taraxacum spp.	1	40.0	13.7	0.0050
	Vaccinium myrtilloides	1	50.4	36.7	0.0210
	Anaphalis margaritacea	1	30.0	10.4	0.0450
	Thuja occidentalis	3	33.9	19.0	0.0460

Appendix IV

Canopy cover and coarse woody debris at conifer clearcut, deciduous clearcut and fire edges. Mean canopy cover or mean coarse woody debris values were compared to their respective interior condition for each forest type. Significant values are less or greater than critical values. Canopy cover was sampled as a discrete variable: 1 = cover, 0 = open.

Response variable	Edge type	Critical Values		Mean values at Edge Position (m)												
				Cut				Edge				Forest				
		2.5th %ile	97.5th %ile	20	15	10	5	0	-5	-10	-15	-20	-25	-30	-35	-40
Canopy cover	Conifer clearcut	0.5	0.9	0	0.15	0	0	0.55	0.6	0.75	0.7	0.65	0.65	0.7	0.65	0.75
	Deciduous clearcut	0.7	1	0.05	0	0	0.05	0.6	0.6	1	0.85	1	0.85	0.9	0.85	0.95
	Fire	0.4	0.9	0	0.15	0.05	0.25	0.55	0.55	0.55	0.85	0.75	0.45	0.7	0.55	0.5
Coarse Woody debris	Conifer clearcut	2.7	17.3	14.3	10.6	11	9.6	16.4	9.7	5	4.45	2.9	4.85	5.95	4.85	5.4
	Deciduous clearcut	3.1	12.5	12.1	11.8	14.7	15.5	13.4	17.3	19.7	14.2	8.65	10.1	11.7	7.1	8.75
	Fire	1.6	10.8	10.6	11.3	10.6	9.7	7.35	6.55	3.25	2.85	4	3.7	4.75	3.2	6.1

Note: Critical values shown are 2.5 and 97.5 percentiles of the 5000 permuted averages of the interior forest data (2 tailed test, sig.= 0.05).

Appendix V

Species with a significant depth of edge influence at conifer clearcut edges

■ = Mean values at given transect locations are lower in comparison to interior reference values.
▨ = Mean values at given transect location are higher in comparison to interior reference values.

Species Group	Species	Critical Values		Mean Values at Edge Position (m)												
				Cut				Edge				Forest				
		2.5th %ile	97.5th %ile	20	15	10	5	0	-5	-10	-15	-20	-25	-30	-35	-40
Conifer saplings	*Picea glauca*	0	0	0.4	0.35	0	3.1	0	0	0	0	0	0	0	0	0
	Pinus banksiana	0	0	2.3	2.9	2.9	0.2	0	0	0	0	0	0	0	0	0
Deciduous saplings	*Betula papyifera*	0	1.3	1.87	2.6	2.75	3.32	1.7	0.8	0.1	0.32	0.32	0.77	0.6	0.7	0.55
	Populus spp.	0	0.5	0.25	0.1	0	0.8	1	0	0	0	0	0	0	0	0
Tall shrubs	*Prunus pensylvanica*	0	0	0.6	0.5	0.85	0.45	0	0.25	0	0	0	1.55	0	0	0
Low-growing shrubs	*Chamaedaphne calyculata*	0.5	5	0	0	0	0	0	0	0	0.65	4.65	3.3	4.2	2.75	2.15
	Gaultheria hispidula	0.6	4.5	0.25	0.25	0.15	0.15	1.67	2.87	3.45	3.12	5.07	5.25	6.12	4.02	4.8
	Vaccinium oxycoccos	0.05	1.1	0	0	0	0	0	0.1	0	0.87	0.45	0.55	0.65	0.52	1.05
	Ribes glandulosum	0	0	0.75	0.62	0.65	0.5	0.1	0	0	0	0	0	0	0	0
	Ribes hirtellum	0	0.2	0.45	0.32	0.4	0	0.05	0	0	0	0	0	0	0	0
	Rubus idaeus	0	0.8	12.5	10.6	7.4	4.55	0.55	0	0.05	0.1	0	0.3	0	0.1	0
Shade-tolerant herbs	*Anemone quinquefolia*	0	0	0.25	0.27	0.15	0	0.05	0	0	0	0	0	0	0	0
	Cornus canadensis	1.45	5.9	7.7	6.7	6.85	5.02	6.35	6.4	5.15	4.8	3.55	4.1	3.55	5.62	3.55
										2.37						1.62
	Maianthemum canadense	0.55	4.6	4.62	5	3.95	1.97	3.3	4.12	5	1.15	1.2	1.2	0.95	0.75	5
	Melampyrum lineare	0	0	0.2	0.1	0.2	0.05	0	0	0.05	0	0	0	0	0	0
	Mitella nuda	0	0.2	0.27	0.17	0	0	0	0.15	0.5	0.45	0.02	0.02	0.3	0.1	0.1
	Petasites frigidus	0	0.5	0.55	0.55	0.55	0	0.35	0.1	0	0.25	0.15	0.5	0.02	0	0
	Streptopus roseus	0	0.3	0.25	0.55	0	0.4	0.4	0.25	0.1	0.15	0	0.05	0.2	0.2	0
Shade-intolerant herbs	*Aster ciliolatus*	0	0	1.25	0.35	0.1	0.05	0	0	0	0	0	0	0	0	0
	Aster puniceus	0	0	0	0	0	0	0	0	0	0	0.1	0	0	0.25	0.25
	Epilobium angustifolium	0	0.6	1.4	1.3	0.85	0.4	0.15	0	0	0	0	0	0	0	0
	Fragaria virginiana	0	0.05	1.35	1.9	1	2	0.25	0.27	0.05	0.1	0	0.05	0	0	0.05
	Polygonum cilinode	0	0	2.2	1.65	1.5	0.32	0	0	0	0	0	0	0	0	0
	Taraxacum spp.	0	0	1.3	0.72	0.9	0.3	0.02	0	0	0	0	0	0	0	0
	Vicia americana	0	0	0.1	0.15	0	0	0	0	0	0	0	0	0	0	0
	Achillea millefolium	0	0	0.1	0.25	0	0	0	0	0	0	0	0	0	0	0
	Anaphalis margaritacea	0	0	0.3	0.05	0	0.15	0	0	0	0	0	0	0	0	0
	Apocynum androsaemifolium	0	0	0	0	0.02	0.15	0	0	0	0	0	0	0	0	0
	Aralia hispida	0	0	0.15	0.25	0.4	0.27	0	0	0	0	0	0	0	0.05	0
	Corydalis sempervirens	0	0	0.15	0	0.15	0.05	0	0	0	0	0	0	0	0	0
	Hieracium caespitosum	0	0	0.3	0.15	0.3	0.02	0	0	0	0	0	0	0	0	0

Appendix V continued

Species Group	Species	Critical Values		Mean Values at Edge Position (m)												
				Cut				Edge				Forest				
		2.5th %ile	97.5th %ile	20	15	10	5	0	-5	-10	-15	-20	-25	-30	-35	-40
Indicator of Moisture	*Mertensia paniculata*	0	0	0.1	0.15	0.5	0	0	0	0	0	0.4	0	0	0	0
	Drosera rotundifolia	0	0	0	0	0	0	0	0	0	0.15	0.1	0	0	0	0
Vascular crytogams	*Equisetum arvense*	0	0	0	0	0	0	0	0	0	0.1	0	0	0.05	0.1	0
	Equisetum sylvaticum	0	1.3	0.15	0.22	0.35	1.05	0.4	0.7	1.95	2.35	2.87	2.3	2.05	1.05	1.125
Grasses	*Bromus ciliatus*	0	1.1	3.4	1.65	2	0.2	0.3	0.12	0.25	0.2	0.1	0.05	0.02	0	0.075
	Calamagrostis canadensis	0	0	2.07	0.52	2.6	0.9	0.3	0.02	0	0	0	0	0.02	0.1	0
	Oryzopsis asperifolia	0	0.3	0.1	0.5	0.8	0.7	1.15	0	0.05	0	0	0	0	0.1	0.05
	Cinna latifolia	0	0	0	0.2	0.2	0	0	0	0	0	0	0	0	0	0
Sedge	*Carex deflexa* group	0	0.7	1.67	1.37	0.7	1.15	0	0.05	0.075	0	0.02	0	0.05	0.2	0.05
Acrocarpous mosses	*Dicranum* spp.	0.7	6.2	0.32	0.22	1.6	1.9	1.1	7.2	2.275	2.15	1.65	2.15	0.6	2.45	1.2
Pleurocarpous mosses	*Pleurozium schreberi*	15.1	43.9	2.35	2.9	4.7	8	20.2	28.2	27.2	23.9	20.9	27.5	20.8	31.0	21.45
	Ptilium crista-canadense	0.8	16.1	0.27	0.02	0.35	0.05	2.35	0.95	7.35	3.5	7.3	3.3	1.92	2.05	2.35
Sphagnum mosses	*Sphagnum* spp.	10	37.2	1.75	1.9	0.3	2.6	1.95	12.2	12.6	26.9	28.1	28.3	37.7	25	27.9

Note: Critical values shown are 2.5 and 97.5 percentiles of the 5000 permuted averages of the interior forest data (2 tailed test, sig.= 0.05).

Appendix VI

Species with a significant depth of edge influence at deciduous clearcut edges

■ = Mean values at given transect locations are lower in comparison to interior reference values.
▨ = Mean values at given transect location are higher in comparison to interior reference values.

Species Group	Species	Critical Values		Mean Values at Edge Position (m)												
				Cut				Edge				Forest				
		2.5th %ile	97.5th %ile	20	15	10	5	0	-5	-10	-15	-20	-25	-30	-35	-40
Conifer sapling	*Picea glauca*	0	0	0	0.2	0.15	0.75	0.1	0	0	0	0	0	0	0	0
Deciduous saplings	*Populus* spp.	0.6	5	1.55	5.85	5.07	2.35	5.45	4.35	4	3.35	3.6	3.9	2.47	2.65	2.95
Tall shrubs	*Acer spicatum*	10	36.6	6.65	2.35	9.35	9.5	13.7	8.1	13	9.1	19	22.4	17.2	18.0	11.3
	Prunus pensylvanica	0	0	0.05	1.8	3.05	0.32	0.3	0.2	0.1	0	0	0.2	0	0.5	0
	Salix spp.	0	0.8	1.1	1.35	0.7	1.1	0	0.25	0	1.9	0.4	1.9	0	0	0.35
Low-lying shrubs	*Ledum groenlandicum*	0	0	0	0	0	0	0	0	0	0	0	1.4	0.25	1.1	0.75
	Rubus idaeus	0	5	15.4	21.5	17	8.1	4.7	1.12	0.15	0	0.55	0.25	0.12	0	0.65
Shade-tolerant herbs	*Aralia nudicaulis*	3.2	12.6	0.25	0.8	1.8	6.55	7.8	7.8	9.1	8.8	7.95	12.1	8.65	6.5	8.05
	Clintonia borealis	7.6	16.4	4.87	2.65	3.7	5.05	9.95	11.1	11.8	9.05	11.3	10.6	10.6	10.5	9.6
	Cornus canadensis	0.95	5.2	5.3	6.05	6.07	9.52	6.95	4.6	4.77	5.35	5.25	4.35	3.8	3.25	3.95
	Trientalis borealis	1.1	4.8	0.62	0.35	1.25	0.6	0.97	1.05	1.35	2.4	1.3	1.95	1.67	3.5	3.32
	Melampyrum lineare	0	0	0	0	0.45	0.25	0.25	0.15	0.15	0	0	0.1	0	0	0.15
	Pyrola spp.	0	0.5	0	0.05	0	0.3	0.1	0	0.6	1.05	1	0.45	0	0	0
Shade-intolerant Herbs	*Aster ciliolatus*	0	0.4	0	1.3	0.7	0.6	0.15	1.2	0.55	0.2	0	1.3	0.15	0.15	0.2
	Cirsium muticum	0	0	0	0.05	0.15	0	0	0	0	0	0	0.15	0	0	0
	Epilobium angustifolium	0	1	3.05	3.45	2.6	2.15	1.45	0.25	1.1	0	0.6	0	0.25	0	0.3
	Polygonum cilinode	0	0	3.1	2.35	3.75	2.2	0.85	0.25	0	0	0	0	0	0	0
	Vicia americana	0	0	0	0.2	0.05	0	0	0	0	0	0	0	0	0	0
	Anaphalis margaritacea	0	0	1.7	1.05	1.3	0	0	0	0	0	0	0	0	0	0
	Apocynum androsaemifolium	0	0	0	0.25	0	0	0	0	0	0.4	0	0.4	0.25	0	0.15
	Epilobium ciliatum	0	0	0.2	0.15	0	0.15	0.15	0	0	0	0	0	0	0	0
	Galeopsis tetrahit	0	0	0.4	0.35	0.45	0	0.6	0.05	0	0	0	0	0	0	0
	Hieracium caespitosum	0	0	0	0.6	0.15	0	0	0	0	0	0	0	0	0	0
	Solidago canadensis	0	0	0.45	0.2	0.1	0	0	0	0	0	0	0	0	0	0
	Taraxacum spp.	0	0.6	0.45	0.77	1.32	0.85	0.9	0.07	0	0.15	0	0.25	0	0	0
Vascular crytogams	*Equisetum pratense*	0	0.1	0.8	0	0.15	0	0	0.05	0.1	0	0	0.2	0.25	0.2	0.1
	Lycopodium dendroideum	1	7.3	0.65	0.42	0.75	3.55	3.15	3.85	4.52	3.1	4.8	3.6	3.8	2.7	1.8

Appendix VI continued

Species Group	Species	Critical Values		Mean Values at Edge Position (m)												
				Cut				Edge				Forest				
		2.5th %ile	97.5th %ile	20	15	10	5	0	-5	-10	-15	-20	-25	-30	-35	-40
Grasses	*Bromus ciliatus*	0	1.3	12.1	5.9	2.4	2.25	1.9	0.85	0.6	1.5	1.65	0.47	1.2	0.92	0.35
	Calamagrostis canadensis	0	0.5	4.7	2.95	8.75	5.1	2.15	0.25	0.02	0.15	0	0	0	0.15	0.25
	Oryzopsis asperifolia	0	0.6	0.8	0.35	0.45	1.05	0.7	0.3	0.37	0.05	0.1	0.1	0	0.1	0.15
	Agrostis scabra	0	0	0	0.1	0.7	0	0	0	0	0	0	0	0	0	0
Sedges	*Carex intumesces*	0	0	0	0	0.75	0.6	0	0	0	0	0	0	0	0	0
	Carex group 1	0	0.3	0.42	2.3	0.4	0.3	0.72	0.6	0	0	0	0.1	0.3	0.15	0
	Scirpus cyperinus	0	0	0	0.3	0.15	0	0	0	0	0	0	0	0	0	0
Acrocarpous mosses	*Ceratodon purpureus*	0	0	1.5	0.15	0.1	0.05	0.05	0	0	0.1	0.05	0	0	0	0
	Polytrichum spp.	0	0.8	1.2	1.15	3.05	1.5	0.3	0.25	0	0	0	0.1	0	0	0
Pleurocarpous mosses	*Pleurozium schreberi*	0	1	0.87	0.8	0.3	0.2	0.82	0.65	0.75	0.8	1.65	1.5	0.4	2.35	0.3
Sphagnum mosses	*Sphagnum* spp.	0	0	0.65	4.2	0.55	0.6	0	0	0	0	0	0	0	0.65	0.02

Note: Critical values shown are 2.5 and 97.5 percentiles of the 5000 permuted averages of the interior forest data (2 tailed test, sig.= 0.05).

Appendix VII

Species with a significant depth of edge influence at fire edges

■ = Mean values at given transect locations are lower in comparison to interior reference values.
▨ = Mean values at given transect location are higher in comparison to interior reference values.

Species Group	Species	Critical Values		Mean Values at Edge Position (m)												
				Cut				Edge				Forest				
		2.5th %ile	97.5th %ile	20	15	10	5	0	-5	-10	-15	-20	-25	-30	-35	-40
Conifer saplings	*Abies balsamea*	0.1	5.7	0.1	0	0	0.1	1.25	1.02	1.85	5.8	2.55	4.9	2	0.9	1.32
	Picea mariana	2.3	15.8	0.82	1.47	0.77	1.32	4.4	3.52	2.25	4.85	8.37	8.47	4.4	7	13.4
Deciduous saplings	*Populus* spp.	0	0.2	0.3	1.05	0	0	0	0	0	0	0	0	0	0	0
	Fraxinus nigra	0	0	0	0	0	0	0	0	0	0	0.4	0.3	1.15	0	0
Tall shrubs	*Cornus stolonifera*	0	1.5	0	1.2	3.65	0	1.95	4.75	3.7	2.95	1.25	0	0.7	0.75	0.65
	Prunus pensylvanica	0	0	0.55	1.6	0.75	0.2	0	0	0	0	0	0	0	0	0
Low-growing shrubs	*Linnaea borealis*	0.4	2.5	0.4	3.75	2.67	1.1	1.3	0.75	1.3	1.75	1	1.52	1.4	0.95	1.4
	Lonicera villosa	0	0.5	0	0.15	0	0.5	0	0.75	0.05	0.05	0.75	0.1	1.1	0.7	2.35
	Ribes glandulosum	0	0	0.2	0.65	0	0	0	0	0	0	0	0	0	0	0
	Ribes triste	0	0.1	0	0	0	0	0.05	0.2	1	0	0.3	0	0	0	0
	Rosa acicularis	0	2	1.4	1.25	2.62	2.15	1.85	0.5	0.2	0.6	0.25	0.25	0.02	0.35	0.1
	Rubus idaeus	0	1	13.8	11.5	8.2	8.25	4.15	2.7	1.85	2.9	2.3	0.15	0.4	0.12	1
	Rubus pubescent	0.2	2.6	1.05	1.35	1.05	1.85	2.5	2.95	5.35	3.15	2.95	2.25	3.25	2.5	0.9
	Vaccinium angustifolium	0.7	5.4	13.7	9	9.65	11.8	4.3	3.55	4	2.35	5.35	6.05	8.35	3	3.7
	Vaccinium myrtilloides	0.55	5.2	8.15	7.45	10.4	9.3	5.8	4.35	2.65	1.9	1.17	3.05	1.75	3.6	3.92
	Viburnum edule	0	0.3	0	0	0.2	0	0	0	0.55	0.75	0	0.2	0.35	0	0.7
	Viburnum trilobum	0	0	0	0	0	0	0	0.3	0.15	0.85	0	0	0	0.2	0
Shade-tolerant herbs	*Cornus canadensis*	1.2	6.8	10.1	9.25	7.95	5.65	6.15	4.27	3.9	4.17	2.57	1.92	3.4	4.7	3.1
	Gallium triflorum	0	0.5	0.22	0.15	0.42	0.35	1.2	1.25	0.6	0.35	0.2	0.05	0.7	0.25	0.1
Shade-intolerant herbs	*Epilobium angustifolium*	0	0.05	3.2	4.95	2.67	2.47	0.2	0	0	0	0	0	0	0	0
	Fragaria virginiana	0	0.3	0	1.5	0.4	0.12	0.15	0.4	0.1	0	0.6	0	0	0.2	0
	Hieracium caespitosum	0	0	0.3	0.15	0.1	0	0	0	0	0	0	0	0	0	0
	Taraxacum spp.	0	0	0.1	0.65	0.05	0.05	0	0	0	0	0	0	0	0	0
	Anaphalis margaritacea	0	0	0.3	0.5	0	0	0	0	0	0	0	0	0	0	0
	Apocynum androsaemifolium	0	0	0.6	0.5	0	0	0	0	0	0	0	0	0	0	0
	Epilobium ciliatum	0	0	0.2	0.1	0	0	0	0	0	0	0	0	0	0	0

Appendix VII continued

Species Group	Species	Critical Values		Mean Values at Edge Position (m)												
				Cut				Edge					Forest			
		2.5th %ile	97.5th %ile	20	15	10	5	0	-5	-10	-15	-20	-25	-30	-35	-40
Indicators of moisture	*Eupatorium maculatum*	0	0	0	0	0	0	0	0	0	0	0	0.35	1	0	0
	Lycopus uniflorus	0	0	0	0	0	0	0	0	0	0	0.7	0.3	0.15	0	0
	Mertensia paniculata	0	0	0	0	0	0	0.4	0.4	0	0.75	0	0	0	0	0
Vascular crytogams	*Equisetum arvense*	0	0.7	1.55	2.75	1.8	1.85	2.25	0.8	1.55	0.6	1.2	0.15	0.5	0.9	0.1
	Lycopodium annotinum	0.5	4.6	0	0.55	0.27	0.3	1.85	1.27	1.92	1.9	1.75	1.15	1.3	1.15	1.62
	Athyrium felix-femina	0	0	0.05	0	0.35	0	0.55	0.02	0.45	0	0.02	0	0.25	0	0
	Phegopteris connectilis	0	0	0	0	0	0	0	0	1.15	0.8	0.6	0	1.4	0.15	0.5
Grasses	*Schizachne purpurascens*	0	0	0	0	0	0	0	0	0.9	0	0.25	0.25	0	0	0
Sedges	*Carex aquatilis*	0	0	0	0	0	0	0	0	0	0	0	0.15	0.15	0.15	0
	Cares deflexa group	0	0.8	1.32	1.3	1.62	0.67	0.05	0.97	0.35	0.2	0.3	0.35	0.75	0	0.2
	Carex group 1	0.25	4.9	3.02	0.85	0.65	0.35	1.15	1	2.75	6.82	5.05	1.67	1.87	1.17	2.52
Acrocarpous mosses	*Dicranum* spp.	1.3	7	1.05	0.6	0.67	1.3	2.05	1.52	1.92	0.4	1.8	2.42	1	1.87	1.8
	Ceratodon purpureus	0	0	20.3	18.7	18.5	12	3.1	0.82	0	0.15	0.1	0	0	0	0
	Polytrichum spp.	0	0.8	3.07	7.15	3.1	2.85	1.22	0.1	0.25	0.1	0.35	0	0.5	0.4	0.02
Pleurocarpous mosses	*Pleurozium schreberi*	7.65	29.3	0.35	0.2	0.37	2.97	4.2	8.72	11.2	4.62	11.5	14.8	19.1	8.3	11.1
Sphagnum sp	*Sphagnum* spp.	24.8	53.4	1	13.0	7.6	14.2	30.9	41.6	39.6	58.3	47.9	46.5	45.1	64.3	53.3
Liverworts	Thallose liverworts	0	0.2	0	0	0	0	0	0.02	0	0.05	0.4	0.25	0.1	0.22	0.2
Lichens	*Cladina* spp.	0.2	3.7	0	0	0.1	0.15	0.9	1.7	0.25	0.2	0.85	2.8	0.35	0.4	1.4

Note: Critical values shown are 2.5 and 97.5 percentiles of the 5000 permuted averages of the interior forest data (2 tailed test, sig.= 0.05).

Appendix VIII

Canopy cover at wide and narrow buffers

▨ = Mean values from transect locations are lower when compared to all reference values (1) and either upland or riparian reference values (2 or 3)
☐ = Mean values at given transect locations are higher when compared to all reference values (1) and either upland or riparian reference values (2 or3)
■ = Mean values at given transect locations are lower only in comparison to upland reference values (2)

Response variable	Buffer width	Critical Values 2.5th %ile	Critical Values 97.5th %ile	Mean Values at Edge Position (m) Cut 20	15	10	5	Cut Edge 0	-5	-10	Critical Values 2.5th %ile	Critical Values 97.5th %ile	Mean Values at Edge Position (m) -15	-20	Riparian Edge -25	-30	-35	-40
Canopy cover	40 m	0.62	0.91	0	0	0.08	0	0.58	0.66	0.83	0.52	0.85	0.91	0.90	0.83	0.75	0.83	0.58
	30 m			0.08	0.08	0.00	0.16	0.50	0.83	0.83			0.83	0.83	0.66	0.16		

Note: Critical values shown are the 2.5 and 97.5 percentiles of the 5000 permuted averages for undisturbed upland data (2) and undisturbed riparian data (3) respectively (2 tailed test, sig.= 0.05).

Appendix IX

Understory species response at narrow buffers

▨ = Mean values from transect locations are lower when compared to all reference values (1) and either upland or riparian reference values (2 or 3)
☐ = Mean values at given transect locations are higher when compared to all reference values (1) and either upland or riparian reference values (2 or3)
■ = Mean values at given transect locations are lower only in comparison to upland reference values (2) or riparian reference values
☐= Mean values at given transect location are higher only in comparison to either upland reference values (2) or riparian reference values (3)

Entire buffer response	Species	Critical Values		Mean values at edge position (m)							Critical Values		Mean values at edge position (m)			
				Cut				Cut Edge						Riparian		
		2.5th %ile	97.5th %ile	20	15	10	5	0	-5	-10	2.5th %ile	97.5th %ile	-15	-20	-25	-30
Increase	*Bromus ciliatus*	0	0.37	1.83	1.58	2.08	5.16	1.33	0	0.75	0	0.79	0.25	0.12	0.29	3.08
	Carex aquatilis	0	0	2.91	1.58	0.66	0.16	0	0	0	0	2.29	0	0	0	2.91
	Carex group 1	0	0.62	0.83	3.33	1.75	0	0	0.66	0.16	0.12	2.41	1.68	0.70	2.5	2.41
	Equisetum pratense	0	0.16	0	0	0	0	0.16	0.5	0.83	0	0.48	0.58	0.04	0.16	0
	Myrica gale	0	0	1.41	7	4.5	1.5	1.25	1.16	0	0	1.54	0	0	0	3.5
	Prunus pensylvanica	0	0	0.83	4.83	5.25	1.58	0.58	0	0	0	0	0.12	0	0	0.66
	Ribes glandulosum	0	0.25	2.5	1	1.33	0.33	2.5	0.33	0	0	0.25	0.12	0	0.5	1.04
	Rubus idaeus	0.08	1.95	7.08	14.2	15.5	11.2	5.16	1	0.66	0.12	1.54	2.45	7.29	9.75	3
	Taraxacum spp.	0	0	1.66	0.83	1.16	0.41	0.08	0	0	0	0.20	0.08	0	0.25	0.58
	Vaccinium oxycoccos	0	0.12	1.33	2	1.5	0.66	0.66	0.25	0.5	0	0	0	0.04	0.08	0
	Vaccinium vitis-idaea	0	0.04	1.33	1.33	1.16	1.91	2.16	1.16	0.91	0	0	0.16	0.29	0.16	0
	Vicia americana	0	0	0	0.16	0.25	0.33	0	0.16	0	0	0	0.16	0	0	0
	Viola spp.	0.18	1.43	2.25	2	2.45	1.70	0.83	0.70	0.5	1.14	4.08	1	2.16	4.25	6.79
	Agrostis scabra	0	0	2.41	0.75	0.33	1.08	0.08	0	0	0	0.37	0	0	0	1.33
	Campanula aparinoides	0	0	0	1.58	1.16	0.33	0	0	0.16	0	0.12	0	0.08	0	1.25
	Mnium pseudopunctatum	0	0.08	0.41	0.58	0.33	0	0	0.83	0.08	0	0.77	3	0.58	0.45	1.37
	Vaccinium myrtilloides	2.70	6.75	6.83	7.91	5.33	2.75	10.3	9.66	5.58	1.16	4.08	4.68	10.0	5.08	0
Decrease	*Acer spicatum*	0.20	2.50	0	0	0	0.25	0	0	0	0.16	3.667	0.04	0	0	0
	Cladina spp.	0.58	7.33	0.08	0.66	1.16	0.41	0.25	1.66	0.58	0.08	4.083	0.62	0.83	0.16	0
	Coptis trifolia	0.37	2.58	0.29	0.50	0.33	0	0	0	1.16	0.54	2.625	1.20	1.45	0.41	0.83
	Dicranum spp.	2.20	5.91	1.66	1.00	2.58	3.33	3.33	3.16	1.50	1.18	4.438	1.29	1.00	0.91	0.75
	Gaultheria hispidula	0.87	4.45	1.00	0	0	0.83	0.25	2.66	2.50	0.79	4.208	4.25	1.79	0.16	0
	Lycopodium annotinum	1.20	5.83	1.25	1.41	0.33	0	0	0.41	2.25	0.79	7.542	6.50	5.37	0.83	0
	Pleurozium schreberi	21.2	37.3	2.29	6.08	7.75	4.41	10.3	24.3	10.8	9.33	24.10	17.7	7.75	4.16	0.91
	Ptilium crista-castrensis	1.08	7.95	0.91	0.83	0.54	0.50	0.58	0.83	2.00	0.87	8.983	4.12	2.00	0.75	0
Decrease-Increase	*Bryophyte* spp. group	1.41	5.708	1.5	2.41	1.33	0.91	1	1.58	2.75	1.83	6.541	3.54	4.16	5.91	10.3

Appendix IX continued

Upland response	Species	Critical Values		Mean values at edge position (m)						
				Cut				Edge	Buffer	
		2.5th %ile	97.5th %ile	*20*	*15*	*10*	*5*	*0*	*-5*	*-10*
Increase	*Aralia hispidula*	0	0.04	0	0.25	0.66	0.91	0	0	0
	Betula papyifera	0.04	3.04	1.25	5.33	5.04	3.75	2.08	0.08	2
	Calamagrostis canadensis	0	0.41	0	0	2.08	1.41	5.87	0.75	0.83
	Cinna latifolia	0	0.04	0.25	0.16	0	0	0.16	0.33	0.08
	Epilobium angustifolium	0	0.29	2.08	0.87	2.25	3.66	2.91	0.83	2.66
	Ceratodon purpureus	0	0	0	1.25	1.5	0	1.08	0	0
	Lonicera hirsuta	0	0	0	0.83	0	0	0	0.41	0.41
	Mertensia paniculata	0	0.12	0.33	0.33	0	1.41	2.33	1.5	1.25
	Oryzopsis asperifolia	0.04	0.41	1.25	0.75	1.33	0.5	0.33	0.16	0
	Picea glauca	0	0	0.83	1.66	0	0	0	0	0.16
	Pinus banksiana	0	0	4.58	1.91	1.33	0.75	0.33	0	0
	Polytrichum spp.	0	1.41	3.66	0.83	3.58	3.5	2.41	0	0.33
	Populus spp.	0	0.87	3.75	1.66	1.25	3.33	1.54	0.5	0.66
	Ribes triste	0	0.20	0.33	1.5	0	0.33	0	0.25	0
	Anaphalis margaritacea	0	0	0.41	0.16	0.5	0.04	0	0	0
	Epilobium ciliatum	0	0	0.25	0.25	0.25	0.16	0	0	0
	Geum spp.	0	0	0	0	0.16	0.16	0.33	0	0
	Hieracium caespitosum	0	0	0.66	0.41	0.83	0.16	0	0	0
	Kalmia polifolia	0	0	1	1	0	1.08	0.25	0	0
	Melampyrum lineare	0	0.04	0.66	0	0	0.16	0.41	0	0.08
	Potentilla norvegica	0	0	1	0	0.08	0.66	0	0	0
	Solidago canadensis	0	0	0	0.5	0.41	0.08	0	0	0
	Urtica dioica	0	0	2.5	2	1.5	0.58	0.16	0	0.04
Decrease	*Lycopodium dendroideum*	0.08	0.91	0	0	0	0.41	0.41	0	1.41
	Maianthemum canadense	3.12	6.37	2	1.91	2.91	4.08	5.08	5.83	4.83
	Rubus pubescens	0.33	1.95	1	0	0	1	0	0.75	0.45
	Trientalis borealis	0.37	1.54	0.16	0.16	0.16	0.5	0.16	1.08	0.33

Appendix IX continued

Riparian response	Species	Critical Values		Mean values at edge position (m)			
				Riparian			
		2.5th %ile	97.5th %ile	-15	-20	-25	*-30*
Increase	*Alnus incana*	5.40	18.2	14.9	17.5	24.2	21.1
	Aster puniceus	0.00	1.62	0.00	0.00	0.08	4.00
	Aster umbellatus	0.00	0.83	0.16	0.08	1.00	2.08
	Galium triflorum	0.29	1.54	0.16	0.50	1.83	3.20
	Lonicera villosa	0.00	0.45	0.00	0.33	0.83	1.33
	Lycopus uniflora	0.00	2.04	0.00	0.00	0.08	3.66
	Mentha arvensis	0.00	1.04	0.00	0.33	0.25	2.00
	Potentilla palustris	0.00	0.12	0.00	0.00	0.00	0.58
	Ribes hirtellum	0.00	0.41	0.00	0.00	0.00	0.50
	Ribes lacustre	0.00	0.00	0.41	0.00	0.16	0.00
	Salix spp.	0.00	1.12	4.58	2.75	2.16	3.33
	Scutellaria galericulata	0.00	1.12	0.00	0.00	0.16	2.08
	Sorbus americana	0.00	0.00	0.00	0.00	0.04	0.33
	Sphagnum spp.	0.70	10.2	8.83	11.8	15.5	5.41
	Thalictrum dasycarpum	0.20	3.41	0.20	1.66	2.50	12.4
	Thallose liverwort group	0.00	0.50	0.00	0.00	0.00	1.00
	Caltha palustris	0.00	0.58	0.00	0.00	0.00	4.41
	Cirsium arvense	0.00	0.20	0.00	0.00	0.00	0.50
	Cirsium muticum	0.00	0.33	0.00	0.00	0.00	1.41
	Glyceria canadensis	0.00	0.00	0.00	0.00	0.00	0.16
	Glyceria striata	0.00	0.83	0.00	0.00	0.00	2.00
	Petasites sagittatus	0.00	0.20	0.00	0.00	0.00	1.25
	Pyrola spp.	0.00	0.14	0.25	0.16	0.04	0.00
	Sagittaria cuneata	0.00	0.33	0.00	0.00	0.00	0.66
	Viburnum edule	0.00	1.20	0.00	0.00	2.08	0.41
Decrease	*Anemone quinquefolia*	0.06	1.00	0.00	0.25	0.00	0.00
	Climacium dendroides	0.08	1.54	0.00	0.00	0.91	0.58
	Clintonia borealis	1.00	3.91	1.66	2.00	1.33	0.25
	Corylus cornuta	0.04	4.62	0.25	0.00	0.00	0.00
	Equisetum sylvaticum	0.25	2.25	0.33	0.66	0.33	0.00
	Leafy liverworts	0.37	3.25	0.00	0.00	0.00	2.41
	Streptopus roseus	0.02	1.29	0.50	0.33	0.00	0.00
	Vaccinium angustifolium	0.20	3.37	2.45	0.00	0.00	0.00

Note: Critical values shown are the 2.5 and 97.5 percentiles of the 5000 permuted averages for undisturbed upland data (2) and undisturbed riparian data (3) respectively (2 tailed test, sig.= 0.05).

Appendix X

Understory species response at wide buffers

▨ = Mean values from transect locations are lower when compared to all reference values (1) and either upland or riparian reference values (2 or 3)
☐ = Mean values at given transect locations are higher when compared to all reference values (1) and either upland or riparian reference values (2 or3)
■ = Mean values at given transect locations are lower only in comparison to upland reference values (2) or riparian reference values
☐ = Mean values at given transect location are higher only in comparison to either upland reference values (2) or riparian reference values (3)

Entire buffer response	Species	Critical Values		Mean values at edge position (m)							Critical Values		Mean values at edge position (m)					
				Cut			Cut Edge								Riparian			
		2.5th %ile	97.5th %ile	20	15	10	5	0	-5	-10	2.5th %ile	97.5th %ile	-15	-20	-25	-30	-35	-40
Increase	*Aralia hispida*	0.00	0.04	0.00	1.08	0.16	0.33	0.00	0.04	0.25	0.00	0.20	0.50	0.00	0.00	0.00	0.00	0.00
	Bromus ciliatus	0.00	0.37	0.41	1.25	1.91	0.83	0.33	0.66	0.33	0.00	0.79	0.25	0.02	0.00	0.50	0.25	1.33
	Clintonia borealis	1.20	4.29	2.50	2.75	2.25	2.08	2.58	4.58	5.16	1.00	3.91	4.33	2.16	2.58	3.41	4.08	4.08
	Ptilium crista-castrensis	1.08	7.95	0.83	2.08	0.16	3.12	9.58	13.0	9.50	0.87	8.98	12.0	4.92	4.16	12.3	3.58	0.50
	Polygala paucifolia	0.00	0.00	0.16	0.16	0.00	0.16	0.00	0.33	0.33	0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.00
	Ribes glandulosum	0.00	0.25	0.16	2.41	0.58	0.33	0.25	0.00	0.00	0.00	0.25	0.00	0.25	0.16	0.00	0.00	0.50
	Thuja occidentalis	0.00	0.04	0.08	4.20	0.66	1.91	0.00	2.50	1.50	0.00	1.79	0.41	1.83	3.33	3.08	1.00	0.00
Decrease	*Abies balsamea*	2.37	11.7	2.08	0.00	1.00	0.00	0.08	0.04	1.25	1.04	6.91	0.75	1.81	1.16	0.54	0.08	0.58
	Acer spicatum	0.20	2.50	0.00	0.00	2.50	1.66	1.50	0.04	2.50	0.16	3.66	3.79	0.64	0.66	0.08	1.58	0.00
	Bryophyte spp. group	1.41	5.70	0.50	0.75	0.83	0.58	0.91	0.91	1.08	1.83	6.54	1.00	1.28	3.08	3.33	1.58	6.41
	Cladina spp.	0.58	7.33	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.08	4.08	0.33	0.00	0.00	0.41	0.00	0.00
	Dicranum sp.p	2.20	5.91	1.41	0.66	0.91	2.66	4.08	3.75	4.08	1.18	4.43	2.29	2.31	1.50	4.16	0.91	0.66
	Ledum groenlandicum	4.70	14.0	0.83	1.66	1.70	6.00	4.58	3.83	6.25	3.00	10.1	5.41	4.74	3.16	3.50	4.00	0.83
	Picea mariana	1.83	11.2	0.00	0.33	0.25	1.91	0.00	2.33	0.75	0.58	7.45	1.08	0.08	0.04	1.16	0.04	0.00
	Trientalis borealis	0.37	1.54	0.45	0.16	0.12	0.25	0.08	0.58	1.25	0.62	2.10	1.83	1.16	0.87	2.00	1.58	0.41
	Vaccinium angustifolium	1.50	6.37	0.41	0.58	0.25	1.16	0.75	1.33	1.00	0.20	3.37	1.25	1.57	1.50	0.50	0.33	0.00
Increase-Decrease	*Mertensia paniculata*	0.00	0.12	0.00	0.75	0.16	0.00	0.25	0.66	0.00	0.20	1.79	0.00	0.03	0.25	0.25	1.25	1.16
	Rubus pubescens	0.33	1.95	3.16	3.25	0.62	0.41	1.08	0.83	0.62	1.47	4.77	0.25	0.44	0.87	1.33	2.91	4.41
Decrease-Increase	*Coptis trifolia*	0.37	2.58	0.50	1.00	0.50	0.62	0.20	0.25	0.91	0.54	2.62	1.41	2.22	1.33	2.58	4.16	1.58
	Cornus canadensis	5.37	9.25	8.50	7.08	4.58	5.33	6.25	7.75	6.16	2.70	7.25	8.33	7.81	6.12	5.45	2.50	1.33
	Pleurozium schreberi	21.2	37.3	3.25	7.58	1.12	9.91	20.8	34.4	32.8	9.33	24.1	38.5	34.4	24.3	18.1	17.1	1.16

Appendix X continued

Upland response	Species	Critical Values		Mean values at edge position (m)						
				Cut				Edge	Buffer	
		2.5th %ile	97.5th %ile	20	15	10	5	0	-5	-10
Increase	*Aster macrophyllus*	0.00	2.87	3.91	1.50	4.41	2.91	0.83	2.75	0.00
	Epilobium angustifolium	0.00	0.29	1.16	1.33	2.75	1.20	0.25	0.50	0.00
	Oryzopsis asperifolia	0.04	0.41	0.75	0.29	2.91	1.16	0.66	0.66	0.25
	Picea glauca	0.00	0.00	4.29	0.66	0.12	0.41	2.54	0.00	0.00
	Pinus banksiana	0.00	0.00	0.16	0.00	1.58	0.33	0.00	0.00	0.00
	Populus spp.	0.00	0.87	1.33	3.00	0.50	0.58	0.20	0.00	0.00
	Prunus pensylvanica	0.00	0.00	0.25	1.25	0.25	0.00	0.00	0.00	0.00
	Rosa acicularis	0.08	1.91	0.83	2.16	0.16	2.50	2.75	2.83	0.33
	Rubus idaeus	0.08	1.95	8.08	4.75	11.9	9.58	2.33	0.70	0.54
	Taraxacum spp.	0.00	0.00	0.33	0.95	0.25	0.08	0.08	0.16	0.00
	Apocynum androsaemifolium	0.00	0.00	0.25	1.00	0.00	0.00	0.00	0.00	0.00
Decrease	*Aralia nudicaulis*	0.79	3.62	1.16	0.50	0.66	1.83	1.75	0.91	2.08
	Lycopodium annotinum	1.20	5.83	0.41	1.08	0.20	0.83	0.41	1.00	2.33
	Lycopodium dendroideum	0.08	0.91	1.16	0.33	0.50	0.00	0.00	0.00	0.00
	Gaultheria hispidula	0.87	4.45	0.41	0.75	0.16	1.83	3.25	2.08	3.08

Appendix X continued

Riparian response	Species	Critical Values		Mean values at edge position (m)					
				Riparian					
		2.5th %ile	97.5th %ile	-15	-20	-25	-30	-35	-40
Increase	*Aster puniceus*	0.00	1.62	0.00	0.00	0.00	0.00	0.50	2.50
	Aster umbellatus	0.00	0.83	0.00	0.00	0.00	0.16	0.33	1.08
	Carex aquatilis	0.00	2.29	0.00	0.00	0.00	0.00	0.00	4.50
	Carex thin group	0.12	2.41	0.00	0.03	1.25	3.58	4.91	2.91
	Diervilla lonicera	0.20	5.23	2.91	7.50	6.91	6.33	2.08	1.00
	Lonicera canadensis	0.00	1.08	0.58	0.00	0.00	0.00	0.00	1.16
	Lonicera villosa	0.00	0.45	0.00	0.03	0.00	0.00	0.83	2.00
	Lycopodium clavatum	0.00	1.45	0.41	0.00	0.00	0.00	0.66	1.66
	Maianthemum canadense	1.63	4.50	7.91	9.27	7.66	7.00	5.29	2.25
	Phegopteris connectilis	0.00	1.95	0.00	0.00	0.00	0.00	0.00	2.50
	Polytrichum spp.	0.00	0.58	0.41	0.50	1.75	0.00	0.08	1.08
	Rhamnus alnifolia	0.00	1.91	0.00	0.00	0.00	0.58	1.83	3.41
	Salix spp.	0.00	1.12	0.00	0.12	0.00	1.16	0.00	3.16
	Agrostis scabra	0.00	0.37	0.00	0.00	0.00	0.00	0.41	0.00
	Cicuta bulbifera	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.16
	Circaea alpina	0.00	0.29	0.00	0.04	0.33	0.00	0.04	1.41
	Equisetum scripoides	0.00	0.00	0.00	0.00	0.08	0.16	0.00	0.66
	Gentiana sp	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.58
	Glyceria striata	0.00	0.83	0.00	0.00	0.00	0.00	0.00	1.16
	Listera cordata	0.00	0.00	0.16	0.02	0.00	0.00	0.00	0.00
	Osmunda claytonia	0.00	0.12	0.00	0.00	0.00	0.00	0.16	2.66
	Pyrola spp.	0.00	0.14	0.00	0.04	0.00	0.16	0.00	0.25
	Sagittaria cuneata	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.58
	Schizachne purpurascens	0.00	0.29	0.00	0.00	0.00	0.00	0.83	0.00
	Solidago canadensis	0.00	0.08	0.00	0.00	0.00	0.00	0.25	0.00
	Viburnum edule	0.00	1.20	0.00	0.00	0.00	0.00	0.00	2.08
Decrease	*Alnus incana*	5.40	18.23	2.50	0.79	1.83	2.58	7.66	9.16
	Anemone quinquefolia	0.06	1.00	0.00	0.01	0.00	0.00	0.50	0.08
	Calamagrostis canadensis	0.04	2.87	0.00	0.00	0.00	0.00	0.58	2.16
	Carex arctata	0.27	2.41	0.00	0.15	0.25	0.25	0.25	0.58
	Cornus stolonifera	0.25	5.87	0.83	0.00	0.00	0.00	0.91	2.50
	Corylus cornuta	0.04	4.62	0.00	1.80	1.00	3.33	0.00	0.00
	Gallium triflorum	0.29	1.54	0.00	0.15	0.25	0.04	1.04	2.16
	Gymnocarpium dryopteris	0.03	0.99	0.25	0.28	0.00	0.00	0.25	0.00
	Hylocomium splendens	0.20	6.83	3.33	3.11	1.83	2.08	0.58	0.00
	Leafy liverworts	0.37	3.25	0.00	0.02	0.16	0.04	0.33	6.41
	Mitella nuda	0.45	3.08	0.00	0.32	1.25	0.87	1.50	2.00
	Petasites frigidus	0.04	2.37	0.08	0.16	0.66	0.00	0.66	0.00
	Streptopus roseus	0.02	1.29	0.33	0.28	0.66	0.16	0.83	0.00
	Thalictrum dasycarpum	0.20	3.41	0.00	0.00	0.00	0.00	0.16	6.83
	Viola spp.	1.14	4.08	0.37	0.26	0.91	1.08	2.87	5.12

Note: Critical values shown are the 2.5 and 97.5 percentiles of the 5000 permuted averages for undisturbed upland data (2) and undisturbed riparian data (3) respectively (2 tailed test, sig.= 0.05).

Appendix XI

ANCOVA comparing moss growth and moss cover between buffers and undisturbed stream edges. Transect distance (i.e. location on the transect) was the covariate.

Dependent Variable	Source	df	Type III Sum of Squares	Mean Square	F	Sig. (<0.05)
Growth of *H. Splendens*(SQRT)	Corrected model	2	4.886	2.443	15.629	0
	Transect	1	3.184	3.184	20.37	0
	Disturbance	1	1.702	1.702	10.888	0.001
	Error	81	12.661	0.156		
Growth of *P. commune*(SQRT)	Corrected model	2	2.481	1.24	9.137	0
	Transect	1	0.526	0.526	3.873	0.052
	Disturbance	1	1.955	1.955	14.4	0
	Error	81	10.997	0.136		
Mean %cover of *H. splendens*	Corrected model	2	79.500	39.75	3.186	0.047
	Transect	1	77.786	77.786	6.234	0.015
	Disturbance	1	1.714	1.714	0.137	0.712
	Error	81	1010.655	12.477		
Mean % cover of *P. commune*	Corrected model	2	51.614	25.807	5.232	0.007
	Transect	1	0.453	0.453	0.092	0.763
	Disturbance	1	51.161	51.161	10.371	0.002
	Error	81	399.571	4.933		

Appendix XII

Spearman's rank-order correlations amongst the bryophyte growth, bryophyte vitality, bryophyte cover, shrub cover and total understory cover. Correlation coefficients are given and N=84 for all correlations. *H.s.* = *Hylocomium splendens* and *P.c.* = *Polytrichum commune*. ** Correlation is significant at the .01 level (2-tailed). * Correlation is significant at the .05 level (2-tailed).

	H.s. growth	*P. c. growth*	*H.s.* # new shoots	*H.s.* vitality	*P. c.* vitality	*H.s.* % cover	*P. c.* % cover	Shrub cover	Total understory cover
H.s. growth	1	.374(**)	.224(*)	.704(**)	.597(**)	.505(**)	.380(**)	.345(**)	.515(**)
P. c. growth	.374(**)	1	0.035	.348(**)	.626(**)	0.168	.410(**)	.342(**)	.470(**)
H.s. # new shoots	.224(*)	0.035	1	0.14	0.143	0.177	.253(*)	0.116	0.196
H.s. vitality	.704(**)	.348(**)	0.14	1	.597(**)	.484(**)	.469(**)	.452(**)	.520(**)
P. c. vitality	.597(**)	.626(**)	0.143	.597(**)	1	.291(**)	.566(**)	.453(**)	.553(**)
H.s. % cover	.505(**)	0.168	0.177	.484(**)	.291(**)	1	0.182	-0.027	0.1
P. c. % cover	.380(**)	.410(**)	.253(*)	.469(**)	.566(**)	0.182	1	.280(**)	.361(**)
Shrub cover	.345(**)	.342(**)	0.116	.452(**)	.453(**)	-0.027	.280(**)	1	.811(**)
Total understory cover	.515(**)	.470(**)	0.196	.520(**)	.553(**)	0.1	.361(**)	.811(**)	1

Appendix XIII

Kruskal-Wallis test of mean rank comparing vitality across buffer and undisturbed stream edges with respect to disturbance treatment and location on the transect.

Grouping variables	Vitality	df	Chi-square	Sig. (<0.05)
Disturbance (buffer/undisturbed)	*H. splendens*	1	17.56	0
	P. commune	1	10.497	0.001
Transect location	*H. splendens*	6	21.588	0.001
	P. commune	6	14.136	0.028

Appendix XIV

Kruskal-Wallis test of mean rank comparing canopy cover across buffer and undisturbed stream edges with respect to disturbance treatment and location on the transect.

Grouping variable	df	Chi-square	Sig. (<0.05)
Disturbance (buffer/undisturbed)	1	1.469	0.226
Transect location	6	15.216	0.019

Appendix XV

Kruskal-Wallis test of mean rank comparing total shrub cover and total understory cover across buffer and undisturbed stream edges with respect to disturbance treatment and location on the transect.

Grouping variable	Total cover	df	Chi-square	Sig. (<0.05)
Disturbance (buffer/undisturbed)	Shrub	1	21.079	0
	Understory	1	24.7	0
Transect location	Shrub	6	22.946	0.001
	Understory	6	18.694	0.005

Appendix XVI

Correlation matrix with the three variables used in the PCA: relative humidity, soil moisture and total understory cover. Correlations are significant ($p < 0.05$), but not highly colinear (<.9).

		Relative humidity	Soil moisture	Understory cover
Correlation	Relative humidity	1.000	.274	.542
	Soil moisture	.274	1.000	.300
	Understory cover	.542	.300	1.000
Sig. (1-tailed)	Relative humidity		.039	.000
	Soil moisture	.039		.027
	Understory cover	.000	.027	

Appendix XVII

Mann-Whitney U test comparing the amount of edge as a proportion of cut and burnt patch area within 250 ha windows. (a) The proportion of edge differed significantly between disturbance patches above and below 150 ha (< 0.05, not corrected for ties).

Disturbance size	N	Mean rank	Sum of ranks	Mann-Whitney U	Z	Exact Sig. [2*(1-tailed Sig.)]
< 150 ha	6	9.5	57	0	-2.882	.002(a)
> 150 ha	6	3.5	21			

Appendix XVIII

Mann-Whitney U test comparing of the Disturbance Index value of near and far edge in 250 ha clearcut and fire disturbance windows. (a) The Fragmentation Index value was significant different between disturbance types (< 0.05, not corrected for ties).

Fragmentation value	Group	N	Mean rank	Sum of ranks	Mann-Whitney U	Z	Exact Sig. [2*(1-tailed Sig.)]
Near edge	Clearcut	6	3.5	21	0	-2.882	.002(a)
	Fire	6	9.5	57			
Far edge	Clearcut	6	4	24	3	-2.402	.015(a)
	Fire	6	9	54			

Appendix XIX

Mann-Whitney U test comparing the total Disturbance Index values as a proportion of the total area disturbed within 250 ha windows. (a) The ratio of Fragmentation Index value to area was significant different between disturbance types (<0.05, not corrected for ties).

Group	N	Mean rank	Sum of ranks	Mann-Whitney U	Z	Exact Sig. [2*(1-tailed Sig.)]
Clearcut	6	9.17	55	2	-2.562	.009(a)
Fire	6	3.83	23			