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**Riparian habitat and vegetation recovery of headwater
streams after clearcut harvesting**

by

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**Thesis submitted in partial fulfillment of the requirements for the
degree of Master of Science in Biology**

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Abstract

In this thesis I examined two important aspects of clearcut harvesting along small headwater streams and their riparian zones. The objectives of the study were: 1) to investigate the impacts of clearcut harvesting on the morphological features of headwater systems and the pattern of recovery of those impacts over time, and 2) to explore the response of headwater riparian understory vegetation to clearcut harvesting over time.

- 1) Study results over 30 small headwater streams of northwestern Ontario indicate that forest harvesting along headwater systems significantly affects stream morphology and associated riparian habitat characteristics. Stream width and number of stream channels were significantly higher while stream depth was lower than reference sites up to 3 years after harvesting. Although impacts on stream width and stream channels were not observed after 3 years, significant difference in stream depth was observed even 23 years after harvesting. Canopy exposure remained significantly high up to 15 years after clearcut. However, headwater streams and their riparian zones need at least 16-18 years to recover from adjacent clearcut harvesting impacts.
- 2) Clearcut harvesting had no significant impact on overall species richness or diversity, but it caused compositional changes in vegetation. It induces local elimination of some late-seral species, recovery of which was not evident even 23 years after harvesting. Species including *Acer spicatum*, *Sorbus americana*, *Circaea alpina*, *Mitella nuda*, *Brachythecium rivulare*, *Dicranum flagellare* and *Rhodobryum roseum* are strongly associated and attain their highest frequency and abundance in late-seral stands.

Results of this study suggest that headwater systems need to be kept under adequate vegetation cover to mitigate harvesting impacts and restore the important ecological services they provide in the protection of biodiversity and water quality.

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Chapter 1

1.1 GENERAL INTRODUCTION

Riparian areas are important components of the natural landscape. These are transition zones between streams and adjacent terrestrial habitats, with ecosystem characteristics and biotic communities distinct from both (Lamb and Mallik, 2003; Naiman and Décamps, 1997). These are areas of reciprocal influences between aquatic and terrestrial components with varying widths depending on the topography (Richardson et al., 2005). The ecological importance of riparian areas greatly exceeds their areal extent on the landscape, because these areas support a wide range of plant, animal and microbial communities (Clary and Medlin, 1993). The structural and functional diversity of the riparian ecosystem is very complex and dynamic, which provides a number of important ecological services including control of surface run-off, mitigation of soil erosion, stabilization of stream and river banks, prevention of sedimentation, maintenance of high water quality and habitat for invertebrate communities (Gould and Walker, 1999; NRC, 2002; Naiman and Décamps, 1997).

Small streams, also called headwater streams are often undetectable by aerial photos. They form a channel network constituting almost 80% of the total stream length in many drainage networks (Sidle et al., 2000), and are typically bordered by hillslopes and zero-order basins (Moore and Richardson, 2003). These are normally first-order channels, with catchments of <100 ha, bank full width <3 m and mean annual discharge <57 l/s (Richardson and Danehy, 2007). Small streams and their riparian areas provide a characteristic structure to the biological communities because of its three distinguishing attributes: small channel dimension, fish abundance and low

flow. Small channel size and closed forest canopy in headwater systems create a physical template of reduced light inputs, strong local microclimate gradients and high input of organic matter (Richardson and Danehy, 2007). Headwater streams process leaf litter into smaller fragments carried downstream, a large part of which are used by the downstream organisms as their primary source of energy (Dieterich et al., 1997; Heard and Richardson, 1995; Wipfli et al., 2007). In addition, headwater systems play a very significant role in biodiversity conservation by maintaining habitat connectivity (Naiman et al., 1993).

Riparian ecosystems are readily affected by a variety of natural and anthropogenic disturbances, which are temporary changes in average environmental conditions causing a pronounced change in an ecosystem. Disturbance is a relatively discrete event in time and space that alters the structure of populations, communities, and ecosystems and/or changes resources, substrate availability, or the physical environment (White and Pickett, 1985). While natural disturbances like fire, flooding, insect defoliation or pathogen activities modify the ecosystem functions, anthropogenic disturbances especially forest harvesting and scarification in and around riparian area accelerate the severity of these disturbances (Naiman et al., 2000; Lamb et al., 2003). The microclimate and floristic composition in clearcuts along riparian areas can be quite different from those of the undisturbed areas and extent of tall shrub and tree species recruitment after a disturbance becomes a controlling factor in forest regeneration (Pontailier et al., 1997; Ulanova, 2000).

Forest management has characteristic influences on the headwater systems. Clearcut harvesting may lead to increased summer maximum stream temperature, changes in near-ground microclimate, higher UV radiation, enhanced algal production and reduced litter inputs

(Richardson, 2008). Forest harvesting increases soil nutrient availability, soil-water retention, soil compaction, disturbance in organic horizon and displacement of mineral horizon (Stark, 1980; Rollerson, 1990; Vitousek et al., 1992). Clearcut harvesting significantly increases water yield especially during May to October and reduces evapotranspiration (Hubbart et al., 2007). Increases in water yield usually takes place immediately after harvesting (Troendle and King, 1885; Stednick, 1996) and the amount of increase depends on climatic regime, vegetation type, percentage of the catchment area harvested and harvesting patterns, and gradually diminishes with regeneration of forest (Bari et al., 1996; Lesch and Scott, 1997). In clearcut areas, buffer zones effectively filter the pollutants from water entering the streams through surface runoff. If small headwater streams are not protected with a buffer, a substantial portion of the flow volume becomes channelized without being filtered (Norris, 1993).

Jackson et al. (2007) reported 0.5 to 2 m deep logging slash deposition in clearcut streams immediately after harvesting, which resulted in increased roughness of the stream and elevated fine sediment deposition. Forest harvesting may result in vegetation typically dominated by ruderal, and in some instances, exotic species (Halpern et al., 1999). On the other hand, it may enhance natural regeneration of tree species which prefer mineral substrates, facilitate recovery of shade-tolerant herbs, planted trees and advanced regeneration (Roberts and Dong, 1993; McInnis and Roberts, 1994). Since plant community recovery is system specific and influenced by numerous biotic and abiotic factors post-harvest community composition in different streams can exhibit marked difference (Battles et al., 2001; Costa and Magnusson, 2002; Sullivan et al., 2001; Roberts, 2004).

Recovery from harvesting impacts refers to returning to initial composition or to a condition where the biophysical conditions are indistinguishable from initial state. The term may be used as a process i.e. a gradual diminishing trend of the impacts of disturbance over time, or as an endpoint where the impacts are indistinguishable from post-disturbance state. In this thesis recovery has been considered as an endpoint to describe biophysical features of clearcut headwater systems in relation to reference forests. Recovery from disturbance impacts largely depends on the nature of disturbance (e.g., its intensity or duration), characteristics of initial community and local environmental conditions. Recovery of vegetation is characterized by its resistance i.e., the extent to which it resists change by disturbance (Sutherland, 1974).

Greenberg et al. (1995) observed an increase in species richness and diversity following post-fire salvage logging. In most cases an initial decrease in diversity, especially among forest interior species, was followed by a quick recovery within a few decades (Gilliam, 2002; Hannerz and Hanell, 1997; Meier et al., 1995; Roberts and Zhu, 2002). However, recovery of some species may take a long time in some managed forests due to short cycle stand rotation (30-60 years) and high soil disturbance associated with logging (Loya and Jules, 2008). Post-harvest species richness and cover of herbaceous plants was found to be lower than primary forests even 87 years after harvesting (Duffy and Meier, 1992). These authors assumed that 87 years is insufficient time to detect recovery as the process is too slow. They also predicted that secondary forests will never recover to match primary forests because of different environmental conditions during their respective establishment period.

Forestry operations adjacent to riparian areas can disrupt the ecological services provided by the riparian zone and cause deterioration of the aquatic environment (Naiman and Décamps, 1997).

Habitat disturbance alters post-disturbance plant communities by providing habitat for exotic and ruderal species (Keeley et al., 2003). When existing plant biomass is removed by a disturbance, resources become available to invading exotic plants (Bataineh et al., 2006). Ruderal species are adapted to environments with high disturbance but low stress, and therefore colonize areas that are high in nutrients and other resources after disturbance (D'Antonio and Chambers, 2006). Riparian management practices typically involve maintaining an unharvested riparian buffer between the stream and the upland. It has been demonstrated that buffers are capable of reducing some adverse effects of clearcut harvesting (Karr and Schlosser, 1978; Norris, 1993; Osborne and Kovacic, 1993). However, near-ground microclimate at the buffer edge and each subsequent location toward the upland remain close to the clearcut state rather than that of the forest interior implying that standard buffer widths may not be adequate for preserving microclimate close to streams (Brosofske et al., 1997).

Much of the riparian research has been conducted on larger, higher order (second order and above) streams (Spackman and Hughes, 1995; Hughes and Cass, 1997). Very little work has been done on small, perennial streams (Goebel et al., 2003; Becker and Pallardy, 2003). The properties of unbuffered headwater streams differ markedly from those of the larger streams and they received relatively little attention (Moore et al., 2005; Anderson et al., 2007). Services provided by the headwater streams in terms of habitat, biota and water quality in natural and managed landscapes are not yet sufficiently understood. Vegetation changes following clearcut harvesting and forest fire is a major issue in the riparian zones. The basic information on vegetation recovery rate after forest harvesting in the riparian areas and its influences on physical structure of headwater systems is still lacking.

In this study, I examined the habitat and biotic differences of headwater systems 3 – 23 years after clearcut harvesting in northwestern Ontario. More specifically, I studied the physical structure of unbuffered post-harvest headwater streams and their riparian zones, floristic composition and their differences over time following forest harvesting without riparian buffers. In the following two chapters of this thesis I addressed two broad questions:

1. How does clearcut harvesting affect the morphological features of small headwater streams and their riparian zones and do these effects differ in relation to time since harvest? This chapter characterizes physical features of small headwater streams and their riparian zones 3 – 23 years since forest harvesting, which will also be used as explanatory variables to illustrate the vegetation recovery pattern dealt in the subsequent chapter.
2. How does the headwater riparian floristic composition differ among streams subject to clearcuts 3-23 years previously? This chapter describes the differences in species richness, abundance, diversity and evenness of ground vegetation after clearcut harvesting and investigates whether any species were restricted to or significantly associated with late successional stands.

1.2 GENERAL METHODS

1.2.1 Study area

The study was conducted in the boreal mixedwood forest located approximately 30 km northeast of Thunder Bay, Ontario, Canada (Figure 1.1). Study sites were spread over four watersheds (Mackenzie River, Current River, Wolf River and Kaministiquia watershed), all of which drain to Lake Superior. The watersheds are part of the Thunder Bay plains eco-region, composed primarily of diabase, greywacke and shale bedrock formations (Wickware and Rubec, 1989). The area is characterized by an undulating terrain with many steep to vertical slopes and extensive rock outcrops, exhibiting poor water retention and soil drainage, numerous small streams and wetlands but few lakes. The area enjoys a boreal temperate climate. Mean temperature varies from -26° to -22° C in January and 21° to 25° C in July and total annual precipitation in the watershed varies from 700 – 850 mm (Baldwin et al., 2000).

All these watersheds are dominated by northern boreal forest. Dominant tree species found on medium textured valley soils include white spruce (*Picea glauca*), balsam fir (*Abies balsamea*), white birch (*Betula papyrifera*) and trembling aspen (*Populus tremuloides*). Tamarack (*Larix laricina*), eastern white cedar (*Thuja occidentalis*) and black spruce (*Picea mariana*) occupy wet soils whereas jack pine (*Pinus banksiana*) and white birch occupy uplands with rocky-outcrops (Rowe, 1972). The understory is dominated by large-leaved aster (*Aster macrophyllus*), bunchberry (*Cornus canadensis*) and blue bead lily (*Clintonia borealis*). Based on the local ecosite classification guidelines the riparian vegetation along the studied streams can be broadly separated into three groups (Harris et al., 1996; Rankin, 2000): *Calamagrostis canadensis* and *Carex aquatilis* dominated meadow marshes, *Alnus incana* dominated swamp thickets, and

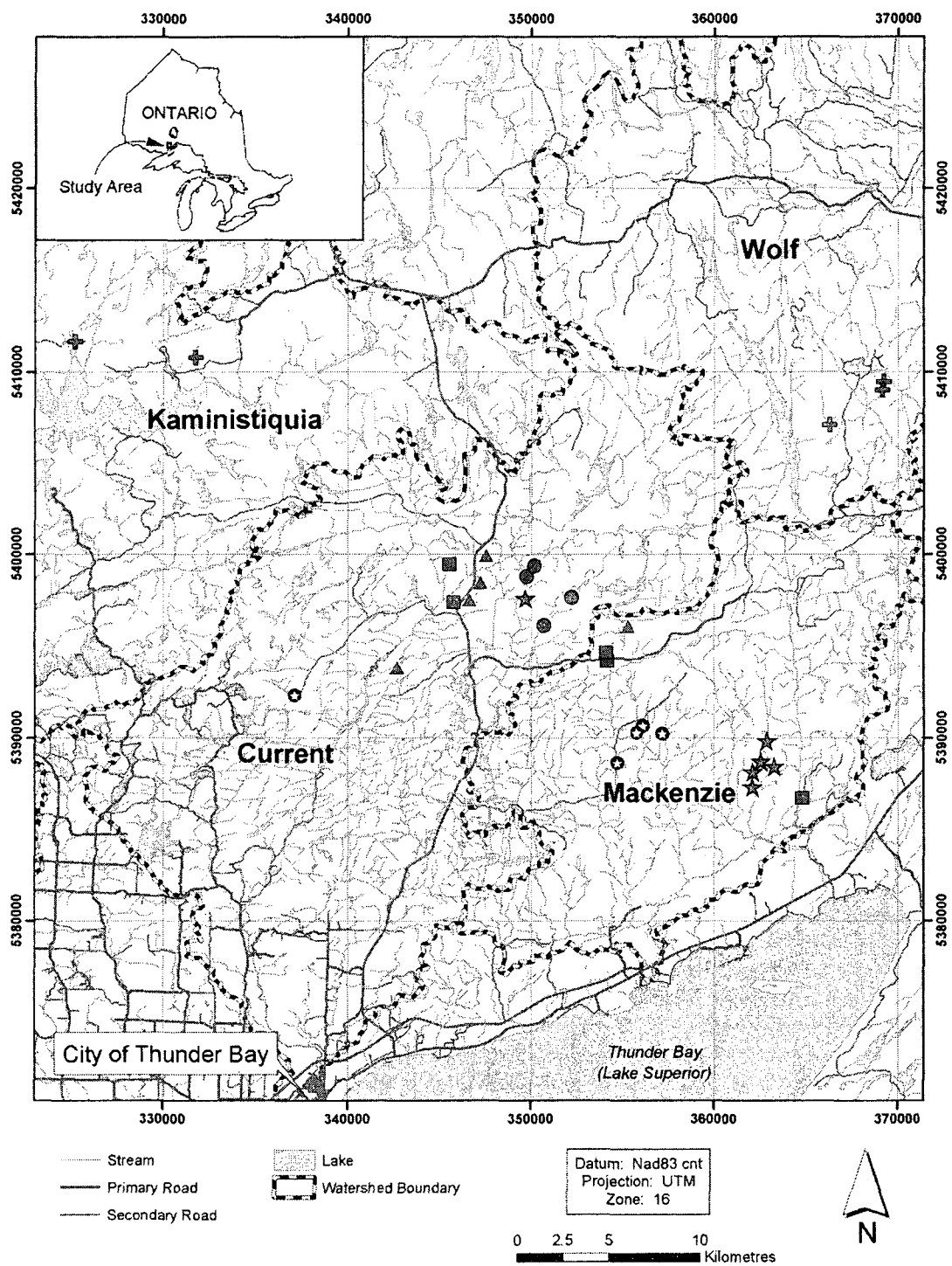


Figure 1.1: Map of the study area, northeast of Thunder Bay, Ontario, Canada, showing study site locations of 3 years (●), 7-10 years (▲), 11-15 years (■), 16-18 years (⊕), 19-23 years (+) post harvest and unharvest reference (★) sites.

occasionally *Thuja occidentalis* dominated conifer swamps. Forestry is the predominant land use in the area, which heavily impacted the upland forests (Perera and Baldwin, 2000).

1.2.2 Site selection

All the sites were selected on small streams with bankfull width less than 3 m and catchment areas less than 100 ha. Potential small streams of the study area were first located using a GIS map (ArcGIS, ArcMap version 9.2, ESRI Inc., Redlands, CA) derived from 20 m resolution digital elevation model (OMNR, 2005). Each of these streams was assigned a number and then following stratified random sampling method 30 of them were selected for the study. Selected streams were then verified in the field through an extensive reconnaissance survey. In case a stream could not be found in the field, another stream was selected randomly. Since small streams in the boreal forest are often characterized by missing channel features due to sub-surface flow (Hupp, 1986), the following criteria were considered in the final selection of study streams: i) presence of a recognizable stream bed with upward slope on either side, ii) bank full width less than 3 m, iii) catchment area less than 100 ha, and iv) connection with a larger stream.

Sites were selected in both harvested and undisturbed areas. Harvested sites had been clearcut between 3 to 23 years previously. Necessary forest harvesting information for the area was collected from the Ontario Ministry of Natural Resources (OMNR) local office in Thunder Bay. Sites with no adjacent forestry activities for at least 90 years within 80-90 m of the clearcut or fire were considered as undisturbed reference sites for comparisons. Sampling was conducted in similar site conditions as much as possible for all available post harvest and reference forests to minimize variations among sites. Site class, ecosite type, average slope, soil texture, landform, relief and drainage conditions were taken into consideration during site selection (Appendix 7).

1.2.3 Sampling Design

Field sampling was conducted across a chronosequence of second-growth clearcuts with ages ranging from 3 to 23 years and adjacent undisturbed mature forest originating from large wild fires 90–100 years ago, referred to as reference forest. To evaluate the variations in the morphology of streams, their riparian habitats and patterns of species re-establishment, I considered a total of 30 streams, 24 in post-harvest and 6 in reference forests. Using records from OMNR I categorized the harvested sites into five age classes based on time since harvesting: 3 years (n=4), 7 to 10 years (n=5), 11 to 15 years (n=5), 16 to 18 years (n=5) and 19 to 23 years (n=5). The study streams were unmapped small streams without any riparian buffer. However, since all the sampled streams were connected to large streams to avoid misidentification, approximately 30 m of their downstream end ran through riparian buffer of the larger streams (Figure 1.2).

A 50 m section of each small stream was selected leaving 10 m from the buffer edge at the downstream end (Figure 1.2). This 50 m section was divided into ten 5 m segments from which 3 segments were selected at random to study stream bed morphology. Three 5 m segments were selected on each stream within the buffered area. Each stream was studied both in clearcut and buffer areas assuming that both parts will be similar in geomorphology and species composition by being part of the same stream. But since the buffered portion is relatively protected compared to the clearcut portion of the stream and the disturbance is considered to be of an intermediate type (Biswas, 2008), any difference between these two parts might be attributed to harvesting. For the study of riparian habitats and their vegetation I established three transects on the clearcut area of each stream, perpendicular to the stream running through riparian zone and extending up

to the riparian-upland transition zone. These transects were then divided into consecutive quadrats of 1x1 m. Since the width of the riparian zone varies among streams, the number of quadrats per transect were not fixed. However, for each transect the minimum number of quadrats in the riparian zone was two and the maximum was ten. Within the buffer zone I laid three more transects: one in the middle and one 10 m away from the center on either side (Figure 1.2). A similar sampling protocol was followed for the unharvested reference sites. To avoid edge effects, quadrats in the reference sites were at least 50 m away from any clearcut edge to avoid edge effects (Murica, 1995). Since aspect was found to influence the microclimate and species composition of a site (Burton, 2002; Chen et al., 1995; Matlack, 1993), the sampling transects were established on both sides of the streams.

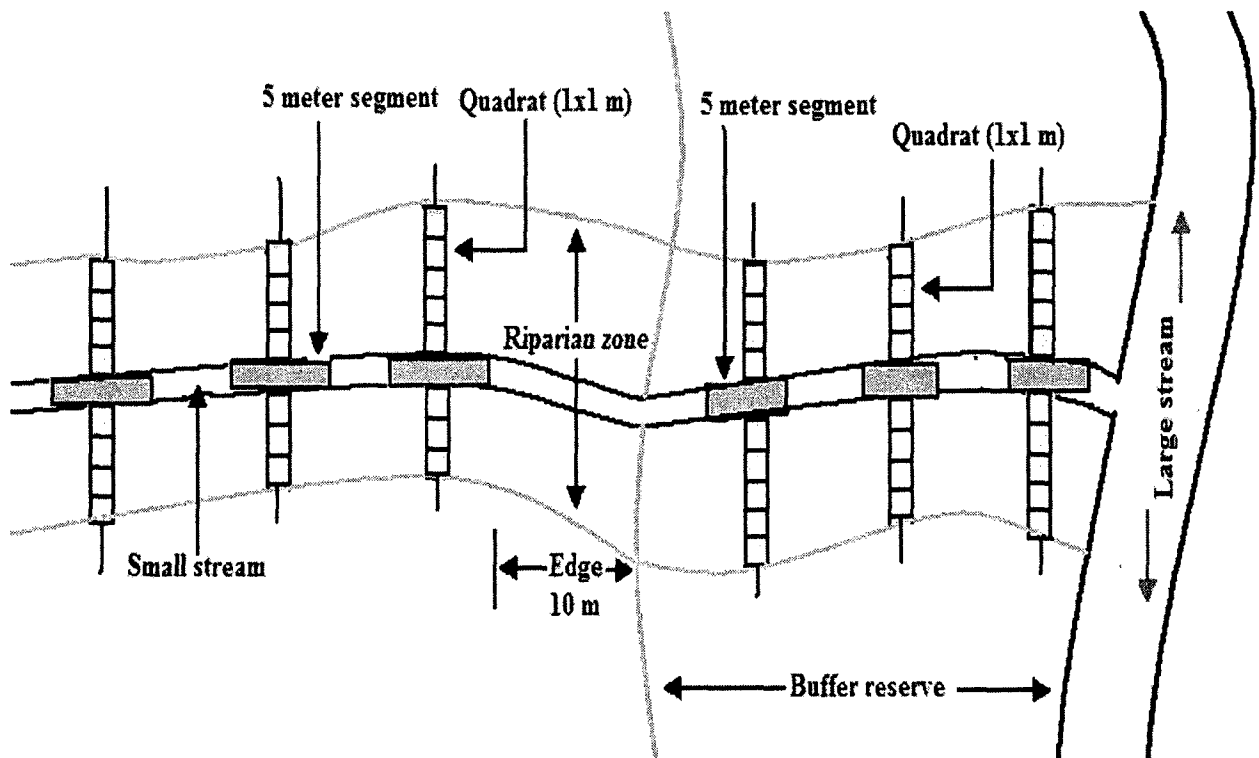


Figure 1.2: A schematic diagram of the sampling design showing sampling protocol for habitat and floristic study at clearcut and buffer areas.

1.2.4 Habitat and floristic variables

Within each study quadrat the following physical and environmental variables were recorded: slope, aspect, stream width and depth, riparian width, number of stream channels, depth of organic matter, distance of quadrat from stream, percent cover of ruts from harvesting equipments, logging slash (≥ 10 cm diameter), exposed rock, exposed mineral soil, vegetation colonization at the edge and center of stream, ground exposure and canopy exposure. Canopy exposure was measured using a concave spherical Densiometer (Model A, 5733 SE Cornell Dr., Bartlesville) held at breast height (1.37 m). Readings were taken in each cardinal direction and averaged to obtain an estimation of canopy exposure above each sampling quadrat. All plants encountered in each quadrat were identified to the species level and their percent cover recorded by visual estimation. Plants that were difficult to identify with certainty in the field were collected and identified in the laboratory by comparing with herbarium specimens.

1.2.5 Data analysis

Prior to statistical analysis, explanatory variables measured at each quadrat were averaged to produce stream level estimates. Data analyses and statistical protocols are described in the respective chapters since these were specific to individual research questions.

Chapter 2

Geomorphic changes and recovery of headwater system 3 to 23 years after clearcutting

2.0 Abstract

Forest harvesting directly affects headwater systems, causing changes in catchment hydrology and riparian habitats. I investigated geomorphological impacts of harvesting on headwater systems and their recovery in the boreal mixedwood forests of northwestern Ontario, Canada. I studied 30 headwater streams (width <3 m), 24 in clearcut sites harvested 3 to 23 years previously and six in undisturbed, mature forests as reference. Each stream had two segments: i) in clearcut 10 m apart from cut edge and ii) in riparian buffer of larger stream to which it flows. Using a nested ANOVA model and discriminant function analysis, I examined the harvesting impacts on and recovery of stream width, depth, number of stream channels, riparian width, ground exposure, canopy exposure, depth of organic matter and disturbance index (derived from percent cover of equipment ruts, logging slash, exposed rock, exposed mineral soil, plant colonization at the edge and center of stream). I found stream width and number of stream channels significantly higher in clearcut sites up to 3 years after clearcutting but recovered within 10 years. Stream depth decreased significantly following harvesting, which was detectable even 23 years after clearcutting. Canopy exposure was the most important factor contributing to harvesting impacts, which remained significantly high up to 15 years after clearcutting. However, overall impacts of harvesting adjacent to headwater streams and their riparian zones were significant at least until 15 years after harvesting. These results demonstrate that headwater systems need to be kept protected by vegetation cover following clearcut harvesting.

2.1 Introduction

Numerous headwater streams occupy an extensive area of a landscape at the fringe of any fluvial network. These are defined as first-order streams, with catchments of <100 ha, and bank full widths <3 m (Richardson and Danehy, 2007). Headwater streams interact very strongly with their surrounding terrestrial areas. They are largely dependent on energy subsidies from the surrounding forest in the form of leaf litter and terrestrial invertebrates (Bilby and Bisson, 1992). Since these streams are very common, small and often unmapped, they are usually overlooked or subject to passive neglect despite their important roles in providing habitat for biota and maintenance of water quality. Although they are numerous and occupy almost 60 – 80% of the total stream length in a watershed, headwater streams may not be protected by buffer reserves (MacDonald and Coe, 2007). In many jurisdictions, only larger streams that appear on the topographic maps receive buffer reserve protection (Hupp, 1986). Small streams are often underappreciated and consequently controversial regarding the management requirement to ensure their conservation as a part of sustainable forestry practice. Kahl (1996) argued that smaller streams may need wider buffers than larger streams since the volume of water flowing through individual stream is low and consequently highly sensitive to environmental changes. However, protecting all headwater streams with buffers may economically be an impractical proposition.

Riparian zones are transitional and semi-terrestrial areas, extending from the edge of water to the edges of upland communities, regularly influenced by fresh water (Naiman et al., 2005). Riparian ecosystems support a high level of floristic diversity relative to upland forests (Décamps and Tabacchi, 1994; Naiman and Décamps, 1997). This greater diversity may be

attributed to stream geomorphology, hydrology and frequency and spatial extent of flooding. Riparian zones help lateral propagule migration, which varies depending on stream size, flow patterns, upland slope, aspect and riparian vegetation (Naiman et al., 2000; Dodds and Oakes, 2008). Riparian ecosystems provide a wide range of ecological services like: i) organic matter input, ii) filtering and buffering of sediment, nutrients and surface runoff, iii) erosion reduction and stabilization of stream banks, iv) maintenance of water quality, v) propagule dispersal corridors, and vi) contribution of energy to the overall ecosystem energy budget (Gregory et al., 1991; Malanson, 1993; Triska et al., 1993; Gould and Walker, 1999; Hannon et al., 2002; Allan et al., 2003; Melody and Richardson, 2004; Shirley, 2004; Sabo et al., 2005). Headwater streams and their riparian areas (collectively constituting the headwater system) differ from larger stream systems in a number of ways (e.g. channel dimension, fish abundance and the disturbance regime associated with low flows) that shape their characteristic biological communities. Therefore, the ecological characteristics of small stream riparian areas are presumably different from those of larger streams (Richardson et al., 2005).

Natural disturbance (mainly fire, insect/pathogen infestation, beaver activity) and anthropogenic disturbance (primarily forest harvesting) are common in the boreal forest (Naiman et al., 2000). Forest harvesting directly affects small streams and their riparian zones due to movement of harvesting equipment and removal of forest canopy, which in turn may cause changes in catchment hydrology and sediment dynamics. The consequent direct and indirect adverse effects on riparian habitat include soil compaction and weakening (Slaymaker and McPherson, 1977), soil erosion, sediment plumes entering riparian zones and streams (Dignan, 1999), increases in fine sediment and organic matter inputs (Davies and Nelson, 1993). Harvest activities may also result in changes in soil structure and subsurface flow dynamics, increased catchment water yield

and higher peak flows in the first few years after harvesting causing decreased stream bank stability, changes in stream channel profiles, decreased sediment retention and increased sediment transport and lower evapotranspiration losses from harvest areas (Vanderwel, 1994). Accumulation of logging slash in streams following harvesting may create habitat for amphibians and aquatic invertebrates by controlling channel structure and stability, creating pools, storing sediment, and dissipating energy (Bilby and Bisson, 1998; Gomi et al., 2001).

Post-harvest vegetation recovery, species composition and ecosystem functioning are related to rate and extent of physical recovery of the habitat. So far studies investigating the effects of forest harvesting on small streams and their riparian areas are mostly confined to the assessment of harvesting impacts on stream water quality and invertebrate communities. Physical response of unbuffered headwater streams and associated riparian zones after clearcutting have not been extensively studied. Gaps in our knowledge of the structure and function of headwater systems, impacts of forestry practices on headwater streams and their riparian areas impede our progress toward meeting management objectives to protect water quality and conserve biodiversity.

In the study, I examined the impacts of forest harvesting on the morphological features of headwater systems. My main objectives were two-fold: (a) to assess how clearcut harvesting alters the physical characteristics of headwater systems, and (b) to examine the patterns of riparian habitat recovery over time. I hypothesized that if forest harvesting has an impact on headwater systems then recently harvested areas will show the greatest difference from reference forest in biophysical factors such as stream size, number of channels, depth of organic matter, vegetation cover. Furthermore, if streams recover over time I expect the deviation from reference forest to be less as time since harvest increases.

2.2 METHODS

2.2.1 Study area

The study was conducted in the Mackenzie River, Current River, Wolf River and Kaministiquia watersheds, about 30 km northeast of Thunder Bay, Ontario, Canada (48°38' - 48°50' N, 88°45' - 89°23' W). The study area has low, rolling relief with a bedrock substrate overlain by glacial tills, exhibiting poor water retention and soil drainage. Ground slope of the study area ranges from 3° to 30°. The area experiences a boreal temperate climate with mean temperature varying from – 26° to –22° C in January and 21° to 25° C in July. Mean annual rainfall ranges between 700 mm to 850 mm (Baldwin et al., 2000).

Vegetation of the area is a range of boreal mixed wood and conifer-dominated stands typical of the southern boreal forest (Rowe, 1972). The overstory is dominated by *Picea mariana*, *Picea glauca*, *Abies balsamea* and *Populus tremuloides*. The understory is dominated by *Alnus incana*, *Aster macrophyllus*, *Cornus canadensis* and *Clintonia borealis* (Stewart and Mallik, 2006).

2.2.2 Site selection

Thirty headwater streams were selected for this study with catchment areas less than 100 ha and bank full widths less than 3 m. Study sites were selected based on similar topographic conditions, aspect, soil type and vegetation. Methods of site selection have been described in details in chapter 1 (1.2.2).

2.2.3 Study design and explanatory variables

From a total of 30 streams, 24 were in post-harvest stands originating from clearcuts 3 to 23 years ago and 6 were in undisturbed mature (90-100 years-old fire originated) forests hereafter called reference streams. The post-harvest streams were categorized into five age classes based

on time since harvesting: age class 1 (3 years, n=4), age class 2 (7 to 10 years, n=5), age class 3 (11 to 15 years, n=5), age class 4 (16 to 18 years, n=5) and age class 5 (19 to 23 years, n=5). Reference streams in undisturbed forests were indicated as age class 6.

On each post-harvest stream six 5 m long segments, three at clearcut site and three within buffered area at the downstream end of the small stream were selected randomly to study stream bed morphology. For the riparian habitat study, six transects, three in the clearcut area and three within the buffered area were established perpendicular to the stream. Consecutive quadrats of 1x1 m were surveyed along each of the transects. Study segments and transects at clearcut sites were at least 10 m away from the buffer edge to avoid edge effects. A similar sampling protocol was followed for the unharvested reference sites (Figure 1.2). The study design has been described in detail in chapter 1 (1.2.3).

Within each study quadrat, the following physical and environmental variables were recorded: bank full width of stream (referred to as stream width), stream channel depth (referred to as stream depth), riparian width, number of water courses (flowing body of water with distinct edges), ground exposure, canopy exposure, depth of organic matter, percent cover of equipment ruts (depression in the soil caused by machine traffic), logging slash (≥ 10 cm diameter), exposed rock, exposed mineral soil, plant colonization at the edge and center of stream. Rooted width, i.e. the point on the bank where the rooted, non-grass vegetation begins, was measured to determine the stream width. For stream depth three measurements were taken at random locations in each section using a metre stick. Stream width and depth were measured in a straight section of the stream to avoid corners and pools and were recorded to the nearest 0.1 cm. Using the point of the most rapid shift from predominantly riparian vegetation to predominantly upland vegetation

riparian width was determined and measured to the nearest 0.1 m. At each quadrat ground exposure was determined by visual estimation. Canopy exposure was measured using a concave hemispherical Densiometer held at breast height (1.37 m). Readings were taken in each cardinal direction and averaged to obtain an estimation of canopy exposure above each sampling quadrat. Depth of organic matter at each quadrat was measured from small soil pits. Percent cover of machine ruts, logging slash, exposed rock, exposed mineral soil, colonized vegetation at the edge and center of stream were determined by visual estimation.

2.2.4 Data analysis

A quantitative disturbance index (DI) was calculated combining the percent cover of harvesting equipment ruts, logging slash, exposed mineral soil, exposed rock, colonized vegetation on stream center and stream edge, which was used as a single variable in the subsequent analyses to assess habitat disturbance from harvesting. Prior to statistical analysis, the explanatory variables measured at each quadrat were averaged to produce stream-level estimates. The data residuals were checked for normality (Kolmogrov-Smirnov test) and homogeneity of the variances (Levene test) to meet the assumptions of ANOVA. To improve the normality stream width and depth data were transformed to \log_{10} . It improved the normality of the data compared to untransformed data.

Simple univariate measures were first calculated at the stream scale to allow for comparison between reference, clearcut and buffer locations of different ages. To test the impacts of clearcut harvesting on the eight response variables, a general linear model was used. Since the design was not completely balanced, in the model type III sum of squares was used. In the model, age classes (years since harvesting) and disturbance types (clearcut and buffer) were used as fixed

factors, streams as random factor and stream width (SW), stream depth (SD), riparian width (RW), number of water courses (WC), ground exposure (GE), canopy exposure (CE), depth of organic matter (DOM) and disturbance index (DI) were used as response variables. The nested model used in the analyses was:

$$Y_{ijk} = \mu + A_i + S_{(ij)} + D_k + AD_{ik} + SD_{(ijk)} + \epsilon_{(ijk)}$$

Where, Y_{ijk} is the response variable (SW/SD/RW/WC/GE/CE/DOM/DI) of the k^{th} disturbance type in the j^{th} stream of i^{th} age class, μ is the overall sample mean, A_i is the fixed effects of i^{th} age class ($i = 1, 2, \dots, 6$), $S_{(ij)}$ is the random effects of j^{th} stream ($j = 1, 2, \dots, 6$) nested within age class i , D_k is the fixed effects of k^{th} disturbance type ($k = 1, 2$), AD_{ik} is the interaction effects of i^{th} age class with k^{th} disturbance type, $SD_{(ijk)}$ is the interaction effects of k^{th} disturbance type with j^{th} stream nested within i^{th} age class, and $\epsilon_{(ijk)}$ is the error term. Applying Sometimes Pooling Rule the interaction effects of stream (nested within age class) and disturbance type was removed from the model when it was insignificant at $\alpha=0.25$ level. The analysis of variance was followed by DUNCAN *post-hoc* test to identify significant differences between age classes. When spanned number of means compared is increased the critical value is decreased in Duncan test, but in Tukey's HSD it remains constant at a high level and hence Duncan *post hoc* test was used.

Multivariate analysis of variance was conducted using the variables to determine which individual variables at the local scale were significantly different between harvested sites of different age classes and reference streams and to investigate any interaction effects between age classes and disturbance types. Finally, discriminant function analysis (DFA) was performed to explore whether the independent variables can be used to distinguish between the age classes and

identify the most important independent variables in differentiating the age classes. All analyses were performed using SPSS version 16.0 (SPSS, 1999).

2.3 Results

General field observations indicate that clearcut harvesting caused physical damage to small streams and their riparian areas. In some cases, especially in the recently harvested areas (3 years post-harvest), stream edges were hard to locate due to severe ground disturbance. Road construction and machine ruts damaged the physical structure of the streams and altered the stream flow regime. In clearcut sites large deposition of logging slash observed in disturbed stream beds interrupted the stream flow pattern compared to reference streams (Figure 2.1A-C). Mean values of habitat parameters measured are shown in Appendix 1.

2.3.1 Stream width and depth

There was a significant difference in stream width between age classes ($p < 0.001$) and disturbance types ($p = 0.014$). Streams in age class 1 were significantly wider than those in all other age classes including the reference streams in clearcut sites ($p = 0.001$). However, for the same age class there was no significant difference in stream width between clearcut and buffer locations. As a whole, streams were wider in harvested sites compared to those at buffer sites and reference sites (mean 87.7, 81.3 and 80.5 cm, respectively). Stream depths were significantly different between age classes ($p < 0.001$) and disturbance types ($p = 0.001$) (Table 2.1). In harvested sites stream depth of age class 1 (14.6 cm) was significantly lower than that of age class 4 (24.5 cm) and reference site (28.2 cm). Stream depth in reference sites was significantly higher than that of all other age classes except 4 ($p = 0.008$). Stream depths were higher in older

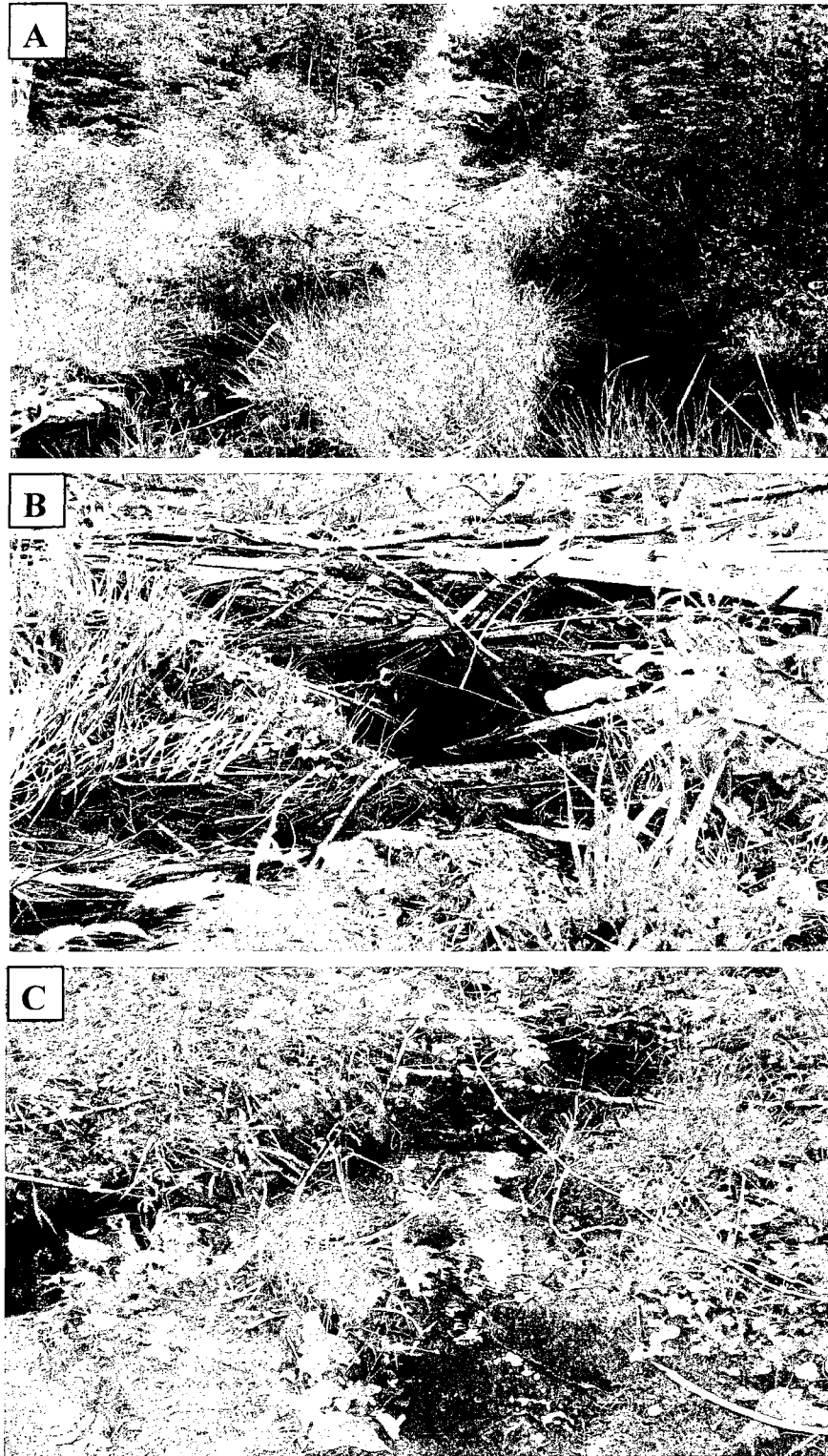


Figure 2.1: Examples of forest harvest impacts on small streams and their riparian areas: (A) slash pile and machine rut damaged stream, (B) accumulated slash disrupted stream flow and (C) undisturbed stream with intact channel bed.

Table 2.1: Results of nested ANOVAs with stream width, stream depth, riparian width, number of water courses, ground exposure, canopy exposure, depth of organic matter and disturbance index as dependent variables and age class and disturbance type as fixed factors, streams nested within age classes as random factor.

Response variable	Sources of variation	df	F-value	p value
Stream width	Age class	5	12.252	<0.001
	Stream(Age class)	24	2.210	0.029
	Disturbance type	1	6.975	0.014
	Age class x Disturbance type	5	1.486	0.231
	Error	24		
Stream depth	Age class	5	9.225	<0.001
	Stream(Age class)	24	2.047	0.043
	Disturbance type	1	14.326	0.001
	Age class x Disturbance type	5	0.781	0.573
	Error	24		
Riparian width	Age class	5	0.329	0.891
	Stream(Age class)	24	1.498	0.164
	Disturbance type	1	0.007	0.936
	Age class x Disturbance type	5	0.555	0.733
	Error	24		
Number of water courses	Age class	5	6.570	0.001
	Stream(Age class)	24	1.000	0.500
	Disturbance type	1	15.117	0.001
	Age class x Disturbance type	5	6.570	0.001
	Error	24		
Ground exposure	Age class	5	5.137	0.002
	Stream(Age class)	24	1.632	0.119
	Disturbance type	1	4.406	0.047
	Age class x Disturbance type	5	0.143	0.980
	Error	24		
Canopy exposure	Age class	5	20.197	<0.001
	Stream(Age class)	24	2.762	0.008
	Disturbance type	1	89.067	<0.001
	Age class x Disturbance type	5	19.240	<0.001
	Error	24		
Depth of organic matter (DOM)	Age class	5	0.897	0.499
	Stream(Age class)	24	2.801	0.007
	Disturbance type	1	7.317	0.012
	Age class x Disturbance type	5	1.216	0.332
	Error	24		
Disturbance Index	Age class	5	15.404	<0.001
	Stream(Age class)	24	5.164	<0.001
	Disturbance type	1	2.920	0.100
	Age class x Disturbance type	5	2.074	0.104
	Error	24		

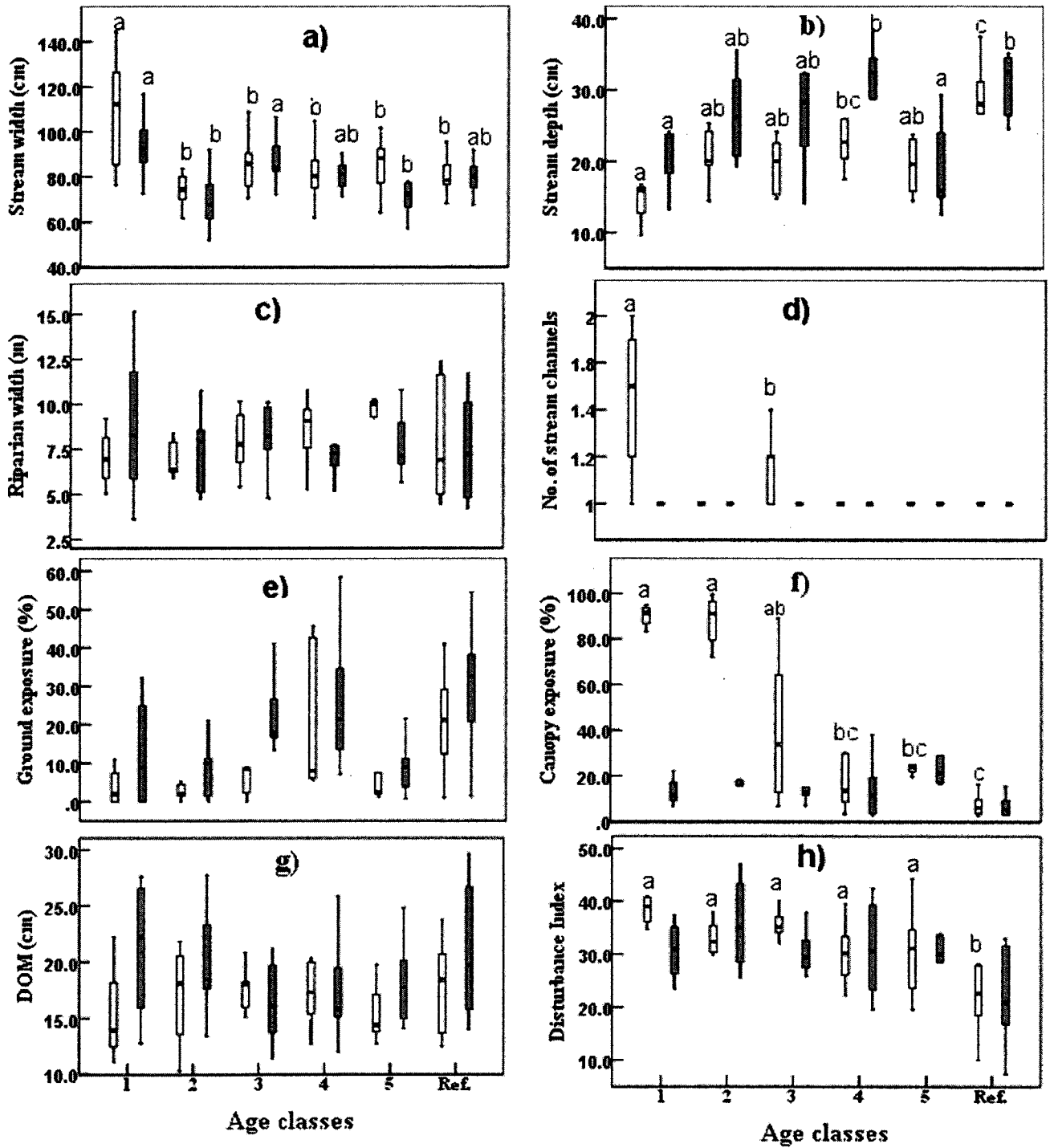


Figure 2.2: Boxplots of a) Stream width, b) stream depth, c) riparian width, d) number of water courses, e) ground exposure, f) canopy exposure, g) depth of organic matter and h) disturbance index at different ages after clearcut harvesting. The shaded and unshaded boxes represent buffer and clearcut locations, respectively. Horizontal bars are median and boxes are quartiles (25 – 75). Superscripts came from the results of Duncan *post hoc* tests.

age classes except the age class 5. Streams were shallow (19.7 cm) in harvested sites, intermediate depth in buffer (24.8 cm) and deepest in reference site (29.6 cm). Distribution of stream width and depth data has been illustrated in Figure 2.2a & 2.2b, respectively.

2.3.2 Riparian width and number of water courses

There was no significant difference in riparian width between age classes (Table 2.1). Mean riparian widths at clearcut, buffer and reference sites were 7.9 m, 7.9 m and 7.7 m, respectively. Riparian zones were slightly wider in older age classes, but there was no significant difference among the age classes. Number of water courses was significantly different between age classes ($p = 0.001$), disturbance types ($p = 0.001$) and interaction effects of age classes and disturbance types ($p = 0.001$) (Table 2.1). Streams in age class 1 of clearcut site had the largest number of water courses (mean 1.55/stream), which was significantly greater than all other age classes. Distribution of riparian width and number of water courses data has been illustrated in Figure 2.2c & 2.2d, respectively.

2.3.3 Ground exposure and canopy exposure

Ground exposure was significantly different between age classes ($p = 0.002$) and between disturbance types ($p = 0.047$) (Table 2.1). Ground exposures at harvested sites of age class 1 and 2 were significantly low (3.68% and 2.57%, respectively) compared to the reference site (20.90%). It was wider in older age classes, except in age class 5 (Appendix 1). Mean ground exposure at harvested, buffer and reference sites were 9.8%, 16.1% and 25.5%, respectively. A highly significant difference ($p < 0.001$) was found in the canopy exposure between age classes as well as between disturbance types ($p < 0.001$) and interaction effects of age classes and

disturbance types ($p < 0.001$) (Table 2.1). Though no significant difference was observed between age classes in buffered sites, canopy exposure in clearcut sites was significantly higher ($p < 0.001$) than that of reference sites up to 15 years after harvesting. It was very high (89.0%) in harvested sites up to 10 years since forest harvesting i.e. in age classes 1 and 2 (90.3% and 87.7%, respectively) (Appendix 1). Canopy exposure was lower in older age classes. Mean canopy exposure was 54.7% in harvested sites, 18.3% in buffered sites and 7.4% in reference sites. Distribution of ground and canopy exposure data has been illustrated in Figure 2.2e & 2.2f, respectively.

2.3.4 Depth of organic matter

Depth of organic matter was significantly lower in clearcut sites compared to buffer sites ($p = 0.012$) (Table 2.10), but there was no significant difference between the age classes either in clearcut sites or in buffer sites. Mean depth of organic matter was lower (15.3 cm) in age class 1 of clearcut sites than in the cut location of the reference sites (17.9 cm). Mean depth of organic matter in clearcut, buffer and reference sites were 16.5, 18.4 and 19.4 cm, respectively. Distribution of organic matter depth data has been illustrated in Figure 2.2g.

2.3.5 Disturbance index

Disturbance index of the reference sites was significantly lower than those of all other age classes ($p < 0.001$) (Table 2.1). Though disturbance indices were significantly higher for all the age classes in the harvested sites compared to reference sites ($p = 0.004$), there was no significant difference ($p = 0.150$) between age classes in buffered sites. Disturbance index for age class 1 of harvested site was 38.43, while it was 21.72 for the cut location of reference site (Appendix 1).

The mean value for clearcut sites was calculated as 33.46, while these values were 31.50 and 21.75 for buffered sites and reference sites, respectively. The distribution of disturbance index data has been illustrated in Figure 2.2h.

2.3.6 Multivariate analysis

The results of MANOVA (Table 2.2) indicate that headwater stream/riparian characteristics are influenced by both harvesting age and disturbance types.

Table 2.2: MANOVA results for stream width, stream depth, riparian width, number of water courses, ground exposure, canopy exposure, depth of organic matter and disturbance index showing significant differences among the group centroids.

Effects	Wilks' Lambda	Hypothesis df	Error df	F	Sig.
Intercept	0.001	8	17	1.453E3	< 0.001
Age class	0.004	40	77	4.978	< 0.001
Stream(Age class)	0.000	192	145	1.908	< 0.001
Disturbance	0.134	8	17	13.696 ^a	< 0.001
Age class * Disturbance	0.034	40	77	2.250	0.001

A is exact statistic.

Design: Intercept + Age class + Stream(Age class) + Disturbance + Age class * Disturbance

2.3.7 Discriminant function analysis

From the tests of equality of group means it is evident that Wilks' lambda values for stream width, stream depth, number of water courses, ground exposure, canopy exposure and disturbance index were low, indicating that these variables played a significant role in discriminating between the age classes. However, riparian width and depth of organic matter were not significant. Smaller Wilks' lambda value of canopy exposure indicates that the mean values of canopy exposure are most different for the age classes and contribute the most to the discriminant function (Table 2.3).

Table 2.3: The amount of variance accounted for in the dependent variable by the independent variables. Wilks' lambda values, ratios of the within-groups sum of squares to the total sum of squares, indicate group differences.

Variables	Wilks' Lambda	F	df1	df2	Sig.
Log stream width	0.524	3.963	11	48	< 0.001
Log stream depth	0.537	3.757	11	48	0.001
Riparian width	0.931	0.324	11	48	0.976
No. of water courses	0.384	6.987	11	48	< 0.001
Ground exposure	0.672	2.134	11	48	0.035
Canopy exposure	0.249	13.190	11	48	< 0.001
Depth of organic matter	0.840	0.832	11	48	0.610
Disturbance index	0.623	2.642	11	48	0.010

In the analysis the first three discriminant functions accounted for 86.1% of the total variation among all sites. Function 1 accounted for 60.0% of the total variance explained by the model, while Function 2 and 3 accounted for 15.3% and 10.7%, respectively (Table 2.4).

Table 2.4: The ratio of the between-groups sum of squares to the within-groups sum of squares showing the spread of the group centroids in the dimension of the multivariate space.

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	4.605 ^a	60.0	60.0	0.906
2	1.174 ^a	15.3	75.3	0.735
3	0.824 ^a	10.7	86.1	0.672

a. First 8 canonical discriminant functions were used in the analysis.

The discriminant function model as a whole (8 axes) significantly separated the groups (Wilks' $\lambda = 0.018$, $p < 0.001$). After removing the first three axes the model no longer separated the groups ($\lambda = 0.406$, $p < 0.3$) (Appendix 1). So only the first three axes were interpreted.

The standardized Canonical Discriminant Function Coefficients were used to assess each independent variable's contribution to the discriminant function, which indicates the relative importance of independent variables in predicting the dependent variables. Canopy exposure,

stream depth and width, ground exposure and number of water courses appeared to have the highest relative contribution to the overall discrimination (Table 2.5). Canopy exposure contributed strongly to group separation along canonical variable 1, stream depth and stream width contributed to group separation along the canonical variable 2. Ground exposure and number of water courses contribute to group separation along the canonical variable 3.

Table 2.5: Standardized canonical discriminant function coefficients indicating the relative contribution of the variables to the overall discrimination.

Response variables	Function		
	1	2	3
Log stream width	0.339	-0.744	0.180
Log stream depth	-0.290	0.811	0.456
No. of water courses	0.316	0.124	0.617
DOM	0.033	-0.231	0.138
Canopy exposure	0.819	0.664	-0.011
Ground exposure	0.051	0.591	0.700
Riparian width	-0.219	-0.057	0.120
Disturbance index	0.159	-0.061	-0.034

The ordination plots (Figure 2.3 & 2.4) show the locations of study streams in the inference space formed by function 1 versus 2 and function 1 versus 3. It contains each of the cases and locates them around the centroid for each group. Discriminant function worked almost equally well for each group of the dependent variables except for age classes 4 and 3 of clearcut sites and age class 5 of buffer sites. It correctly classified 63.3% of original grouped cases. Along axis one clearcut sites of age class 1, 2 and 3 (group 1, 3 and 5, respectively) differed the most and all other age classes including the buffered sites differed the least. Along axis two (Figure 2.3) clearcut sites of age class 2 (group 3) and buffered site of age class 1 (group 2) differed the most. Along axis 3 (Figure 2.4) clearcut sites of age class 2 (group 3), 5 (group 9) and buffered sites of age class 5 (group 10) differed the most from other sites. From the above results it can be

inferred that though different variables recover from harvesting impacts at different spatial scales, overall recovery takes at least 18 years since harvesting.

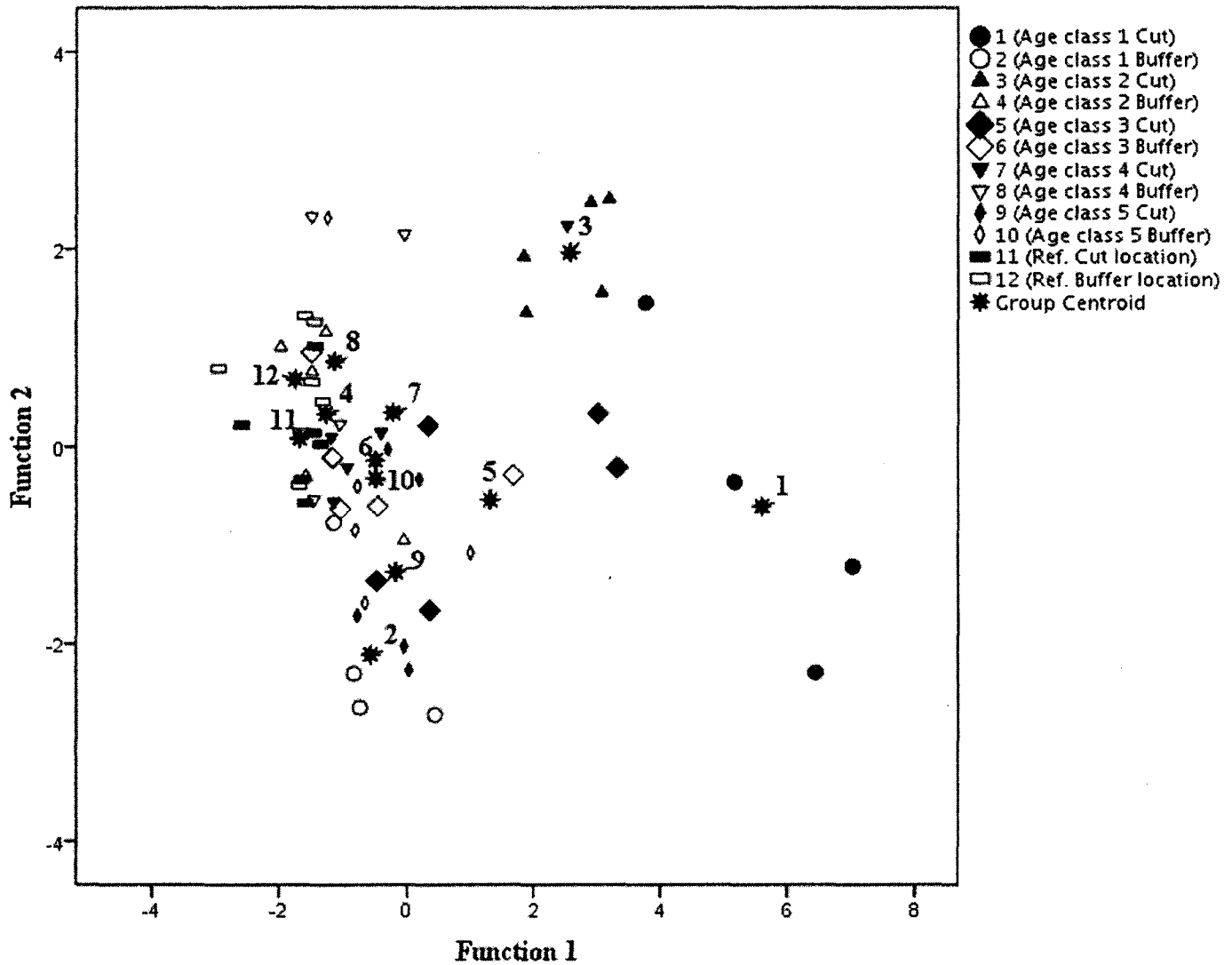


Figure 2.3: Ordination plot of the study streams in discriminant function space. The interspersed centroids of age classes 1, 2 and 3 of clearcut site from other group centroids along Function 1 indicate significant impacts of clearcutting up to 15 years since harvesting. Approximately 80% (canonical correlation = 0.906) of variation on function 1 was among groups while approximately 50% (canonical correlation = 0.735) on function 2 was among groups.

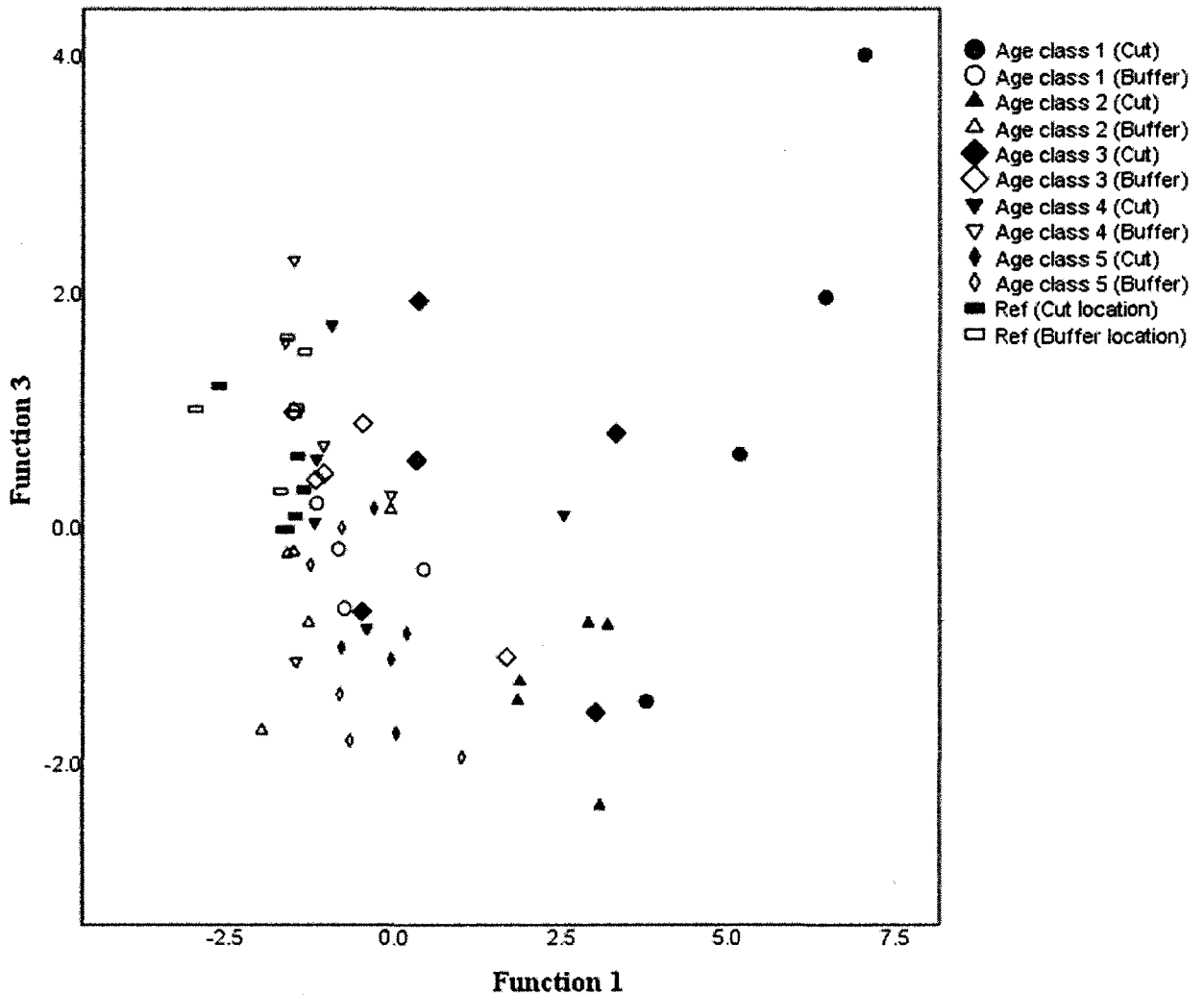


Figure 2.4: Ordination plot of the study streams in discriminant function space, Function 1 versus Function 3. Canopy exposure along Function 1 separated age classes 1 (3 years) and 2 (7-10 years) of clearcut sites from other age classes. Approximately 80% (canonical correlation = 0.906) of variation on function 1 was among groups while approximately 45% (canonical correlation = 0.672) on function 2 was among groups.

2.4 Discussion

In this study impacts of clearcutting on headwater systems and the differences among different ages of cut was explored. I found significant differences in the variables I examined such as stream width, stream depth, number of water courses, canopy exposure, ground exposure and disturbance index between clearcut sites of different ages since harvesting and reference sites. Stream channels in recently harvested areas were wider but shallower compared to undisturbed forested streams. Streams in older cut areas were narrower and deeper. However, age class 2 was an exception with streams narrower than the older age classes. The reasons may be lower logging slash accumulation (3.96% compared to an average of 7.93% in the older and reference streams) in these channel beds.

Studies documenting the effects of harvesting on riparian zones have often found differences between harvested and unharvested streams when harvesting right to the stream edge (Newbold et al., 1980). In a riparian study in North America, Sweeney et al. (2004) showed that forested stream channels in piedmont region were wider and had lower average water velocity and higher bed roughness than adjacent deforested channels. A similar process has been described by Hession et al. (2003) in urban watersheds of the region. My findings contradict their findings. Sweeney et al. (2004) noticed bank encroachment by herbaceous plants as the reason for stream channel narrowing. But I found herbaceous vegetation on stream banks overhanging from the banks creating indented stream edges. In my study streams recently harvested areas had higher levels of in-stream logging slash (10.59% in age class 1) than older age classes, helping trap fine sediment on the channel beds. Moreover, following slash and sediment deposition some vegetation colonized within the stream channel. These processes, in combination with stream

bank damage by harvesting equipment, might result in increased width and decreased depth of streams.

Forest harvesting can affect stream bed characteristics either directly by removal of vegetation which in turn increases water yield due to loss of evapotranspiration (Vanderwel, 1994), and loading of slash into the stream (Jackson et al, 2007) or indirectly via logging related slash transport and accumulation on the channel bed causing multiple channels or changing its path. In this study multiple water courses were observed in the clearcut sites of age classes 1; a mean of 1.55 channels per stream was significantly higher than all other age classes including reference sites (mean 1.03). The reason behind this may be the higher logging slash accumulation (10.59%) in the stream beds of recently clearcut sites. The number of water courses decreased with time since disturbance. However, multiple channels were also observed in age classes 3 and 4 (mean 1.16 and 1.04, respectively) but not significantly different from reference sites. Logging slash accumulations in these two age classes were 8.70% and 7.92%, respectively, which was 7.55% in reference sites. Several authors have suggested changes in channel routing as a potential driver of changes to peak flows. Cheng et al. (1975) stated that increased channel roughness due to slash loading within the stream could have contributed to the increase in time to peak. Conversely, Jones and Grant (1996) and Thomas and Megahan (1998) suggested that smoothing of the channel by road-related slash flows could have contributed to peak flow magnitude by decreasing travel time in the channel. However, no studies examined these influences quantitatively.

Worldwide studies show that water yield usually increases immediately after timber harvest (Stednick, 1996). Bosch and Hewlett (1982) stated that a reduction in canopy cover increases water yield and following afforestation it decreases with increasing canopy cover. Hubbard et al. (2007) reported an increase of water yield by 36% after clearcut harvesting, however, the relative amount of increase depends on climate and forest types and tends to diminish as forests regenerate (Bari et al., 1996). Hassan et al. (2005) stated that headwater streams may store sediment depending on stream morphology and timber harvesting pattern. Jackson and Sturm (2002) reported slash-filled streams following harvesting. Jackson and Sturm (2002) and Haggerty et al. (2004) reported that high slash loads may have various effects, like slowing flow, retaining and storing fine sediment, redirecting flow to create bank erosion and blocking insolation. They also mentioned that sediment detained within logging slash dams will be temporary, so post-harvest pulses of fine sediment as slash dams deteriorate are likely. Jackson et al. (2001) identified the introduction of large amounts of harvest slash to the channel as the dominant effect of clearcutting adjacent to small headwater streams. They reported that, two years after harvest, the total amount of buried and covered channel length in the clearcut streams decreased from 94% immediately after harvest in 1999 to 79% in 2001. The deposition of sediment in channels alters channel gradient (Hogan et al., 1998) and a large accumulation of sediment may force a lateral shift in unconfined channels, diverting the flow and causing bank erosion. All these observations are in agreement with my findings of shallow, wider stream channels with higher number of water courses immediately after harvesting.

The importance of riparian shade in controlling stream temperature is well documented (Beschta 1997; Johnson, 2004). Increase in stream temperature after harvesting is mainly due to increased solar radiation following canopy removal (Kiffney et al., 2003). In a study on the influence of

multiple spatial scales, Sponseller et al. (2001) showed that 93% of variation in stream temperature could be explained by forest cover. In my study I found canopy exposure most strongly associated with variation in riparian habitat, contributing highest (82%) to the canonical variable 1 in discriminant function analysis. Canopy exposure was very high in age classes 1 and 2. It was much lower in age class 3, though still significantly higher than reference sites (Appendix 1). Streamside shade recovery can be attributed entirely to low-lying understory species, as evidenced by the increase in understory/deciduous cover of 26% in 2003 to 39% and 37% in 2004 and 2005, respectively (Gravelle and Link, 2007). In my study I found very low ground exposure up to 10 years since harvesting and then it gradually increased with an exception in age class 5 (Appendix 1). In age class 5 sites richness and abundance of moss was comparatively high (described in next chapter), resulting in lower ground exposure. Understory vegetation appears to be higher after harvesting, as the removal of the forest overstory canopy allows more incoming solar energy to reach the forest floor. Moola and Vasseur (2004) reported a three-fold increase in ground vegetation cover in 6-year old clearcuts compared to late successional stands. Following harvesting increased light stimulated streamside vegetation (Jackson et al., 2007), resulting in lower ground exposure, which is in line with my findings of higher canopy and lower ground exposure in the early stage of headwater system recovery.

2.5 Conclusion

Timber harvest practices adjacent to headwater streams and their riparian zone have major impacts on stream bed structure. Spatial scales of recovery varied widely among the habitat parameters. Impacts of clearcut on stream width and number of water courses were significant only up to 3 years since harvesting. Whereas, after 23 years harvesting impacts on stream depths and disturbance indices were still significant. Significant impact on canopy exposure was pronounced up to 15 years since harvesting. However, overall recovery from impacts of clearcutting adjacent to small headwater streams and their riparian zones takes at least 18 years after harvesting. Indeed in the recovery process geographical locations of the streams are also important inferential factors. The study result implies that headwater streams need adequate protection from anthropogenic disturbances, especially from clearcut harvesting. Leaving headwater streams unattended may mean not meeting the objectives of sustainable forest management.

Chapter 3

Recovery of riparian vegetation along headwater streams after clearcut harvesting

3.0 Abstract

The study of the recovery of understory plant communities after clearcut harvesting has received much attention. However, most of these studies have ignored the recovery of riparian understory vegetation especially along headwater streams despite its critical role in the protection of stream water quality and biota. I studied 30 headwater streams, 24 in clearcut sites and 6 in reference sites of 90–100 year-old undisturbed forest. Each stream was studied at two locations: i) within clearcut areas and ii) within buffer zone of a larger stream where it flows. I quantified species richness, abundance, diversity and evenness of riparian understory vegetation at different stages of recovery ranging from 3 to 23 years since harvesting and at reference sites. Using nested model and Non-metric Multidimensional Scaling (NMS) I examined the effect of clearcut age on the plant composition. I found that clearcut harvesting had no immediate impact on overall species richness or diversity, but it caused compositional changes in the subsequent vegetation, dominated by ruderal invading species. Some late-seral species were locally eliminated and showed no evidence of recovery over 23 years after harvesting. Species like *Acer spicatum*, *Sorbus americana*, *Circaea alpina*, *Mitella nuda*, *Brachythecium rivulare*, *Dicranum flagellare* and *Rhodobryum roseum* attained their highest frequency and abundance in older age-classes. These results indicate that for the conservation of rich riparian biodiversity clearcutting along headwater systems should be replaced by selective/partial harvesting.

3.1 Introduction

The effects of forest harvesting on headwater systems (consisting of headwater streams and their riparian areas) have not been extensively studied although headwater streams compose almost 80% of total stream length in many drainage networks and drain a high proportion of the catchment area (Naiman et al., 2005). Management needs of these streams are still neglected partly because of insufficient understanding of the benefits they provide in terms of biotic habitat, ecosystem services and water quality. Since headwater streams hold a small volume of water they are highly sensitive to environmental changes, and may need more attention than larger streams.

Being transitional between streams and adjacent terrestrial habitats, riparian zones possess biotic communities distinct from both (Lamb and Mallik, 2003; Naiman and Décamps, 1997) and are generally considered to be biodiversity hotspots (Naiman et al., 2005). Their high biodiversity may be due to the juxtaposition of aquatic and terrestrial habitats (Sabo et al., 2005) and occurrence of biota associated with the edge environment (Naiman and Décamps, 1997). Riparian areas provide unique floristic communities that are more herbaceous than upland habitats, but also provide cover from many shrub species (Pabst and Spies, 1998).

Riparian ecosystems are constantly affected by a variety of natural and anthropogenic disturbances. Clearcut harvesting is the most important anthropogenic disturbance that adds to the severity of natural disturbances and can modify ecosystem functions (Naiman et al., 2000; Lamb et al., 2003). Forest harvesting results in a significant difference in plant communities compared to uncut forests causing loss of a portion of old-growth flora immediately after logging

(Loya and Jules, 2008). It may result in vegetation typically dominated by ruderal species and in some instances, exotic species (Halpern et al., 1999). On the other hand, it may enhance natural regeneration of tree species which prefer mineral substrates, facilitate recovery of shade tolerant herbs, planted trees and advanced regeneration (Roberts and Dong, 1993; McInnis and Roberts, 1994).

Recovery of plant communities after forest harvesting differ markedly since community recovery is system specific and influenced by numerous biotic and abiotic factors (Battles et al., 2001; Costa and Magnusson, 2002; Sullivan et al., 2001; Roberts, 2004). Greenberg et al. (1995) reported an increase in species richness and diversity following post-fire salvage logging. Duffy and Meier (1992) reported a lower post-harvest species richness and cover of herbaceous plants compared to primary forests even 87 years after harvesting. In most cases an initial decrease in diversity, particularly interior forest species, was followed by a quick recovery within a few decades (Gilliam, 2002; Hannerz and Hanell, 1997; Meier et al., 1995; Roberts and Zhu, 2002). However, recovery of some species may take a long time in managed forests (Loya and Jules, 2008).

Lamb (2002) stated that harvesting disturbance in adjacent uplands does not strongly affect the riparian vegetation along buffer-protected streams. Perhaps hydrology is the primary factor that determines the distribution and abundance of riparian species (Bendix, 1994; Naiman and Décamps, 1997). Biswas (2008) stated that disturbance intensity (clearcut and clearcut plus scarification as extreme and buffers as moderate disturbance) significantly affects the riparian plant colonization. He reported that both species diversity and functional diversity reach their peak under moderate intensity of disturbance. Since the hydrology of unbuffered headwater

streams may be quite different from buffered larger streams and is highly sensitive to adjacent harvesting disturbance, response of riparian understory plant communities along headwater streams might also be different from those of larger streams.

Understory vegetation plays a critical role in boreal ecosystems, influencing nutrient cycling, overstory succession, and long-term stand productivity (Zackrisson et al., 1995; Wardle et al., 2004; Kolari et al., 2006). For sustainable management of boreal forests, understanding factors that affect diversity, abundance and composition of understory vegetation is very important. Although vegetation changes following clearcut harvesting is a major issue in the riparian zones, basic information on the effects of clearcut harvesting on the vegetation of headwater systems and the rate of their recovery after harvesting are still inadequately documented.

In this study I explored the alpha diversity and composition of understory riparian vegetation along 24 boreal headwater streams at different stages after clearcut harvesting and compared that of 6 undisturbed mature forests. I hypothesized that if forest harvesting alters riparian understory vegetation then differences in floristic composition will be greatest between recently harvested sites and reference forests. I hypothesized that with increasing time since harvest, differences in floristic composition compared to reference forest would be less. Also, the ruderal species dominating recently harvested sites will gradually be replaced by old-growth species.

3.2 METHODS

3.2.1 Study area

The study was conducted in the boreal mixedwood forests spread over four watersheds, Mackenzie River, Current River, Wolf River and Kaministiquia watersheds located between 48°38' - 48°50' N latitude and 88°45' - 89°23' W longitude (Figure 1.1). The area is characterized by low relief with underlying bedrock composed of primarily Precambrian granite and gneiss.

Overstory vegetation is dominated by black spruce (*Picea mariana*), balsam fir (*Abies balsamea*), jack pine (*Pinus banksiana*), white birch (*Betula papyrifera*) and trembling aspen (*Populus tremuloides*). The understory is dominated by speckled alder (*Alnus incana*), large-leaved aster (*Aster macrophyllus*), bunchberry (*Cornus canadensis*) and blue bead lily (*Clintonia borealis*). (Details in chapter 1).

3.2.2 Site selection

Twenty four headwater streams were selected in clearcut sites of age 3 to 23 years since harvesting. Six more undisturbed streams with no adjacent forestry activities within 80-90 m were used as reference sites. During site selection physical conditions of the sites such as elevation, slope, aspect, soil type as well as vegetation of the sites were taken into consideration to reduce among site variation (Refer to chapter 1 for detailed site selection methods).

3.2.3 Sampling Design

To evaluate the patterns of species re-establishment, a total of 30 streams were sampled covering 24 post-clearcut stands and 6 undisturbed stands. Sites were categorized into five age classes based on time since harvesting: 3 years (n=4), 7 to 10 years (n=5), 11 to 15 years (n=5), 16 to 18 years (n=5) and 19 to 23 years (n=5).

Six transects were established on each stream, three in the clearcut area and three in the buffer area, for the study of vegetation and habitat parameters. Transects laid perpendicular to the stream extended up to the transition zone through the riparian zone and were divided into consecutive quadrats of 1x1 m for detailed study. A similar protocol was followed for the reference sites (Figure 1.2). In the study, a total of 1211 quadrats were sampled on 180 transects. To avoid edge effects, quadrats in the reference sites were at least 50 m away from edge of the stand (See chapter 1 for detailed sampling design).

3.2.4 Field sampling

Plants encountered in each quadrat were identified to the species level and their percent cover was recorded by visual estimation. For each study quadrat the following physical and environmental variables were also recorded: slope, aspect, stream width and depth, depth of organic matter, distance of quadrat from stream, riparian width, percent cover of logging slash, exposed rock and exposed mineral soil, and canopy exposure. These parameters were used as explanatory variables in the analysis. (Details in chapter 1).

3.2.5 Data analysis

Simple univariate measures were first calculated at the stream scale to determine the level of alpha-diversity and to allow for comparison between reference and clearcut sites of different ages since clearcut. Three diversity indices: species richness (S), Shannon-Wiener index of diversity (H'), and evenness (E), as well as percent total cover (abundance) were calculated. To test the impacts of clearcut harvesting on species richness, diversity, evenness and abundance, a nested model of ANOVA with type III sum of squares was used. In the model, age classes (time

since harvesting) and disturbance types (clearcut and buffer) were used as fixed factors, streams as random factor and species richness, diversity, evenness and abundance were used as response variables. The model used in the analyses was:

$$Y_{ijk} = \mu + A_i + S_{(ij)} + D_k + AD_{ik} + SD_{(ij)k} + \epsilon_{(ijk)}$$

Where, Y_{ijk} is the response variable (species richness/diversity/evenness/abundance) at k^{th} disturbance type in the j^{th} stream of i^{th} age class, μ is the overall sample mean, A_i is the fixed effects of i^{th} age class ($i = 1, 2, \dots, 6$), $S_{(ij)}$ is the random effects of j^{th} stream ($j = 1, 2, \dots, 6$) nested within age class i , D_k is the fixed effects of k^{th} disturbance type ($k = 1, 2$), AD_{ik} is the interaction effects of i^{th} age class with k^{th} disturbance type, $SD_{(ij)k}$ is the interaction effects of k^{th} disturbance type with j^{th} stream nested within i^{th} age class, and $\epsilon_{(ijk)}$ is the error term. Applying Sometimes Pooling Rule the interaction effects of stream (nested within age class) and disturbance type was removed from the model when it was insignificant at $\alpha=0.25$ level. The analysis of variances was then followed by DUNCAN *post-hoc* test to identify significant differences between age classes and disturbance types. SPSS version 16.0 (SPSS, 1999) was used for the analyses.

The overall structure and trends in the data were explored using Non-Metric Multidimensional Scaling (NMS), a non-parametric ordination method well suited to community data that avoids many of the assumptions about the underlying structure of the data made by traditional ordination methods (Clarke, 1993), using the autopilot option with a slow and thorough analysis and the default settings. Despite the difficulties in detecting discontinuities and failing to find the best solution because of intervening local minima, NMS was used since it tends to linearize the relation between environmental distance and ecological distance relieving the “zero-truncation problem” that plagues all ordinations of heterogeneous data sets. The hypothesis of no significant

floristic differences between the age classes was tested using Multiple Response Permutation Procedure (MRPP) (Zimmerman et al., 1985), which is a non-parametric analogue of Discriminant Function Analysis (DFA) that supports a multivariate test of the null hypothesis of no significant difference between *a priori* groups of samples. An Indicator Species Analysis (INSPAN) was used to classify the species into different harvest age classes according to their occurrence and abundance based on a comparison of the mean relative frequency and cover of a species in a pre-defined group to the same values calculated for all groups. For each individual species the strength of its association with a specified age group was tested with Monte Carlo permutations of 1000 runs where samples are randomly reassigned to groups and the indicator values are recalculated. Mean percent cover for all understory species were used as the response variable. Species found in less than 5% quadrats were removed from the analysis. A total of 135 species was used in the analysis. All multivariate tests were carried out using the PC-ORD program version 4 (McCune and Mefford, 1999).

3.3 Results

Highly diverse vegetation was observed in the riparian zones of small headwater streams in northwestern Ontario. A total of 259 species from 146 genera and 71 families were recorded (Appendix 4). The maximum number of species (25) was recorded from the family Cyperaceae, followed by Rosaceae (21) and Compositae (20). The number of species was highest for herbs (85) followed by mosses, shrubs and grasses with 55, 46 and 44 species, respectively. *Alnus incana*, *Acer spicatum*, *Rubus idaeus*, *Corylus cornuta* and *Cornus stolonifera* were the most abundant shrub species in the area. Among the herbs *Aster macrophyllus*, *Clintonia borealis*, *Thalictrum dasycarpum*, *Galium asprellum* and *Mertensia paniculata* were the most abundant. *Calamagrostis canadensis* and *Carex intumescens* were the most dominant grass species. *Athyrium felix-femina* was dominant among the ferns. *Eurhynchium pulchellum* was the most abundant moss in the study area. *Carex crinita* was fairly common in the area although it is considered locally rare in the Thunder Bay District (Thunder Bay Naturalists, 1998). *Rubus idaeus* and *Aster macrophyllus*, two upland species, were found to be dominant in the clearcut sites immediately after harvesting.

3.3.1 Species richness

There was no significant difference in overall species richness between age classes (Table 3.1). However, in buffer sites overall species richness in age class 5 (16.1 species/m²) was significantly higher than that of age class 4 (12.4). There was no significant difference in species richness between clearcut and buffer sites of the same age class or reference sites. Mean overall species richness in clearcut sites varied from 14.0 to 15.8 species per m² as compared to 14.3 species per m² at cut locations of reference sites (Appendix 3). No gradual shift in overall species

richness was observed over time since harvesting either in clearcut site or in buffer sites (Figure 3.1).

In life-form based analysis, there was no significant difference in species richness between age classes ($p = 0.283$), but species richness in clearcut sites was significantly higher ($p = 0.001$) than that in buffer sites (Table 3.1). In clearcut sites richness of tree species was significantly higher in age class 4 than age class 1 and reference site ($p = 0.051$). There was a gradual increase in the richness of tree species towards older age classes. However, in buffer sites there was no significant difference between age classes. There was no significant difference in richness of shrubs either in between age classes or between clearcut and buffer sites. For herbs there was no significant difference in their richness among age classes ($p = 0.081$) and disturbance types ($p = 0.816$) (Table 3.1). But, in clearcut sites the richness of herbs was significantly lower in age class 5 than age classes 6, 1 and 2 (Figure 3.1). In clearcut sites mean richness of herbs was 3.3 for age class 5, which were 5.6, 5.1 and 5.2 for age classes 1, 2 and 6, respectively. Richness of herbs was lower in older age classes (Appendix 3). However, in buffer sites there was no significant difference in the richness of herbs among age classes. Though there was no significant difference in the richness of fern between age classes, in the clearcut sites it was significantly lower in age class 1 and 2 compared to age classes 3 and 6 (Figure 3.1). Richness of grass was significantly different between clearcut sites and buffer sites ($p < 0.001$). In clearcut sites richness of grasses differed significantly between age classes. It reached the peak in age class 2 and then gradually decreased (Figure 3.1). In clearcut sites richness of moss was lowest (1.4) in age class 2 and highest (2.5) in age class 5. In buffer sites moss richness was significantly higher in age class 5 (4.5) compared to other age classes (2.7, 2.1, 2.3, 2.0 and 3.0 in age classes 1, 2, 3, 4 and 6,

respectively) (Appendix 3). Distribution of species richness data has been illustrated in Figure 3.1.

Table 3.1: Results of nested ANOVAs with species richness as dependent variable and age class and disturbance type as fixed factors, streams nested within age classes as random factor.

Life form	Sources of variation	df	F- value	p value
All species	Age class	5	0.470	0.795
	Stream(Age class)	24	3.250	0.003
	Disturbance type	1	2.854	0.104
	Age class x Disturbance type	5	1.752	0.161
	Error	24		
Tree	Age class	5	1.336	0.283
	Stream(Age class)	24	1.336	0.242
	Disturbance type	1	13.948	0.001
	Age class x Disturbance type	5	1.836	0.144
	Error	24		
Shrub	Age class	5	0.259	0.931
	Stream(Age class)	24	3.606	0.001
	Disturbance type	1	0.057	0.813
	Age class x Disturbance type	5	1.082	0.395
	Error	24		
Herb	Age class	5	2.257	0.081
	Stream(Age class)	24	2.110	0.037
	Disturbance type	1	0.055	0.816
	Age class x Disturbance type	5	0.728	0.609
	Error	24		
Fern	Age class	5	0.919	0.485
	Stream(Age class)	24	2.435	0.017
	Disturbance type	1	1.762	0.197
	Age class x Disturbance type	5	2.193	0.089
	Error	24		
Grass	Age class	5	2.283	0.078
	Stream(Age class)	24	1.975	0.051
	Disturbance type	1	35.861	<0.001
	Age class x Disturbance type	5	5.154	0.002
	Error	24		
Moss	Age class	5	3.859	0.010
	Stream(Age class)	24	2.380	0.019
	Disturbance type	1	15.357	0.001
	Age class x Disturbance type	5	3.359	0.019
	Error	24		

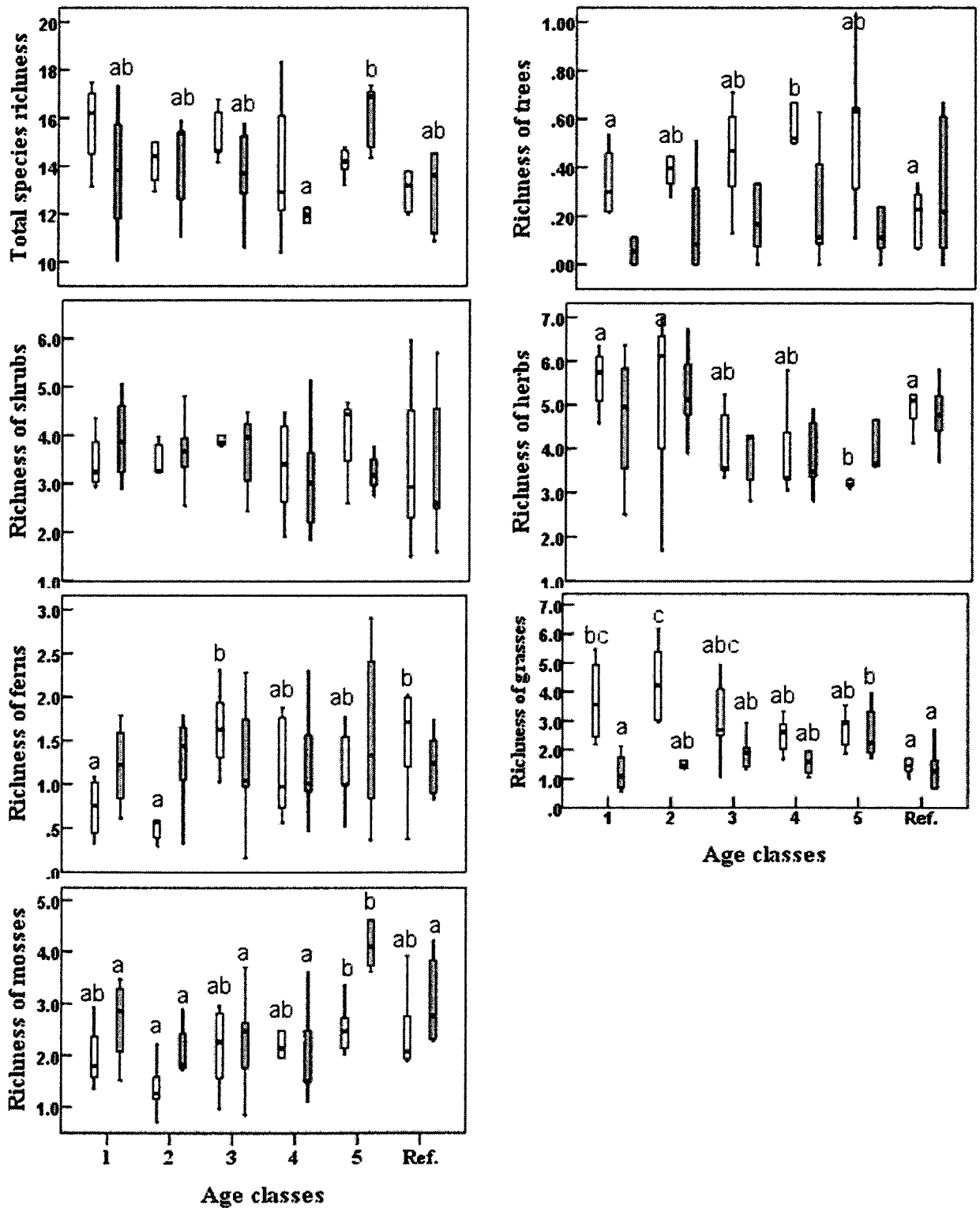


Figure 3.1: Species richness of sites differing in time since harvesting disturbance. The shaded boxes represent buffer locations while unshaded boxes represent clearcut locations. Horizontal bars are median and boxes are quartiles (25 – 75). Superscripts came from the results of Duncan *post hoc* tests.

3.3.2 Species abundance

There was a significant difference in overall species abundance between clearcut and buffer sites ($p = 0.049$), but between the age classes it was not significant ($p = 0.172$) (Table 3.2). In clearcut sites species abundance was lowest in age class 1 (232.0) and highest in age class 3 (277.1). However, in buffer sites overall species abundance was significantly different between the age classes. In buffer sites overall abundance was highest in age class 5 (275.6) and lowest in age class 1 (186.8) (Appendix 3). Species abundance data has been illustrated in Figure 3.2.

There was significant difference in the abundance of tree species between clearcut and buffer sites ($p = 0.017$). In clearcut sites age class 4 had the highest abundance (24.7) and lowest in the reference sites (3.9). In buffer sites abundance of tree species gradually increased up to age class 3 and then started decreasing. Age class 3 had the highest abundance (9.4) and age class 1 had the lowest (1.5). Abundance of shrub almost gradually increased towards older age classes, but there was no significant difference between age classes. In both cut and buffer sites abundance of herb was highest (76.9 and 77.8, respectively) in age class 2 and then gradually decreased towards older age classes (Appendix 3). Abundance of fern was significantly lower in age classes 1 and 2 in clearcut sites, however, in buffer sites there was no significant difference between age classes. Abundance of grasses was significantly different between age classes ($p = 0.012$) and clearcut and buffer sites ($p < 0.001$) (Table 3.2). In clearcut sites mean grass abundance was highest (79.3) in age class 2 which gradually decreased over time and lowest (14.2) in reference sites (Appendix 3). Abundance of mosses were significantly different between disturbance types ($p = 0.001$). Abundance of moss gradually increased towards older age classes both in clearcut and buffer sites (Appendix 3).

Table 3.2: Results of nested ANOVAs with species abundance as dependent variable and age class and disturbance type as fixed factors, streams nested within age classes as random factor.

Life form	Sources of variation	df	F- value	p value
All species	Age class	5	1.703	0.172
	Stream(Age class)	24	2.564	0.012
	Disturbance type	1	4.297	0.049
	Age class x Disturbance type	5	1.641	0.187
	Error	24		
Tree	Age class	5	1.451	0.242
	Stream(Age class)	24	1.300	0.263
	Disturbance type	1	6.520	0.017
	Age class x Disturbance type	5	2.573	0.053
	Error	24		
Shrub	Age class	5	1.446	0.244
	Stream(Age class)	24	0.909	0.591
	Disturbance type	1	0.064	0.802
	Age class x Disturbance type	5	0.716	0.618
	Error	24		
Herb	Age class	5	1.845	0.142
	Stream(Age class)	24	2.377	0.019
	Disturbance type	1	0.885	0.356
	Age class x Disturbance type	5	1.488	0.231
	Error	24		
Fern	Age class	5	1.606	0.197
	Stream(Age class)	24	2.620	0.011
	Disturbance type	1	1.295	0.266
	Age class x Disturbance type	5	2.551	0.055
	Error	24		
Grass	Age class	5	3.755	0.012
	Stream(Age class)	24	1.542	0.148
	Disturbance type	1	37.302	<0.001
	Age class x Disturbance type	5	6.483	0.001
	Error	24		
Moss	Age class	5	1.968	0.120
	Stream(Age class)	24	3.208	0.003
	Disturbance type	1	13.921	0.001
	Age class x Disturbance type	5	1.477	0.234
	Error	24		

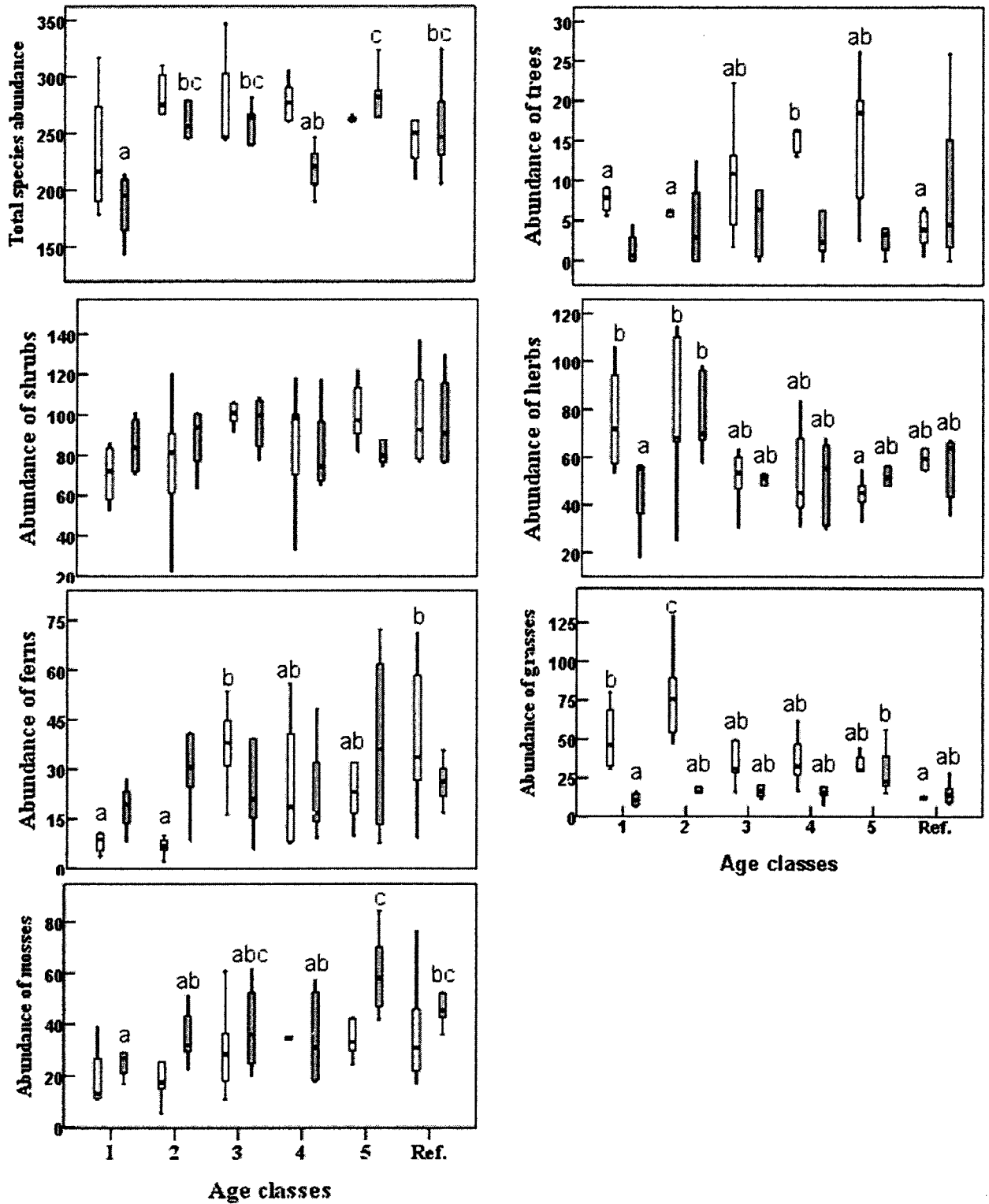


Figure 3.2: Species abundance of sites differing in time since harvesting disturbance. The shaded boxes represent buffer locations while unshaded boxes represent clearcut locations. Horizontal bars are median and boxes are quartiles (25 – 75). Superscripts came from the results of Duncan *post hoc* tests.

3.3.3 Species diversity

There was no significant difference in overall species diversity between age classes ($p = 0.530$), but it was significantly different between disturbance types ($p = 0.019$) (Table 3.3). In clearcut sites age class 1 had the highest overall species diversity (2.5) and lowest in reference sites (2.3). Species diversity gradually decreased towards the older age classes. In buffer sites age class 5 had significantly higher diversity (2.5) than that of age class 4 (2.2) (Appendix 3).

In the study area diversity of tree species was very low compared to other life forms (Appendix 3). There was no significant difference in the diversity of trees or shrubs among age classes either in clearcut sites or in buffer sites. In clearcut sites diversity of shrubs varied from 0.8 in reference sites to 1.1 in age class 3. However, diversity of herbs differed significantly between age classes ($p = 0.047$). In clearcut sites diversity of herbs was highest in age class 1 (1.5), which gradually decreased towards the older age classes and was lowest in age class 5 (1.0). There was no significant difference in the diversity of ferns between age classes ($p = 0.630$) and disturbance types ($p = 0.345$). In clearcut sites diversity of ferns was highest in age class 3 and lowest in age class 2. Diversity of grasses was significantly different between clearcut and buffer sites ($p < 0.001$). However, it was not significant between age classes ($p = 0.145$). In clearcut sites, diversity of grasses was significantly higher in age classes 1 and 2 than that of the reference sites. In clearcut sites diversity of grasses decreased gradually towards the older age classes, whereas in buffer there was a gradual increase in grass diversity towards the older age classes. Diversity of mosses was significantly different between age classes ($p = 0.019$) as well as between clearcut and buffer sites ($p = 0.002$). In buffer sites moss diversity was significantly higher in age class 5 than all other age classes. Figure 3.3 illustrates the distribution of species diversity data.

Table 3.3: Results of nested ANOVAs with species diversity as dependent variable and age class and disturbance type as fixed factors, streams nested within age classes as random factor.

Life form	Sources of variation	df	F- value	p value
All species	Age class	5	0.847	0.530
	Stream(Age class)	24	3.153	0.003
	Disturbance type	1	6.362	0.019
	Age class x Disturbance type	5	2.728	0.043
	Error	24		
Tree	Age class	5	0.820	0.547
	Stream(Age class)	24	1.420	0.198
	Disturbance type	1	3.014	0.095
	Age class x Disturbance type	5	2.530	0.056
	Error	24		
Shrub	Age class	5	0.364	0.868
	Stream(Age class)	24	2.741	0.008
	Disturbance type	1	1.531	0.228
	Age class x Disturbance type	5	0.852	0.527
	Error	24		
Herb	Age class	5	2.674	0.047
	Stream(Age class)	24	1.682	0.105
	Disturbance type	1	0.008	0.931
	Age class x Disturbance type	5	0.565	0.726
	Error	24		
Fern	Age class	5	0.698	0.630
	Stream(Age class)	24	1.918	0.059
	Disturbance type	1	0.929	0.345
	Age class x Disturbance type	5	2.157	0.093
	Error	24		
Grass	Age class	5	1.827	0.145
	Stream(Age class)	24	2.641	0.010
	Disturbance type	1	36.162	<0.001
	Age class x Disturbance type	5	5.061	0.003
	Error	24		
Moss	Age class	5	3.361	0.019
	Stream(Age class)	24	2.301	0.023
	Disturbance type	1	11.429	0.002
	Age class x Disturbance type	5	3.130	0.026
	Error	24		

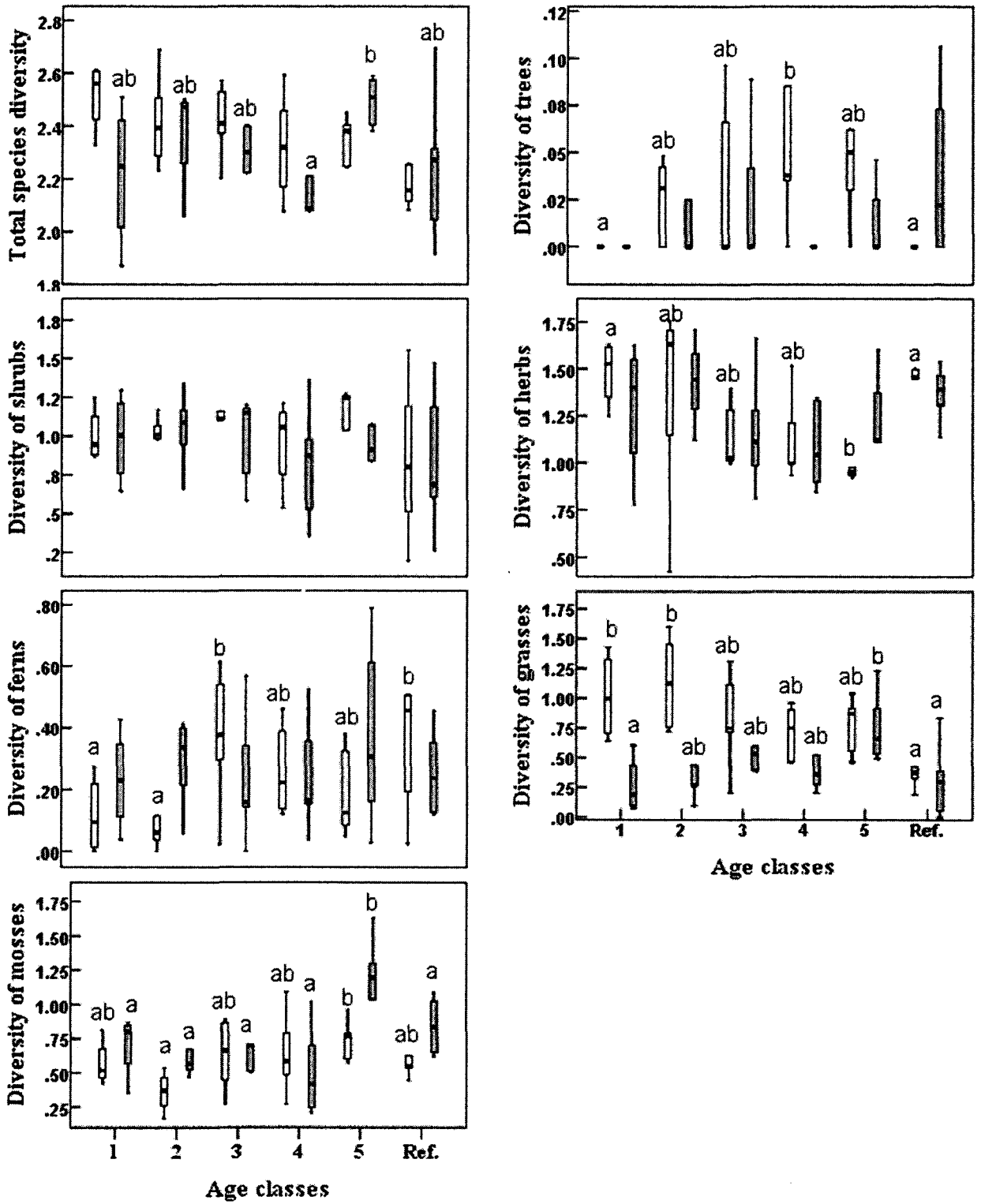


Figure 3.3: Species diversity of sites differing in time since harvesting disturbance. The shaded boxes represent buffer locations while unshaded boxes represent clearcut locations. Horizontal bars are median and boxes are quartiles (25 – 75). Superscripts came from the results of Duncan *post hoc* tests.

3.3.4 Evenness of species

Overall evenness of species or any of the life forms was not significantly different between the age classes. It was also not significantly different between disturbance types except for grasses (Table 3.4). However, species evenness of age class 5 was significantly lower than that of age class 4 in buffer sites. Herbs were comparatively evenly distributed in reference sites than other age classes. Evenness of grasses was significantly different between clearcut sites and buffer sites ($p < 0.001$). In clearcut sites evenness of grasses was significantly higher in age class 1 than age class 6. But, in buffer sites evenness of grasses was highest in age class 5 and lowest in age class 1 (Appendix 3). In clearcut sites age class 2 had significantly lower evenness of mosses than age classes 3 and 5. In buffer sites evenness of mosses was significantly lower in age class 4 than age class 5 (Appendix 3). Distribution of species evenness data has been illustrated in Figure 3.4.

Table 3.4: Results of nested ANOVAs with species evenness as dependent variable and age class and disturbance type as fixed factors, streams nested within age classes as random factor.

Life form	Sources of variation	df	F- value	p value
All species	Age class	5	0.681	0.642
	Stream(Age class)	24	2.791	0.007
	Disturbance type	1	0.780	0.386
	Age class x Disturbance type	5	1.405	0.258
	Error	24		
Tree	Age class	5	0.836	0.537
	Stream(Age class)	24	1.420	0.198
	Disturbance type	1	2.869	0.103
	Age class x Disturbance type	5	2.570	0.053
	Error	24		
Shrub	Age class	5	1.125	0.374
	Stream(Age class)	24	2.484	0.015
	Disturbance type	1	2.339	0.139
	Age class x Disturbance type	5	0.459	0.803
	Error	24		
Herb	Age class	5	2.269	0.080
	Stream(Age class)	24	1.033	0.469
	Disturbance type	1	0.119	0.733
	Age class x Disturbance type	5	0.786	0.570
	Error	24		
Fern	Age class	5	0.879	0.510
	Stream(Age class)	24	1.900	0.061
	Disturbance type	1	0.974	0.333
	Age class x Disturbance type	5	1.846	0.142
	Error	24		
Grass	Age class	5	1.344	0.280
	Stream(Age class)	24	2.817	0.007
	Disturbance type	1	17.809	<0.001
	Age class x Disturbance type	5	3.379	0.019
	Error	24		
Moss	Age class	5	1.323	0.288
	Stream(Age class)	24	2.253	0.026
	Disturbance type	1	2.444	0.131
	Age class x Disturbance type	5	2.735	0.043
	Error	24		

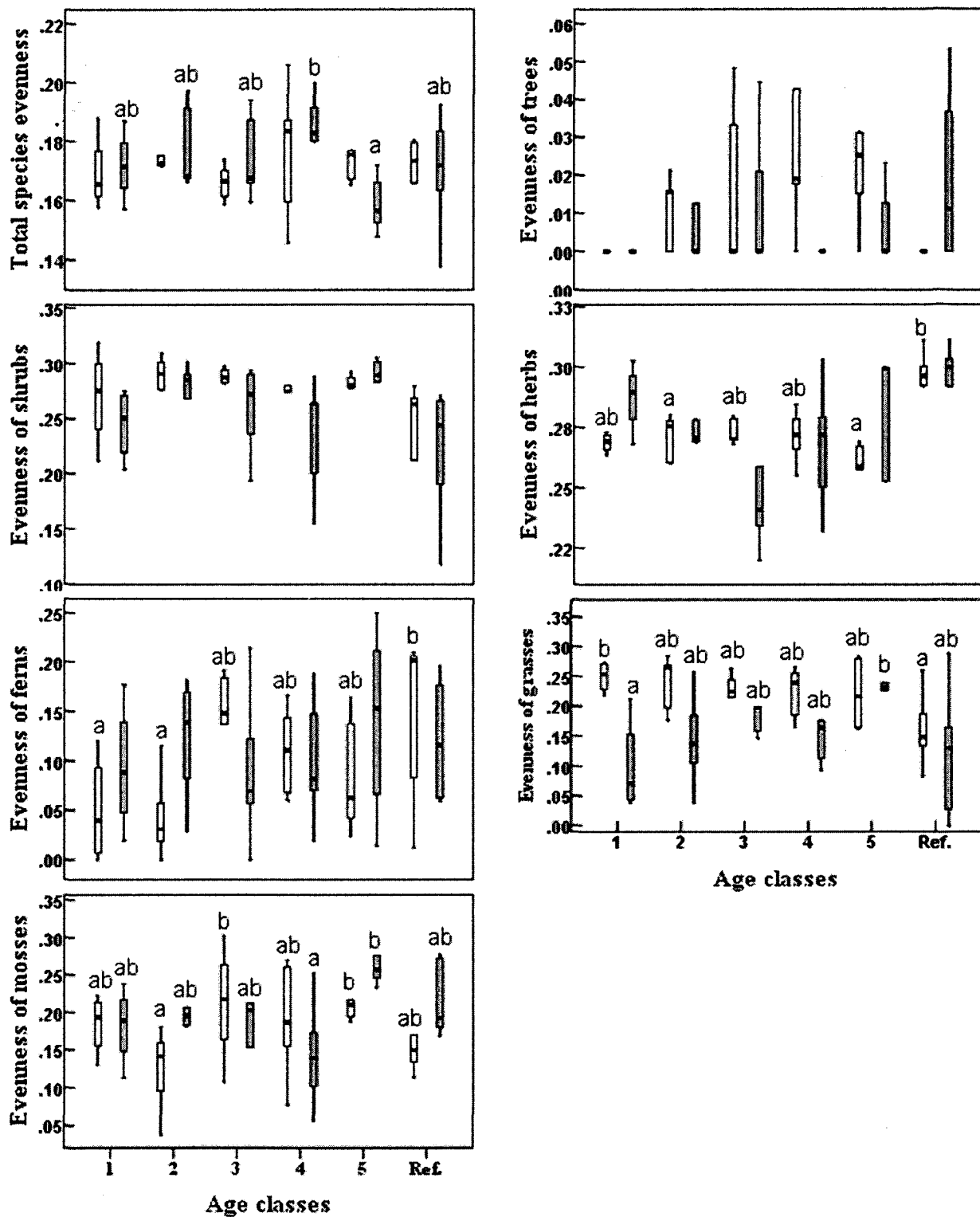


Figure 3.4: Species evenness of sites differing in time since harvesting disturbance. The shaded boxes represent buffer locations while unshaded boxes represent clearcut locations. Horizontal bars are median and boxes are quartiles (25 – 75). Superscripts came from the results of Duncan *post hoc* tests.

3.3.5 NMS ordination, MRPP and Indicator Species Analysis

The Non-metric Multidimensional Scaling (NMS) of species composition within streams identified a 2-dimensional optimum solution (Figure 3.5). The final stress was 18.273, which is fairly low. Since the correlations (r^2) between ordination distances in the final solution and distances in the original n-dimensional space are 0.561 and 0.236 for the first and second axes, respectively the solution is very strong. These two axes together give a cumulative r^2 of 0.797, accounting for most of the variance structuring the data set. In the ordination space Axis 1 is strongly negatively correlated with canopy exposure and positively correlated with ground exposure. Axis 2 is positively correlated with distance from stream and negatively correlated with exposed rock cover. Species with high scores on NMS axis 1 appear in the right quadrant of the ordination (Figure 3.6). These are mostly shade tolerant species e.g., *Acer spicatum*, *Circaea alpina*, *Osmunda claytoniana*, *Viola nephrophylla*, etc. Species with low scores on NMS axis 1 (Figure 3.6) appear in the left quadrant of the ordination. These plants attained their maximum abundance in exposed sites following clearcut harvesting, i.e. *Epilobium angustifolium*, *Calamagrostis canadensis*, *Elymus repens*, *Equisetum pretense*, *Carex lasiocarpum*, *Fragaria vesca*, *Aster ciliolatus*, etc. Plants with low scores on NMS axis 2 are mostly typical of disturbed sites like *Cinna latifolia*, *Oryzopsis asperifolia*, *Fragaria vesca*, etc. *Polytrichum commune* grows well on exposed rocks. Plants preferring moist upland sites appeared towards the high score end of NMS axis 2 (Figure 3.6).

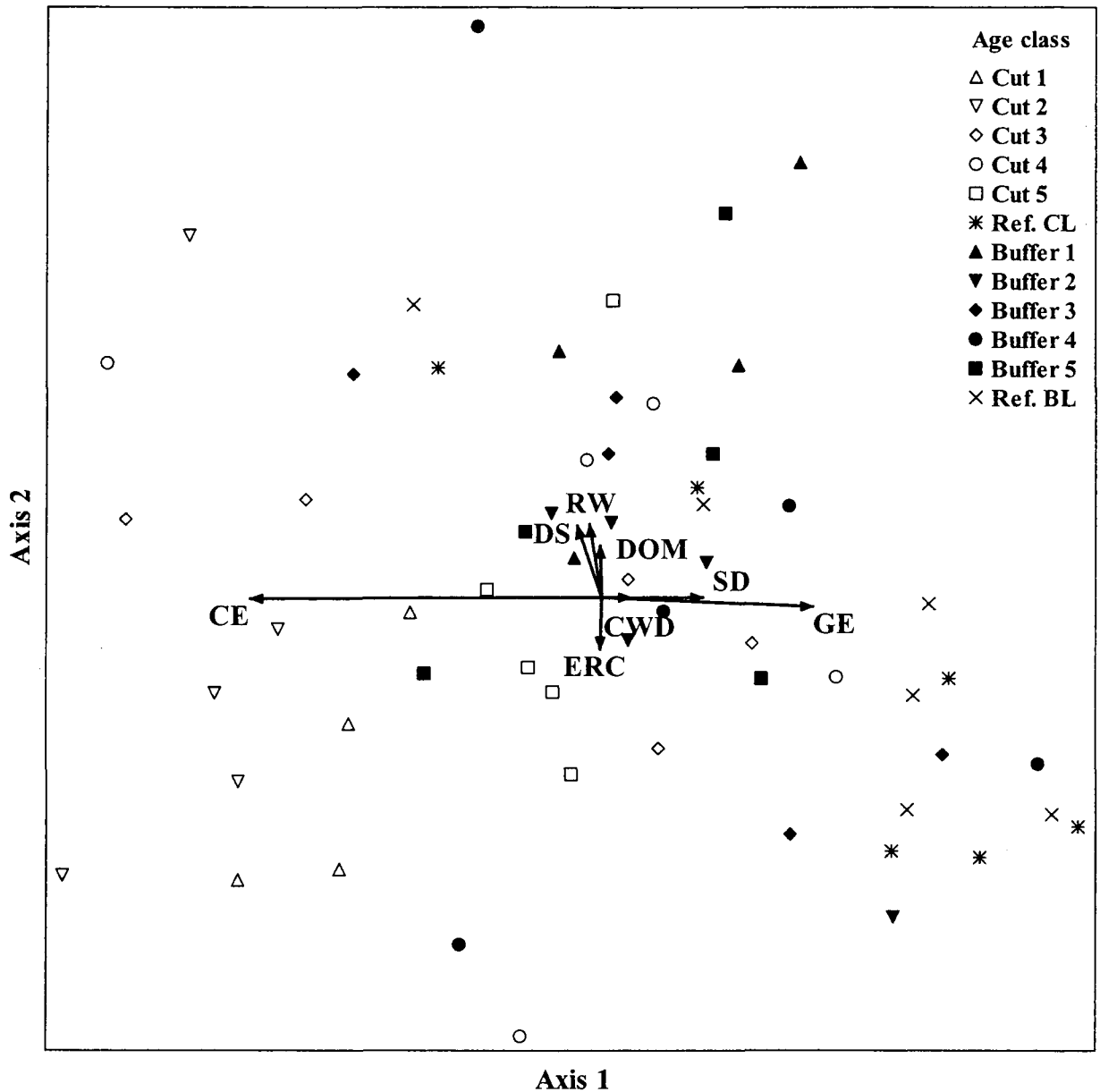
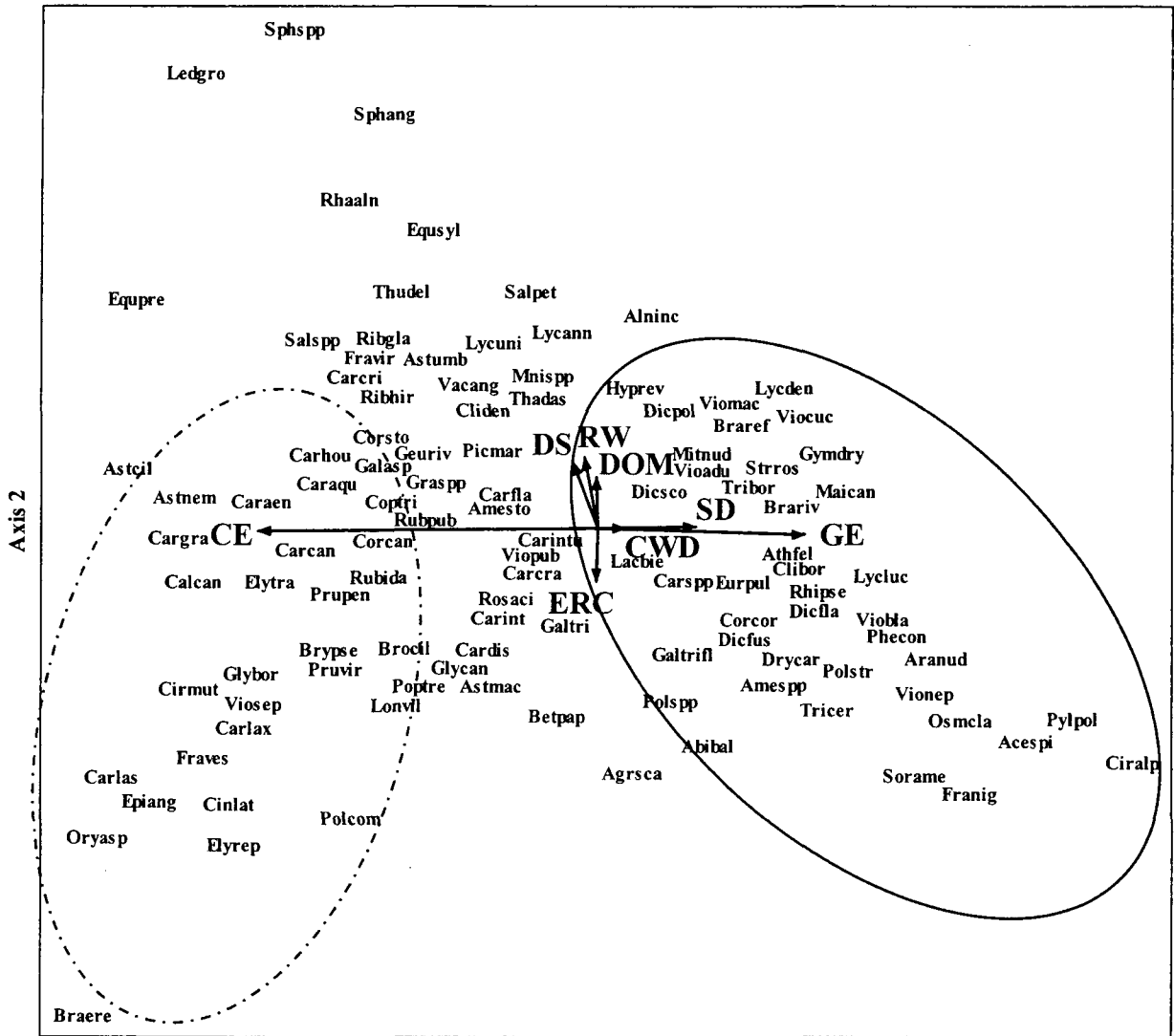


Figure 3.5: NMS ordination of average species composition within age classes and disturbance types. Younger sites are structured towards high canopy exposure and older sites along with buffered and reference sites towards low canopy exposure and high ground exposure in the ordination space. Ref.CL and Ref.BL represent reference sites at clearcut and buffer locations, respectively. CE = canopy exposure, GE = ground exposure, ERC = exposed rock cover, CWD = logging slash, SD = stream depth, DOM = depth of organic matter, RW = riparian width and DS = distance from stream.



Axis 1

Figure 3.6: NMS species ordination using the mean percent cover of 135 species within 30 streams. Species scores are shown for the first two axes of the ordination. Axis 1 explains 56.1% and Axis 2 explains 23.6% variation of the species data. Species are represented by codes that are the first three letters of the generic name followed by first three letters of the species name. Species within the dashed and compact ovals are mostly shade intolerant ruderal and shade tolerant old-growth species, respectively.

The MRPP showed significant differences in floristic compositions between sites of different age classes since harvesting ($p < 0.001$) and low within-group homogeneity ($A = 0.089$). This indicates overall differences in riparian community composition at different stages of recovery

from harvesting disturbances; however there is also a great deal of variation within age classes. The distance values indicate that age class 5 in clearcut sites is most different from other age classes (Table 3.5).

Table 3.5: Results of MRPP testing the null hypothesis of no significant differences in floristic composition between age classes and disturbance types.

Age classes	Average distance	MRPP statistics
1 (Cut)	0.55372091	Observed delta = 0.59451201
2 (Cut)	0.59745064	
3 (Cut)	0.59587736	Expected delta = 0.65225391
4 (Cut)	0.68197275	
5 (Cut)	0.49387498	T = -7.0901302
1 (Buffer)	0.51341548	A = 0.08852671
2 (Buffer)	0.55037705	
3 (Buffer)	0.62808828	p = 0.00000005
4 (Buffer)	0.71122472	
5 (Buffer)	0.55747233	
Ref. (Cut location)	0.61957014	
Ref. (Buffer location)	0.60051063	

Indicator Species Analysis results showed that out of 135 species in the analysis (Appendix 5), 23 were significantly associated with any particular age class. Eighteen species showed almost a complete lack of association with any particular age class. Most of the species associated with the young clearcut sites were ruderal invading species, shade intolerant in nature. Species with special affinity for buffered sites were mostly mosses. Commonly known as mid-seral species *Lycopodium dendroideum* and late-seral species *Maianthemum canadense* were found associated with age class 1 in the buffer sites. *Acer spicatum* was the only species significantly associated with the reference age at clearcut location (Table 3.6). *Sorbus americana*, *Circaea alpina*, *Mitella nuda*, *Brachythecium rivulare*, *Dicranum flagellare* and *Rhodobryum roseum* attained their highest frequency and abundance in reference forest.

Table 3.6: Affinity of species for a particular age class and disturbance type as revealed by the Indicator Species Analysis. For each species the significance of the association was tested in a Monte Carlo permutation test (999 permutations).

Age class	Clearcut site		Buffer site	
	Species	p value	Species	p value
1	<i>Populus tremuloides</i>	0.0056	<i>Maianthemum canadense</i>	0.0040
	<i>Prunus virginiana</i>	0.0072	<i>Climacium dendroides</i>	0.0256
	<i>Prunus pensylvanica</i>	0.0474	<i>Lycopodium dendroideum</i>	0.0480
2	<i>Epilobium angustifolium</i>	0.0008	<i>Plagiomnium spp.</i>	0.0180
	<i>Calamagrostis canadensis</i>	0.0034		
	<i>Carex lasiocarpum</i>	0.0044		
	<i>Rubus idaeus</i>	0.0262		
	<i>Brachyelytrum erectum</i>	0.0462		
3	<i>Equisetum pretense</i>	0.0128		
4	<i>Abies balsamea</i>	0.0116		
5			<i>Dicranum polysetum</i>	0.0072
			<i>Dicranum scoparium</i>	0.0228
			<i>Viola macloskeyi</i>	0.0272
			<i>Rubus pubescens</i>	0.0346
			<i>Sphagnum angustifolium</i>	0.0504
Reference	<i>Acer spicatum</i>	0.0500	<i>Eurhynchium pulchellum</i>	0.0038
			<i>Fissidens spp.</i>	0.0126
			<i>Brachythecium rivulare</i>	0.0260

3.3.6 Differences in species composition among age classes

The study revealed that after clearcut harvesting (up to 10 years) total number of species was higher in the cut over areas. At the age of 23 years after harvesting total number of species was equal to that of the reference sites at cut location. In buffer sites the number of species in different age classes was slightly lower than the reference site of buffer location, except in age class 5, which was slightly higher. With these differences in species number a remarkable difference was also observed in the species composition between harvested sites and reference sites. Some species like *Betula papyrifera*, *Amelanchier spp.*, *Diervilla lonicera*, *Salix petiolaris*, *Vaccinium angustifolium*, *Cirsium muticum*, *Epilobium angustifolium*, *Hieracium aurantiacum*,

Carex crinita, *C. houghtoniana* and *Calamagrostis canadensis* were found to invade the cut area whereas several old-growth species like *Actaea rubra*, *Atrichum* spp., *Dicranum montanum*, *Gentiana rubricaulis*, *Distichium capillaceum* and *Myurella julacea* locally disappeared after clearcut harvesting. Sixty five new species were recruited and 36 had disappeared from age class 1 of clearcut site as compared to the reference sites of cut location. Towards the older age classes both the number of new species recruitment and disappearance was reduced (Figure 3.7 & Appendix 4).

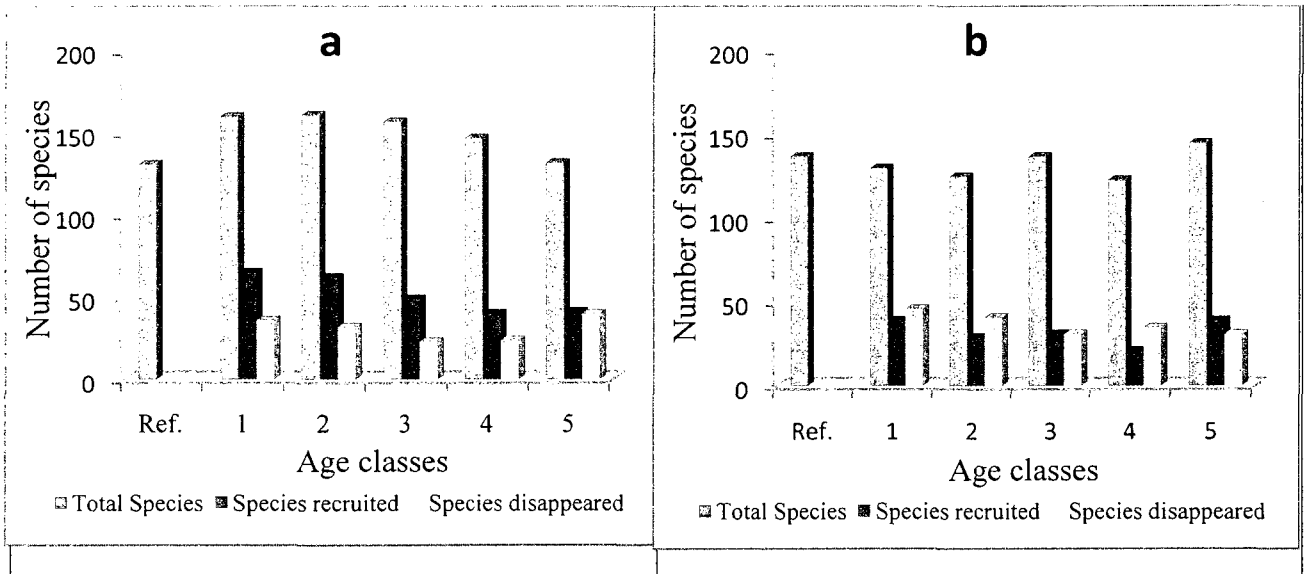


Figure 3.7: Number of species recruited and disappeared at different clearcut ages as compared to the reference sites (Figures a and b indicate clearcut and buffer sites, respectively).

A substantial difference was also observed in the composition of life forms between cut and reference sites. In clearcut sites mean total cover of grass was very high up to 10 years after harvesting and then gradually decreased towards the older age classes. An opposite trend was observed for moss and fern cover. Herb cover was very high up to 3 years and then gradually declined towards the older age classes. Differences in the composition of life forms among age

classes have been illustrated in Appendix 6a and 6b. A shift in species dominance was also observed between the age classes. *Rubus idaeus* was the most dominant species in age class 1 and 2 of clear cut sites, while *Alnus incana* was the dominant species in the subsequent age classes. *Alnus incana* was also most dominant in all the five age classes in buffered sites. *Acer spicatum* was the most dominant species in the reference sites of both cut and buffer locations.

3.4 Discussion

I found that clearcut harvesting along headwater streams had no significant effect on overall diversity indices (species richness, abundance, diversity or evenness) of riparian vegetation. Overall species richness and diversity were slightly higher immediately after harvesting in age class 1 compared to other age classes and the reference sites. This result may be due to a short-term increase in both indices due to the survival of generalist species, tolerant of disturbance along with the addition of a remarkable number of invading species to the community. Crawford et al. (2001) also observed a higher species richness after moderate to high severity disturbance due to exotic species and native ruderal species. A similar conclusion was drawn by Roberts and Zhu (2002). Although clearcut harvesting had no significant impact on overall species richness and diversity, has caused local elimination of some late-seral species like *Actaea rubra*, *Atrichum* spp., *Dicranum montanum*, *Gentiana rubricaulis*, *Distichium capillaceum*, *Myurella julacea*, etc. The absence of these species from all later harvest age classes may be evidence of a lack of recovery over 23 years after harvesting. In a study Moola and Vasseur (2004) found no immediate impact of clearcutting on overall alpha richness or diversity. But, richness and diversity of residual plants declined after canopy removal, which showed no evidence of recovery over 54 years of secondary succession. Immediately after clearcut harvesting some

species disappeared but recovered within 10 years and some others took 23 years to re-establish. Some ruderal species invaded the area after harvesting and was found surviving even until 23 years after harvesting while some others disappeared at different stages of habitat recovery, which might lead to a compositional change in the riparian vegetation following harvesting. These results are quite consistent with the findings of Peterken (1996) and Battles et al. (2001). Their results show that although overall species richness and diversity recovers rapidly during secondary succession, many of the typical residual species are eliminated from the plant communities of secondary forests. Loya and Jules (2008) concluded that forest harvesting results in a significant difference in plant communities compared to old-growth forests causing loss of a portion of old-growth flora immediately after logging. Moola and Vasseur (2004) also stated that clearcut harvesting results in compositional differences between secondary and late-seral stands, which persist for many decades after clearcutting. As stated by McLachlan and Bazely (2001) even if significant number of residual species is lost after clearcutting, diversity indices will not change if the plants eliminated are replaced by an equal or greater number of new invading species.

Species composition differences of different age classes may suggest vegetation recovery. MRPP results showed age class 5 of clearcut sites most different from other age classes. This may be attributed to the disappearance of some of the initially invaded ruderal species due to decreased canopy exposure at this stage and failure of some late-seral species to re-establish. Immediately after harvesting herb and grass cover was very high that decreased gradually over time. Most of these species are shade intolerant. On the other hand shade tolerant fern and moss cover was low initially, which increased gradually over time. Invading species are predominantly intolerant to shade and rapid reduction in light availability results in their elimination (Klinka et al., 1985).

Again, relatively open canopy of immature stands favor the persistence of invading ruderal species with an intermediate tolerance to shade (De Grandpré et al., 2000). Schoonmaker and McKee (1988) found richness of shrubs and herbs at their peak two to five years after harvesting. Following clearcut harvesting a shift in the species dominance was also observed. *Acer spicatum* was the most dominant species in the reference site of both cut and buffer locations. But, in age classes one and two *Rubus idaeus* became the dominant species, which is an early successional species. Ten years after disturbance *Rubus idaeus* was replaced by *Alnus incana*, which developed extensive thickets and maintained its dominance until 23 years. In buffered sites *Alnus incana* was also the most dominant species from age class 1 through age class 5. *Alnus incana* is a clonal species spread by layering and maintains dominance by stem-base re-sprouting (Bell, 1991) and thus once established maintains dominance for a long time (Huenneke, 1987).

Through the Indicator Species Analysis *Populus tremuloides*, *Prunus virginiana* and *P. pensylvanica* were found to be associated with very young (up to 3 years) clearcut sites and *Epilobium angustifolium*, *Calamagrostis canadensis*, *Carex lasiocarpum*, *Rubus idaeus* and *Brachyelytrum erectum* were indicators of moderately young (7 – 10 years) clearcut sites, all of which are shade intolerant early successional species. Shade tolerant *Acer spicatum* is the only species that showed its affinity to undisturbed reference sites at comparable clearcut location.

3.5 Conclusions

This study suggested that immediately after clearcut harvesting riparian vegetation becomes dominated by shade-intolerant ruderal species. Though some of these invaders disappear over time, others persist for a long period of time. No evidence of recovery of some typical riparian species was found over a period of 23 years. Although clearcut harvesting along small headwater stream does not affect the overall diversity indices of the riparian vegetation significantly, it alters the composition of the vegetation. Following harvesting disturbance a shift in species dominance may cause long-term effects on the future structure of the riparian vegetation, which in turn may cause significant changes in the ecological services they provide. Therefore, it is important to bring these headwater streams and associated riparian vegetations under necessary management actions for the maintenance of important ecological services they provide. In this case selective/partial harvesting or cultivating fast growing cover crops along headwater systems immediately after clearcutting may be the potential management options.

Chapter 4

GENERAL DISCUSSION

Most riparian research focuses on the consequences of forest harvesting on stream temperature, aquatic communities and regeneration of commercially valuable, shade-tolerant canopy species and on the effectiveness of buffers in preventing these consequences (Schuler and Gillespie, 2000). Relatively less attention has been given to unbuffered headwater streams, the properties of which differ markedly from those of the larger streams (Anderson et al., 2007). In this study I investigated the impacts of clearcutting on geomorphology and understory vegetation of headwater systems in the boreal forests of northwestern Ontario with main focuses on: 1) biophysical response of headwater systems to clearcutting and 2) differences in riparian understory vegetation over time after clearcut harvesting.

I found that clearcutting along headwater stream significantly influenced the biophysical features of the headwater system and their overall recovery appeared to take at least 16-18 years after harvesting. Clearcutting does not affect the overall diversity indices significantly, but resulted in changes in floristic compositions. Several residual species appeared to be locally eliminated and had not recovered within 23 years after harvesting.

Streams were significantly wider in clearcut sites up to 3 years after clearcutting but after 10 years there was no significant difference between subsequent age classes and reference streams. There was no significant difference in stream width between clearcut and buffer sites of the same age class. In clearcut sites stream depth was significantly less in harvested sites, which was detectable even 23 years after clearcutting. Both in clearcut and buffer sites stream depth

increased almost gradually towards the older age classes, with an exception of age class five. In age class 5 the riparian zone was the widest compared to other age classes and slash accumulation was also highest, which may have resulted in lower stream depth. Immediately after clearcutting (up to 3 years after harvesting) the number of stream channels was significantly greater in clearcut sites than in other age classes. These results support the first hypothesis that recently harvested areas will show the greatest difference from reference forest in biophysical factors. Immediately after clearcut water yield increases significantly due to loss of evapotranspiration (Bosch and Hewlett, 1982; Stednick, 1996; Sun et al., 2005; Hubbart et al., 2007). Moreover, clearcut harvesting may increase slash loads in stream channels resulting in slowing stream flow, retaining and storing fine sediments and redirecting flow to create bank erosion (Jackson et al., 2001; Jackson and Sturm, 2002; Haggerty et al., 2004; Hassan et al., 2005). Therefore, immediately after harvesting stream depth may decrease and consequently stream width will increase to hold and discharge an increased volume of water. Over time water yield decreases with increasing canopy cover (Bosch and Hewlett, 1982; Bari et al., 1996) and accumulated harvest slash and sediments detained within slash deteriorate (Jackson et al., 2001; Jackson and Sturm, 2002; Haggerty et al., 2004). As a result stream depth is expected to increase gradually. My findings are consistent with these observations. However, Sweeney et al. (2004) and Hession et al. (2003) demonstrated an opposite result that forested stream channels are wider than deforested stream channels. They argued that stream bank encroachment by grasses narrows down the stream channels. But, my observations suggest that water yield, bank erosion and sediment and slash accumulation in the streambed have more influence on stream structure than bank encroachment by herbaceous plants.

Immediately after harvesting multiple water channels were observed in clearcut sites, which was significantly higher in age class 1 compared to other age classes and reference sites. Sediment deposition in channels alters channel gradient (Hogan et al., 1998) and a large accumulation of sediment may force a lateral shift in unconfined channels, diverting the flow and resulting in the formation of multiple channels (Jackson et al., 2007). Among multiple channels, the channels towards the upward slope acts as cross drainage, which hold sediments eroded from up slope and gradually silted up. Consequently, in course of time one channel perpetuates and side channels disappear.

Canopy exposure was significantly higher up to 15 years after harvest compared to reference and older cut sites (18 years after harvesting). An opposite trend was observed in case of ground exposure, which was very low up to 10 years following clearcutting and then increased with an exception of age class 5. Increased light availability following clearcutting stimulates understory vegetation, resulting in lower ground exposure (Jackson et al., 2007). In age class 5 high abundance of moss resulted in lower ground exposure.

I found no significant effect of harvesting age on overall species richness, abundance, diversity or evenness of riparian understory vegetation. However, there was significant difference in species abundance and species diversity between clearcut and buffer sites. Overall species diversity of clearcut sites was higher than that of buffer sites in all the age classes except age class 5. This result contradicts with the findings of Biswas and Mallik (2009). They reported a higher species diversity and functional diversity of riparian understory vegetation in buffer sites compared to 3 to 6 year-old clearcut and reference sites. In my study I found a large number of invading ruderal species added to the community along with the survival of disturbance-tolerant

generalist species in clearcut sites of younger ages (3-10 years after clearcut), which resulted in higher species diversity in clearcut sites than in buffer sites. Moreover, riparian vegetation is highly resilient to changes in microclimate that occur following removal of the adjacent forest canopy (Brososke et al., 1997). Riparian species frequently have mechanisms to survive flooding due to their tolerance for anoxic rooting zones (Blom and Voeselek, 1996). These species also have dispersal and establishment strategies such as the ability to rapidly colonize bare sediments and aggressive clonal growth that allow rapid recovery from disturbance (Naiman and Décamps, 1997). All these might result in higher species richness at clearcut sites of early stage compared to the buffer sites.

Although clearcut harvesting had no significant impact on overall species richness and diversity, it may have caused local elimination of some residual species such as *Actaea rubra*, *Atrichum* spp., *Dicranum montanum*, *Gentiana rubricaulis*, *Distichium capillaceum* and *Myurella julacea*. These species showed no evidence of recovery since 23 years after harvesting. On the other hand though some invading species disappeared at different stages of habitat recovery, some remained even until 23 years after harvesting resulting a compositional change over time. These results are consistent with that of Loya and Jules (2008) who reported that forest harvesting results in a significant difference in plant communities compared to old-growth forests due to loss of a portion of old-growth flora immediately after logging. As stated by McLachlan and Bazely (2001) even if significant numbers of residual species are lost after clearcutting, diversity indices will not change if the plants eliminated are replaced by an equal or greater number of new invading species.

Generalist species had a complete lack of association with any particular age classes or disturbance types. These species were found throughout all age classes and disturbance types with relatively little changes in their abundance following clearcut harvesting. A similar conclusion was also made by Moola and Vasseur (2004). Ruderal species, which are shade intolerant early successional species, were found to be indicator of younger (3–10 years) clearcut sites. Moola and Vasseur (2004) also found that ruderal invading species originating from wind dispersed seeds or spores were associated or restricted to the young clearcut sites. Shade tolerant *Acer spicatum* is the only species showed its affinity to undisturbed reference sites of clearcut location.

The study result implies that anthropogenic disturbance, especially clearcut harvesting along headwater system significantly alter the biophysical conditions of the system. Leaving the headwater system unattended, protection of water quality and aquatic environment and conservation of biodiversity may not be possible, which is the prime objective of sustainable forest management. Therefore, it is important to bring these headwater streams and associated riparian vegetations under necessary management actions for the maintenance of important ecological services they provide. Potential management options may be selective/partial harvesting along headwater systems instead of clearcutting or cultivation of suitable fast growing cover crops immediately after clearcut harvesting.

FUTURE RESEARCH DIRECTIONS

Much research is still needed to fill the gaps in the basic understanding of the riparian ecology of headwater system which are much more sensitive than larger streams. Some of the important issues that need to be addressed are:

- 1) Since habitat heterogeneity is an important factor to the biophysical response to disturbance, study of habitat and vegetation recovery based on different streams for different age classes might result some noises. To eliminate that and to provide better insights to harvesting impacts on headwater system and their recovery patterns pre- and post-harvest study along same stream is needed.
- 2) In this study canopy exposure was found to play a vital role in the recovery of headwater system. After clearcut harvesting taking the advantages of high canopy exposure invading species replaces shade tolerant old-growth species. Therefore, after harvesting it is important to bring these highly sensitive zones under close vegetation cover as soon as possible. Protection of all headwater systems through treed buffer is not economically feasible. Therefore, researches might be directed to test whether these zones can effectively be protected by raising some suitable cover crops along headwater systems immediately after clearcut harvesting instead of treed buffer.
- 3) Findings of this study suggest that clearcutting brings compositional changes in the headwater riparian understory vegetations and locally eliminate some old-growth species. So, to ensure conservation of rich riparian biodiversity, it is important to investigate the duration over which such compositional changes persist. And it is also important to investigate the influence of such changes on subsequent ecosystem functioning.

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Appendix 1: Mean values (\pm standard deviations) of some habitat parameters of the sampling sites

Age class & location	Stream Width (cm)	Stream Depth (cm)	Riparian width (m)	Ground exposure (%)	Canopy exposure (%)	DOM (cm)	Disturbance Index
1 Cut	107.3 \pm 22.5	14.6 \pm 4.5	7.0 \pm 1.9	3.7 \pm 5.0	90.3 \pm 11.5	15.3 \pm 5.2	38.43 \pm 2.91
1 Buffer	93.1 \pm 11.9	21.1 \pm 8.1	8.8 \pm 5.3	12.5 \pm 17.9	13.1 \pm 7.6	21.2 \pm 6.6	30.73 \pm 5.84
2 Cut	74.9 \pm 9.4	20.7 \pm 7.0	6.9 \pm 1.6	2.6 \pm 4.3	87.7 \pm 16.0	16.9 \pm 5.4	33.17 \pm 3.45
2 Buffer	71.9 \pm 16.5	26.7 \pm 7.2	7.3 \pm 3.0	8.8 \pm 9.9	15.7 \pm 5.1	18.9 \pm 7.2	35.91 \pm 9.24
3 Cut	88.2 \pm 14.6	19.4 \pm 7.2	7.9 \pm 2.4	13.7 \pm 22.5	41.4 \pm 35.4	17.6 \pm 4.3	35.73 \pm 3.02
3 Buffer	87.6 \pm 10.0	25.9 \pm 7.6	8.0 \pm 2.8	23.1 \pm 19.7	21.1 \pm 20.2	16.0 \pm 5.1	30.68 \pm 4.69
4 Cut	82.5 \pm 11.9	24.5 \pm 8.3	8.5 \pm 2.7	21.6 \pm 24.1	28.3 \pm 32.6	17.1 \pm 4.5	30.31 \pm 6.62
4 Buffer	80.7 \pm 6.4	30.8 \pm 7.8	7.3 \pm 2.2	27.0 \pm 23.4	15.1 \pm 15.7	17.7 \pm 5.5	31.08 \pm 9.86
5 Cut	85.5 \pm 10.0	19.3 \pm 4.9	9.0 \pm 2.4	7.5 \pm 11.4	25.7 \pm 11.2	15.5 \pm 4.1	30.69 \pm 9.68
5 Buffer	73.1 \pm 12.1	19.4 \pm 7.2	7.9 \pm 2.2	9.2 \pm 10.9	26.5 \pm 15.1	18.3 \pm 5.6	28.93 \pm 6.20
Ref. CL	80.6 \pm 6.7	28.2 \pm 8.4	7.9 \pm 3.3	20.9 \pm 21.5	7.6 \pm 5.6	17.9 \pm 5.1	21.72 \pm 7.13
Ref. BL	80.4 \pm 8.1	31.0 \pm 5.8	7.5 \pm 3.2	30.0 \pm 24.9	7.2 \pm 4.8	20.9 \pm 6.9	21.80 \pm 9.89

Note: CL = clearcut location (supposed to be clearcut in case of harvesting); BL = buffer location (closed to large stream and supposed to be left as buffer in case of harvesting); DOM = Depth of organic matter.

Appendix 2: The proportion of the total variance in the discriminant scores not explained by differences among the groups and their level of significance.

Test of Function(s)	Wilks' lambda	Chi-square	df	Sig.
1 through 8	.018	196.137	88	.000
2 through 8	.102	111.674	70	.001
3 through 8	.223	73.617	54	.039
4 through 8	.406	44.168	40	.300
5 through 8	.635	22.251	28	.770
6 through 8	.829	9.211	18	.955
7 through 8	.950	2.511	10	.991
8	.992	.413	4	.981

Appendix 3: Mean species richness, abundance, diversity and evenness at quadrat level for different age classes and disturbance types.

Life form	Diversity indices	Age classes and disturbance types											
		1		2		3		4		5		Reference	
		Cut	Buffer	Cut	Buffer	Cut	Buffer	Cut	Buffer	Cut	Buffer	Cut	Buffer
All species	Richness	15.76	13.77	14.92	14.07	15.27	13.63	13.97	12.35	14.15	16.10	14.32	13.96
	Abundance	232.03	186.78	269.54	261.46	277.09	248.75	260.39	218.89	256.77	275.59	252.69	255.12
	Diversity	2.52	2.22	2.42	2.36	2.42	2.24	2.32	2.15	2.35	2.49	2.26	2.25
	Evenness	0.17	0.17	0.17	0.18	0.17	0.17	0.18	0.18	0.17	0.16	0.17	0.17
Tree	Richness	0.34	0.06	0.41	0.18	0.45	0.29	0.73	0.25	0.55	0.20	0.20	0.30
	Abundance	7.61	1.44	6.38	4.78	10.53	9.42	24.65	5.09	15.03	4.01	3.93	8.61
	Diversity	0.00	0.00	0.02	0.02	0.03	0.03	0.10	0.00	0.06	0.01	0.01	0.04
	Evenness	0.00	0.00	0.01	0.01	0.02	0.01	0.05	0.00	0.03	0.01	0.00	0.02
Shrub	Richness	3.44	3.92	3.12	3.66	3.92	3.63	3.32	3.17	3.94	3.23	3.36	3.26
	Abundance	70.71	84.79	75.15	96.04	106.26	95.49	84.16	84.25	101.02	89.38	99.15	96.68
	Diversity	1.00	0.99	0.92	1.04	1.10	0.97	0.94	0.82	1.10	0.78	0.84	0.82
	Evenness	0.27	0.25	0.27	0.27	0.28	0.26	0.27	0.23	0.28	0.28	0.23	0.22
Herb	Richness	5.60	4.69	5.07	5.29	4.08	4.26	3.98	3.83	3.26	3.95	5.20	4.77
	Abundance	75.82	46.24	76.94	77.76	50.74	53.04	53.40	49.90	44.35	52.93	59.51	56.69
	Diversity	1.48	1.30	1.33	1.43	1.14	1.17	1.13	1.09	0.95	1.11	1.47	1.37
	Evenness	0.27	0.29	0.25	0.27	0.27	0.25	0.27	0.27	0.26	0.26	0.29	0.29
Fern	Richness	0.73	1.22	0.57	1.26	1.64	1.24	1.18	1.25	1.17	1.57	1.50	1.24
	Abundance	7.96	18.46	6.52	29.08	36.72	31.43	26.25	24.09	27.42	38.28	38.83	26.29
	Diversity	0.12	0.23	0.10	0.28	0.37	0.24	0.27	0.25	0.19	0.38	0.36	0.25
	Evenness	0.05	0.09	0.04	0.12	0.13	0.09	0.11	0.10	0.09	0.14	0.15	0.12
Grass	Richness	3.68	1.21	4.35	1.56	3.05	1.92	2.50	1.80	2.70	2.62	1.62	1.37
	Abundance	50.90	10.87	79.28	18.08	41.91	20.41	36.95	20.14	34.50	30.83	14.16	15.70
	Diversity	1.02	0.27	1.13	0.37	0.82	0.56	0.71	0.48	0.77	0.77	0.42	0.31
	Evenness	0.25	0.10	0.24	0.14	0.20	0.20	0.22	0.17	0.22	0.24	0.16	0.12
Moss	Richness	1.97	2.68	1.39	2.12	2.12	2.28	2.26	2.04	2.54	4.54	2.44	3.02
	Abundance	19.03	24.98	25.28	35.73	30.93	38.97	34.98	35.41	34.43	60.16	37.11	51.15
	Diversity	0.57	0.71	0.36	0.64	0.63	0.64	0.64	0.52	0.74	1.24	0.63	0.84
	Evenness	0.18	0.18	0.12	0.21	0.21	0.19	0.19	0.14	0.21	0.26	0.16	0.21

Appendix 4: Complete list of species observed in the study area along with their status in different age classes following clearcut harvesting.

Family	Species	Status of species in different age classes											
		RC	1C	2C	3C	4C	5C	RB	1B	2B	3B	4B	5B
Pinaceae	<i>Abies balsamea</i>	P	P	D	P	P	P	P	D	P	P	P	P
Betulaceae	<i>Betula papyrifera</i>	A	A	R	R	R	R	P	D	D	P	P	P
Oleaceae	<i>Fraxinus nigra</i>	P	D	D	P	P	D	P	D	P	P	D	P
Pinaceae	<i>Larix laricina</i>	A	A	A	A	A	A	A	A	A	A	R	A
Pinaceae	<i>Picea glauca</i>	A	A	R	A	R	A	A	A	A	A	A	A
Pinaceae	<i>Picea mariana</i>	P	P	P	P	P	P	P	P	P	P	P	P
Pinaceae	<i>Pinus banksiana</i>	A	R	R	R	A	A	A	A	A	A	A	A
Salicaceae	<i>Populus balsamifera</i>	A	A	R	A	A	A	A	A	A	R	A	A
Salicaceae	<i>Populus tremuloides</i>	P	P	P	P	P	P	A	R	R	R	R	A
Aceraceae	<i>Acer spicatum</i>	P	P	P	P	P	P	P	P	P	P	P	P
Betulaceae	<i>Alnus incana</i>	P	P	P	P	P	P	P	P	P	P	P	P
Betulaceae	<i>Alnus viridis</i>	P	P	P	P	P	D	P	P	D	P	P	P
Rosaceae	<i>Amelanchier stolonifera</i>	P	P	P	P	P	D	P	P	P	P	P	P
Rosaceae	<i>Amelanchier spp.</i>	A	R	R	R	R	R	A	A	R	R	R	A
Ericaceae	<i>Arctostaphylos uva-ursi</i>	P	D	P	D	D	P	P	D	D	D	P	P
Ericaceae	<i>Chamaedaphne calyculata</i>	P	D	D	P	D	D	P	P	P	P	P	D
Cornaceae	<i>Cornus stolonifera</i>	P	P	P	P	P	P	P	P	P	P	P	P
Betulaceae	<i>Corylus cornuta</i>	P	P	P	P	P	P	P	P	P	P	P	P
Caprifoliaceae	<i>Diervilla lonicera</i>	A	R	R	R	R	R	P	P	P	P	P	P
Ericaceae	<i>Gaultheria hispidula</i>	A	A	R	A	A	A	P	D	P	D	P	D
Ericaceae	<i>Kalmia spp.</i>	A	A	A	R	A	A	A	A	A	A	A	A
Ericaceae	<i>Ledum groenlandicum</i>	P	D	P	P	D	P	P	P	P	P	P	P
Caprifoliaceae	<i>Linnaea borealis</i>	A	A	A	A	A	R	P	D	D	D	D	P
Caprifoliaceae	<i>Lonicera canadensis</i>	A	A	A	A	A	R	A	R	R	A	A	A
Caprifoliaceae	<i>Lonicera hirsuta</i>	P	P	D	D	P	D	A	A	R	R	R	A
Caprifoliaceae	<i>Lonicera involucrata</i>	A	A	R	A	A	A	P	D	D	D	D	D
Caprifoliaceae	<i>Lonicera villosa</i>	P	D	P	P	P	P	P	P	P	P	P	P
Caprifoliaceae	<i>Lonicera spp.</i>	A	A	A	A	A	A	A	R	A	A	A	A
Rosaceae	<i>Physocarpus opulifolius</i>	A	R	A	A	A	A	P	P	D	D	D	D
Rosaceae	<i>Potentilla fruticosa</i>	P	D	P	D	D	D	A	A	A	A	A	A
Rosaceae	<i>Prunus pensylvanica</i>	P	P	P	P	P	P	A	R	A	A	A	A
Rosaceae	<i>Prunus virginiana</i>	A	R	R	R	A	R	A	R	R	R	R	A
Rhamnaceae	<i>Rhamnus alnifolia</i>	P	D	P	P	P	D	P	D	P	P	P	P
Rhamnaceae	<i>Rhamnus spp.</i>	A	A	A	A	A	A	A	R	A	A	A	A
Grossulariaceae	<i>Ribes glandulosum</i>	P	P	P	P	P	P	P	P	P	P	P	P
Grossulariaceae	<i>Ribes hirtellum</i>	P	P	P	P	P	P	P	P	P	P	P	P
Grossulariaceae	<i>Ribes lacustre</i>	A	A	A	A	A	R	A	R	R	A	A	A
Grossulariaceae	<i>Ribes oxyacanthoides</i>	A	R	A	A	A	A	A	R	R	A	A	R
Grossulariaceae	<i>Ribes triste</i>	A	R	R	A	R	R	A	R	R	R	A	A
Rosaceae	<i>Rosa acicularis</i>	P	P	P	P	P	P	P	P	P	P	P	P
Rosaceae	<i>Rubus acaulis</i>	P	P	P	P	P	D	P	P	P	P	P	P
Rosaceae	<i>Rubus chamaemorus</i>	A	A	R	A	A	A	A	R	R	A	A	A

Family	Species	RC	1C	2C	3C	4C	5C	RB	1B	2B	3B	4B	5B
Rosaceae	<i>Rubus idaeus</i>	P	P	P	P	P	P	P	P	P	P	P	P
Rosaceae	<i>Rubus parviflorus</i>	A	A	A	A	A	A	P	D	P	D	D	D
Rosaceae	<i>Rubus pubescens</i>	P	P	P	P	P	P	P	P	P	P	P	P
Salicaceae	<i>Salix petiolaris</i>	A	A	R	R	R	R	A	R	R	R	A	A
Salicaceae	<i>Salix pyrofolia</i>	A	A	R	R	A	R	A	R	A	A	A	A
Salicaceae	<i>Salix spp.</i>	P	P	P	P	P	P	P	P	P	P	D	D
Rosaceae	<i>Sorbus americana</i>	P	D	D	P	D	P	P	D	P	P	D	P
Rosaceae	<i>Sorbus decora</i>	A	R	R	R	R	R	P	P	P	P	P	P
Taxaceae	<i>Taxus canadensis</i>	A	A	A	A	R	A	A	A	A	A	A	A
Ericaceae	<i>Vaccinium angustifolium</i>	A	R	R	R	R	R	P	P	P	P	P	P
Ericaceae	<i>Vaccinium myrtilloides</i>	A	A	R	A	A	R	A	A	A	A	A	A
Caprifoliaceae	<i>Viburnum edule</i>	P	P	P	P	P	P	P	P	P	P	P	P
Caprifoliaceae	<i>Viburnum trilobum</i>	A	R	R	R	A	A	A	R	A	R	R	A
Ranunculaceae	<i>Actaea rubra</i>	P	P	P	D	D	D	P	P	P	P	P	P
Labiatae	<i>Ajuga reptans</i>	A	R	R	A	A	A	P	P	D	D	D	D
Compositae	<i>Anaphalis margaritacea</i>	A	R	R	A	A	R	A	A	A	A	R	R
Ranunculaceae	<i>Anemone quinquefolia</i>	A	R	A	A	A	R	A	A	A	A	R	A
Ranunculaceae	<i>Anemone riparia</i>	A	R	A	A	A	A	A	A	A	A	A	A
Ranunculaceae	<i>Aquilegia canadensis</i>	A	R	R	A	A	A	A	A	A	A	A	R
Araliaceae	<i>Aralia nudicaulis</i>	P	P	P	P	P	D	P	P	P	P	P	P
Compositae	<i>Aster ciliolatus</i>	P	P	P	P	P	P	P	P	P	P	P	P
Compositae	<i>Aster lateriflorus</i>	P	D	P	P	P	D	P	D	P	D	D	D
Compositae	<i>Aster macrophyllus</i>	P	P	P	P	P	P	P	P	P	P	P	P
Compositae	<i>Aster modestus</i>	A	R	A	R	A	A	A	A	A	R	A	A
Compositae	<i>Aster nemoralis</i>	A	R	R	R	R	A	A	R	R	R	A	R
Compositae	<i>Aster puniceus</i>	A	A	R	R	A	A	A	A	A	A	A	A
Compositae	<i>Aster umbellatus</i>	P	P	D	P	P	P	P	P	P	D	P	P
Ranunculaceae	<i>Caltha palustris</i>	P	D	D	P	D	P	P	D	D	P	D	P
Onagraceae	<i>Circaea alpina</i>	P	D	P	P	D	D	P	D	D	P	P	D
Compositae	<i>Cirsium muticum</i>	A	R	R	R	R	R	A	R	R	R	R	R
Liliaceae	<i>Clintonia borealis</i>	P	P	P	P	P	P	P	P	P	P	P	P
Lamiaceae	<i>Collinsonia canadensis</i>	A	R	R	A	A	A	A	A	A	A	A	A
Ranunculaceae	<i>Coptis trifolia</i>	P	P	P	D	P	P	P	P	P	P	P	P
Cornaceae	<i>Cornus canadensis</i>	P	P	P	P	P	P	P	P	P	P	P	P
Papaveraceae	<i>Corydalis spp.</i>	A	A	R	A	A	A	A	A	A	A	A	A
Droseraceae	<i>Drosera rotundifolia</i>	P	D	D	D	P	D	A	A	A	A	A	A
Onagraceae	<i>Epilobium angustifolium</i>	A	R	R	R	R	R	A	A	A	R	A	R
Onagraceae	<i>Epilobium ciliatum</i>	P	D	D	D	D	D	A	A	A	A	A	A
Onagraceae	<i>Epilobium glandulosum</i>	A	A	A	A	R	A	A	A	A	A	A	A
Brassicaceae	<i>Erysimum cheiranthoides</i>	A	A	A	A	A	A	A	R	A	A	A	A
Compositae	<i>Eupatorium maculatum</i>	A	A	A	R	R	R	A	A	A	R	A	R
Rosaceae	<i>Fragaria vesca</i>	A	R	A	R	A	R	A	R	R	R	A	R
Rosaceae	<i>Fragaria virginiana</i>	P	P	D	P	D	D	P	P	P	P	D	D
Rubiaceae	<i>Galium asprellum</i>	P	P	P	P	P	P	P	P	P	P	P	P
Rubiaceae	<i>Galium trifidum</i>	P	P	P	P	P	P	A	R	R	R	R	R
Rubiaceae	<i>Galium triflorum</i>	P	P	P	P	P	P	P	P	P	P	P	P

Family	Species	RC	1C	2C	3C	4C	5C	RB	1B	2B	3B	4B	5B
Gentianaceae	<i>Gentiana rubricaulis</i>	P	D	D	D	D	D	A	A	A	A	A	A
Geraniaceae	<i>Geranium bicknellii</i>	A	R	A	A	A	A	A	A	A	A	A	A
Rosaceae	<i>Geum rivale</i>	P	P	P	P	P	D	P	P	P	D	P	D
Orchidaceae	<i>Goodyera repens</i>	A	A	A	A	A	A	A	R	A	A	A	A
Compositae	<i>Hieracium aurantiacum</i>	A	R	R	R	R	R	A	A	A	A	A	A
Compositae	<i>Hieracium caespitosum</i>	A	A	A	R	A	A	A	A	A	A	A	A
Balsaminaceae	<i>Impatiens capensis</i>	A	A	A	A	A	A	P	D	D	D	D	D
Iridaceae	<i>Iris versicolor</i>	A	R	A	A	A	A	A	A	A	A	A	A
Compositae	<i>Lactuca biennis</i>	P	P	P	P	P	P	P	D	D	D	D	P
Compositae	<i>Lactuca virosa</i>	A	R	R	A	A	A	A	A	A	A	A	A
Compositae	<i>Lactuca spp.</i>	A	A	R	A	A	A	A	A	A	A	A	A
Orchidaceae	<i>Listera cordata</i>	A	R	A	A	A	A	A	A	A	A	A	R
Labiatae	<i>Lycopus uniflorus</i>	P	D	P	P	P	P	P	D	P	P	P	P
Liliaceae	<i>Maianthemum canadense</i>	P	P	P	P	P	P	P	P	P	P	P	P
Scrophulariaceae	<i>Melampyrum lineare</i>	A	A	A	R	A	A	A	A	A	A	A	A
Scrophulariaceae	<i>Melampyrum pratense</i>	A	R	A	A	A	A	A	A	A	A	A	A
Labiatae	<i>Mentha arvensis</i>	P	P	P	D	P	D	P	P	P	P	D	P
Menyanthaceae	<i>Menyanthes trifoliata</i>	A	A	R	A	R	A	A	A	R	A	A	A
Boraginaceae	<i>Mertensia paniculata</i>	P	P	P	P	P	P	P	P	P	P	P	P
Saxifragaceae	<i>Mitella nuda</i>	P	P	P	P	P	P	P	P	P	P	P	P
Pyrolaceae	<i>Moneses uniflora</i>	A	A	A	R	A	A	A	A	A	A	A	A
Pyrolaceae	<i>Orthilia secunda</i>	A	A	A	R	A	A	A	A	A	A	A	A
Compositae	<i>Petasites frigidus</i>	P	P	P	P	P	P	P	P	P	P	P	P
Orchidaceae	<i>Platanthera hyperborea</i>	A	A	A	A	A	R	A	A	A	A	A	R
Polygonaceae	<i>Polygonum cilinode</i>	A	A	R	R	A	A	A	A	A	R	A	R
Rosaceae	<i>Potentilla gracilis</i>	A	A	R	A	A	A	A	A	A	A	A	A
Rosaceae	<i>Potentilla norvegica</i>	A	R	A	A	A	A	A	A	A	A	A	R
Rosaceae	<i>Potentilla palustris</i>	A	A	A	A	A	A	A	A	A	A	R	A
Rosaceae	<i>Potentilla spp.</i>	A	R	A	A	A	A	A	A	A	A	A	A
Pyrolaceae	<i>Pyrola elliptica</i>	A	A	A	A	A	A	A	A	R	A	A	R
Apiaceae	<i>Sanicula marilandica</i>	A	R	A	A	A	A	A	A	A	A	A	A
Labiatae	<i>Scutellaria galericulata</i>	A	R	R	R	R	A	A	R	A	A	A	A
Umbelliferae	<i>Sium suave</i>	A	R	A	A	R	A	A	A	A	A	A	A
Compositae	<i>Solidago canadensis</i>	A	R	R	R	R	A	A	A	A	A	A	A
Compositae	<i>Solidago graminifolia</i>	A	A	R	R	A	A	A	A	A	A	A	A
Compositae	<i>Solidago uliginosa</i>	A	R	R	A	A	A	A	A	A	A	A	A
Liliaceae	<i>Streptopus roseus</i>	P	P	P	P	P	P	P	P	P	P	P	P
Compositae	<i>Taraxacum officianale</i>	A	R	A	A	A	A	A	R	A	A	R	A
Ranunculaceae	<i>Thalictrum dasycarpum</i>	P	P	P	P	P	P	P	P	P	P	P	P
Clusiaceae	<i>Triadenum fraseri</i>	A	A	A	A	R	A	A	A	A	A	A	A
Primulaceae	<i>Trientalis borealis</i>	P	P	P	P	P	P	P	P	P	P	P	P
Liliaceae	<i>Trillium cernuum</i>	P	P	P	P	P	D	P	P	P	P	P	D
Typhaceae	<i>Typha latifolia</i>	A	R	R	A	A	A	A	A	A	A	A	A
Violaceae	<i>Viola adunca</i>	P	D	P	P	P	P	P	P	P	P	P	P
Violaceae	<i>Viola blanda</i>	P	P	P	P	P	P	P	P	P	P	D	P
Violaceae	<i>Viola cucullata</i>	A	A	A	A	R	A	P	D	P	P	P	D

Family	Species	RC	1C	2C	3C	4C	5C	RB	1B	2B	3B	4B	5B
Violaceae	<i>Viola macloskeyi</i>	A	R	A	A	R	A	P	P	D	D	D	P
Violaceae	<i>Viola nephrophylla</i>	P	P	P	P	P	D	P	P	P	P	D	P
Violaceae	<i>Viola pubescens</i>	P	P	P	P	P	P	P	P	P	P	P	P
Violaceae	<i>Viola renifolia</i>	P	P	P	P	P	P	P	P	P	P	P	P
Violaceae	<i>Viola septentrionalis</i>	A	R	A	R	R	A	A	R	A	A	A	A
Violaceae	<i>Viola septoradis</i>	A	R	R	R	A	R	A	R	R	R	R	R
Dryopteridaceae	<i>Athyrium felix-femina</i>	P	P	P	P	P	P	P	P	P	P	P	P
Adiantaceae	<i>Cryptogramma acrostichoides</i>	P	D	D	P	P	D	P	D	D	P	P	D
Dryopteridaceae	<i>Dryopteris carthusiana</i>	P	P	P	D	P	D	P	P	P	P	P	D
Dryopteridaceae	<i>Dryopteris expansa</i>	A	R	R	R	A	R	A	A	R	A	A	R
Equisetaceae	<i>Equisetum arvense</i>	P	D	P	P	D	D	A	R	R	R	A	A
Equisetaceae	<i>Equisetum fluviatile</i>	A	A	R	A	R	A	A	A	A	A	A	R
Equisetaceae	<i>Equisetum pretense</i>	P	D	P	P	P	D	P	P	D	P	D	D
Equisetaceae	<i>Equisetum sylvaticum</i>	P	P	P	D	P	P	P	P	P	P	P	P
Dryopteridaceae	<i>Gymnocarpium dryopteris</i>	P	P	D	P	D	P	P	P	P	P	P	P
Lycopodiaceae	<i>Lycopodium annotinum</i>	P	D	P	P	P	P	P	P	P	P	P	P
Lycopodiaceae	<i>Lycopodium clavatum</i>	A	R	A	A	R	A	P	P	D	D	P	D
Lycopodiaceae	<i>Lycopodium dendroideum</i>	A	R	A	R	R	A	P	P	P	P	P	P
Lycopodiaceae	<i>Lycopodium lucidulum</i>	P	D	D	P	P	P	P	P	P	P	P	P
Onocleaceae	<i>Matteuccia struthiopteris</i>	P	P	P	P	P	P	P	D	P	P	P	P
Dryopteridaceae	<i>Onoclea sensibilis</i>	P	P	D	D	P	D	A	A	A	R	A	A
Osmundaceae	<i>Osmunda claytoniana</i>	P	D	D	P	P	P	P	P	D	P	D	P
Osmundaceae	<i>Osmunda regalia</i>	A	A	A	A	A	A	A	A	A	A	A	R
Thelypteridaceae	<i>Phegopteris connectilis</i>	P	D	P	P	P	P	P	P	P	P	P	P
Polypodiaceae	<i>Pteridium aquilinum</i>	A	R	A	A	R	A	A	A	A	A	A	A
Thelypteridaceae	<i>Thelypteris palustris</i>	A	A	R	R	R	A	P	D	D	D	D	D
Cyperaceae	<i>Carex adusta</i>	A	A	R	A	A	R	A	A	A	A	A	R
Cyperaceae	<i>Carex aenea</i>	P	P	P	P	P	P	P	P	D	P	P	P
Cyperaceae	<i>Carex aquatilis</i>	P	P	P	P	P	P	P	D	D	P	P	P
Cyperaceae	<i>Carex arcta</i>	P	D	P	P	P	D	A	A	A	R	A	R
Cyperaceae	<i>Carex canescens</i>	A	R	R	R	R	R	P	P	D	P	P	D
Cyperaceae	<i>Carex crawfordii</i>	P	P	P	P	P	P	P	D	P	P	D	P
Cyperaceae	<i>Carex crinita</i>	A	R	R	R	R	R	P	D	P	D	P	P
Cyperaceae	<i>Carex deflexa</i>	P	P	P	P	P	P	P	P	P	P	P	P
Cyperaceae	<i>Carex disperma</i>	P	P	P	P	P	P	A	R	R	A	R	R
Cyperaceae	<i>Carex flava</i>	P	P	P	P	P	P	P	P	P	P	P	P
Cyperaceae	<i>Carex gracillima</i>	P	P	P	P	P	P	A	R	R	R	R	R
Cyperaceae	<i>Carex houghtoniana</i>	A	R	R	R	R	R	P	D	D	P	P	P
Cyperaceae	<i>Carex interior</i>	A	R	R	A	R	R	P	P	P	P	P	D
Cyperaceae	<i>Carex intumescens</i>	P	P	P	P	P	P	P	P	P	P	P	P
Cyperaceae	<i>Carex lasiocarpum</i>	A	R	R	A	A	R	A	R	R	A	A	A
Cyperaceae	<i>Carex laxiflora</i>	P	P	P	D	P	P	A	R	R	R	A	R
Cyperaceae	<i>Carex leptalea</i>	A	R	R	A	A	A	A	A	A	R	A	A
Cyperaceae	<i>Carex oligosperma</i>	P	P	D	D	P	D	P	P	D	D	D	D
Cyperaceae	<i>Carex retrogosa</i>	A	R	R	R	A	A	A	R	A	A	A	A
Cyperaceae	<i>Carex rostrata</i>	A	R	A	R	A	R	A	R	A	R	A	A

Family	Species	RC	1C	2C	3C	4C	5C	RB	1B	2B	3B	4B	5B
Cyperaceae	<i>Carex stipata</i>	A	R	R	A	A	A	A	A	A	A	A	R
Cyperaceae	<i>Carex trisperma</i>	A	R	A	A	A	A	A	R	A	R	R	R
Cyperaceae	<i>Carex spp.</i>	P	P	P	P	P	D	P	P	P	P	D	P
Cyperaceae	<i>Scirpus cyperinus</i>	A	R	R	R	A	A	A	A	A	R	A	A
Cyperaceae	<i>Scirpus hudsonianus</i>	A	A	R	R	A	A	A	A	A	A	A	A
Juncaceae	<i>Juncus brevicaudatus</i>	A	A	A	R	A	A	A	A	A	A	A	A
Juncaceae	<i>Juncus effuses</i>	A	A	A	R	A	A	A	A	A	A	A	A
Juncaceae	<i>Juncus filiformis</i>	A	A	A	R	A	A	A	A	A	A	A	A
Gramineae	<i>Agropyron repens</i>	A	A	A	A	A	A	A	R	A	A	A	A
Gramineae	<i>Agrostis scabra</i>	A	R	R	A	R	R	A	A	R	R	A	R
Poaceae	<i>Brachyelytrum erectum</i>	P	D	P	P	P	D	P	D	D	D	D	P
Gramineae	<i>Bromus ciliatus</i>	P	P	P	P	P	P	P	P	P	P	P	P
Gramineae	<i>Calamagrostis canadensis</i>	A	R	R	R	R	R	A	R	R	R	R	R
Gramineae	<i>Cinna latifolia</i>	P	P	P	D	P	P	P	D	D	P	P	P
Gramineae	<i>Elymus trachycaulus</i>	P	P	P	P	P	P	A	R	R	A	A	R
Gramineae	<i>Elymus repens</i>	P	P	P	P	P	P	P	P	P	P	P	P
Gramineae	<i>Glyceria borealis</i>	P	P	P	P	P	D	A	A	A	A	R	R
Gramineae	<i>Glyceria canadensis</i>	P	P	P	P	D	D	P	D	P	P	D	D
Gramineae	<i>Oryzopsis asperifolia</i>	P	P	P	P	D	D	P	D	P	P	P	P
Poaceae	<i>Phalaris arundinacea</i>	A	A	R	R	R	A	A	A	R	A	A	A
Gramineae	<i>Poa compressa</i>	A	R	A	A	A	A	A	A	A	A	A	R
Gramineae	<i>Poa spp.</i>	A	R	A	R	A	A	A	A	A	R	A	R
Gramineae	<i>Schizachne purpurascens</i>	A	A	R	R	R	A	A	A	A	A	A	A
Gramineae	<i>Graminoide spp.</i>	P	P	P	P	P	P	P	P	P	P	P	P
Polytrichaceae	<i>Atrichum spp.</i>	P	D	D	D	D	D	P	D	D	D	D	D
Aulacomniaceae	<i>Aulacomnium palustre</i>	P	P	P	P	P	P	P	P	P	P	P	P
Brachytheciaceae	<i>Brachythecium reflexum</i>	P	P	D	P	P	P	P	P	D	D	P	P
Brachytheciaceae	<i>Brachythecium rivulare</i>	P	P	P	P	P	P	P	P	P	P	P	P
Brachytheciaceae	<i>Brachythecium turgidum</i>	P	P	D	P	P	P	P	D	D	D	P	P
Brachytheciaceae	<i>Brachythecium spp.</i>	A	A	A	A	A	R	A	A	A	A	A	A
Bryaceae	<i>Bryum pseudotriquetrum</i>	P	P	P	P	P	P	P	D	P	P	D	P
Bryaceae	<i>Bryum spp.</i>	A	R	A	A	A	A	A	A	A	A	A	A
Amblystegiaceae	<i>Calliargon giganteum</i>	A	R	R	A	A	A	P	D	D	D	D	D
Hypnaceae	<i>Callicladium haldanianum</i>	A	A	A	A	A	A	A	R	A	A	A	A
Hypnaceae	<i>Callicladium spp.</i>	P	D	P	P	P	P	P	D	P	P	P	P
Ditrichaceae	<i>Ceratodon purpureus</i>	A	R	R	A	R	A	A	A	A	A	A	A
Climaceaceae	<i>Climacium dendroides</i>	P	P	P	P	P	D	P	P	P	P	P	P
Dicranaceae	<i>Dicranum flagellare</i>	P	D	P	P	P	P	P	D	D	P	P	P
Dicranaceae	<i>Dicranum fuscescens</i>	P	P	P	P	P	P	P	D	P	P	P	P
Dicranaceae	<i>Dicranum montanum</i>	P	D	D	D	D	D	A	A	A	A	A	A
Dicranaceae	<i>Dicranum ontariense</i>	A	A	A	A	R	R	P	D	D	D	P	D
Dicranaceae	<i>Dicranum polysetum</i>	P	P	P	P	D	P	P	P	P	P	P	P
Dicranaceae	<i>Dicranum scoparium</i>	P	D	D	D	P	P	A	A	R	R	A	R
Dicranaceae	<i>Dicranum undulatum</i>	A	A	A	R	R	A	P	D	D	D	D	P
Dicranaceae	<i>Dicranum spp.</i>	P	P	D	D	P	P	P	P	P	D	P	P
Ditrichaceae	<i>Distichium capillaceum</i>	P	D	D	D	D	D	P	D	D	D	D	D

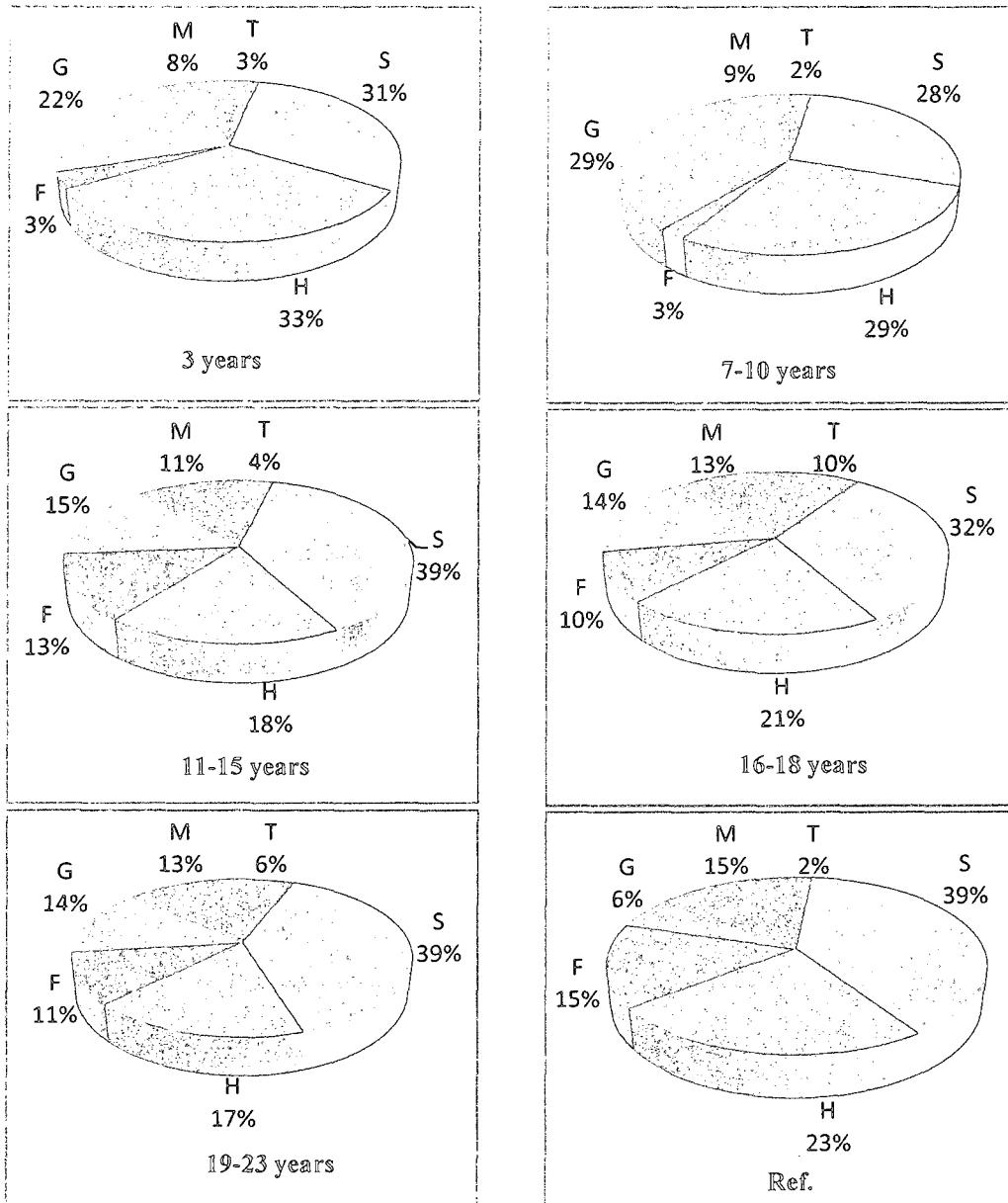
Family	Species	RC	1C	2C	3C	4C	5C	RB	1B	2B	3B	4B	5B
Amblystegiaceae	<i>Drepanocladus fluitans</i>	A	R	A	A	A	A	A	A	A	A	A	A
Amblystegiaceae	<i>Drepanocladus uncinatus</i>	P	P	P	P	P	P	P	P	P	P	P	P
Brachytheciaceae	<i>Eurhynchium pulchellum</i>	P	P	P	P	P	P	P	P	P	P	P	P
Fissidentaceae	<i>Fissidens spp.</i>	P	P	P	P	P	P	P	P	P	P	P	P
Helodiaceae	<i>Helodium blandowii</i>	P	P	D	P	D	P	P	D	D	D	D	P
Hylocomiaceae	<i>Hylocomium splendens</i>	A	A	A	A	A	R	A	A	A	A	A	R
Hypnaceae	<i>Hypnum revolutum</i>	P	D	D	P	P	D	P	P	P	P	P	P
Pterigynandraceae	<i>Myurella julacea</i>	P	D	D	D	D	D	P	D	D	D	D	D
Mniaceae	<i>Mnium spp.</i>	P	P	P	P	P	P	P	P	D	P	P	P
Dicranaceae	<i>Onchophorus wahlenbergii</i>	A	A	A	R	A	R	P	D	D	D	D	P
Bartramiaceae	<i>Philonotis fontana</i>	A	A	A	R	R	R	A	A	A	A	R	A
Mniaceae	<i>Plagiomnium spp.</i>	P	P	P	P	P	P	P	P	P	P	P	P
Hylocomiaceae	<i>Pleurozium schreberi</i>	P	P	P	P	P	P	P	P	P	P	P	P
Polytrichaceae	<i>Polytrichum commune</i>	P	P	P	P	D	P	A	A	A	A	R	R
Polytrichaceae	<i>Polytrichum juniperinum</i>	A	R	R	A	A	A	A	A	A	A	A	A
Polytrichaceae	<i>Polytrichum strictum</i>	P	D	P	D	P	D	P	D	D	P	P	D
Polytrichaceae	<i>Polytrichum spp.</i>	P	P	D	P	P	D	A	R	A	A	R	R
Hypnaceae	<i>Ptilium crista-castrensis</i>	P	D	D	D	D	P	P	D	P	P	P	P
Hypnaceae	<i>Pylaisiella polyantha</i>	P	D	D	P	D	P	P	D	D	P	D	P
Mniaceae	<i>Rhizomnium pseudopunctatum</i>	P	P	D	P	P	P	P	P	P	P	P	P
Mniaceae	<i>Rhizomnium punctatum</i>	P	P	P	P	P	P	P	P	P	P	P	P
Mniaceae	<i>Rhizomnium spp.</i>	A	A	A	A	A	A	A	R	A	A	A	A
Bryaceae	<i>Rhodobryum roseum</i>	P	P	D	P	P	P	P	P	P	P	P	P
Hylocomiaceae	<i>Rhytidiadelphus triquetrus</i>	P	P	P	P	P	P	P	P	P	P	P	P
Amblystegiaceae	<i>Scorpidium scorpioides</i>	A	R	A	A	A	A	A	R	A	R	A	R
Sphagnaceae	<i>Sphagnum angustifolium</i>	A	A	R	A	A	R	A	A	A	A	A	R
Sphagnaceae	<i>Sphagnum capillifolium</i>	A	A	R	A	A	R	A	A	A	A	A	R
Sphagnaceae	<i>Sphagnum girgensohnii</i>	A	R	A	A	A	R	A	R	R	A	A	A
Sphagnaceae	<i>Sphagnum warnstorffii</i>	A	A	R	A	A	R	A	A	A	A	A	R
Sphagnaceae	<i>Sphagnum spp.</i>	P	P	P	P	P	P	P	P	D	P	P	P
Thuidiaceae	<i>Thuidium delicatulum</i>	P	P	P	P	P	P	P	P	P	P	P	P
Lepidoziaceae	<i>Lepidozia spp.</i>	A	A	A	A	A	A	P	D	D	D	D	D
Vitaceae	<i>Parthenocissus quinquefolia</i>	A	A	A	A	A	A	P	D	D	D	P	D
Total number of species recorded		131	160	161	157	147	132	137	130	125	137	123	145
Total number of species recruited		-	65	62	49	40	41	-	39	29	31	21	39
Total number of species disappeared		-	36	32	23	24	40	-	46	41	31	35	31

Note: RC= reference site at cut location; RB= reference site at buffer location; 1C-5C and 1B-5B = age classes 1-5 at cut and buffer, respectively; A= absent; P= present; D = disappeared and R = recruited. Recruitment or disappearance of a species was determined for cut and buffer sites based on the absence or presence of that species at reference sites of cut and buffer locations, respectively.

Appendix 5: List of species and their codes used in NMS ordination space.

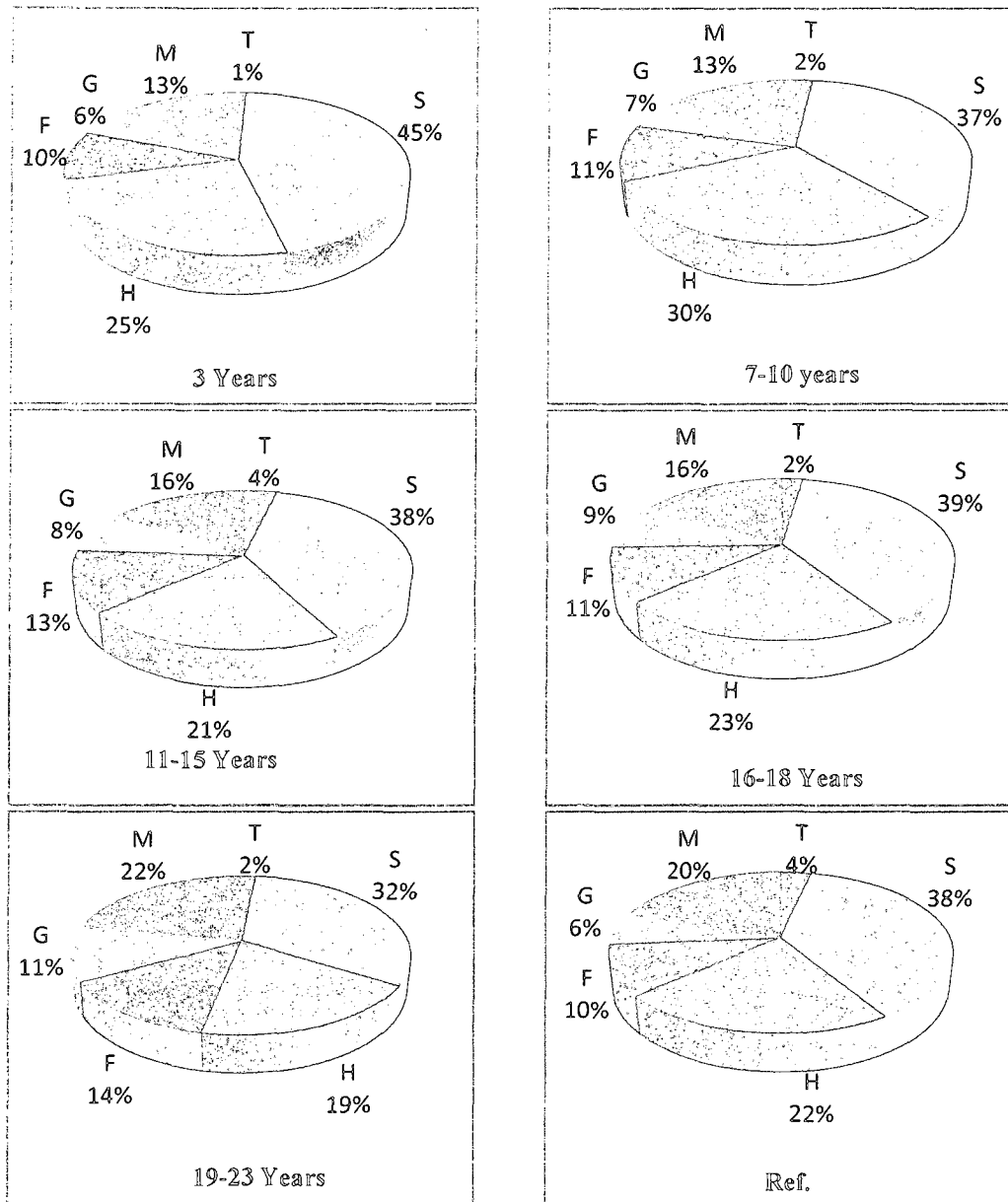
Code	Species	Code	Species	Code	Species
Abibal	<i>Abies balsamea</i>	Corcan	<i>Cornus canadensis</i>	Petfri	<i>Petasites frigidus</i>
Acespi	<i>Acer spicatum</i>	Corcor	<i>Corylus cornuta</i>	Phecon	<i>Phegopteris connectilis</i>
Actrub	<i>Actaea rubra</i>	Corsto	<i>Cornus stolonifera</i>	Picmar	<i>Picea mariana</i>
Agrsca	<i>Agrostis scabra</i>	Dicfla	<i>Dicranum flagellare</i>	Plaspp	<i>Plagiomnium spp.</i>
Alninc	<i>Alnus incana</i>	Dicfus	<i>Dicranum fuscescens</i>	Plesch	<i>Pleurozium schreberi</i>
Alnvir	<i>Alnus viridis</i>	Dicpol	<i>Dicranum polysetum</i>	Polcom	<i>Polytrichum commune</i>
Amespp	<i>Amelanchier spp.</i>	Dicsco	<i>Dicranum scoparium</i>	Polsp	<i>Polytrichum spp.</i>
Amesto	<i>Amelanchier stolonifera</i>	Dicspp	<i>Dicranum spp.</i>	Polstr	<i>Polytrichum strictum</i>
Aranud	<i>Aralia nudicaulis</i>	Dielon	<i>Diervilla lonicera</i>	Poptre	<i>Populus tremuloides</i>
Astcil	<i>Aster ciliolatus</i>	Dreunc	<i>Drepanocladus uncinatus</i>	Prupen	<i>Prunus pennsylvanica</i>
Astmac	<i>Aster macrophyllus</i>	Drycar	<i>Dryopteris carthusiana</i>	Pruvir	<i>Prunus virginiana</i>
Astnem	<i>Aster nemoralis</i>	Elyrep	<i>Elymus repens</i>	Pticri	<i>Ptilium crista-castrensis</i>
Astumb	<i>Aster umbellatus</i>	Elytra	<i>Elymus trachycaulus</i>	Pylpol	<i>Pylaisiella polyantha</i>
Athfel	<i>Athyrium felix-femina</i>	Epiang	<i>Epilobium angustifolium</i>	Rhaaln	<i>Rhamnus alnifolia</i>
Aulpal	<i>Aulacomnium palustre</i>	Equpre	<i>Equisetum pretense</i>	Rhipse	<i>Rhizomnium pseudopunctatum</i>
Betpap	<i>Betula papyrifera</i>	Equsyl	<i>Equisetum sylvaticum</i>	Rhipun	<i>Rhizomnium punctatum</i>
Braere	<i>Brachyelytrum erectum</i>	Eurpul	<i>Eurhynchium pulchellum</i>	Rhoros	<i>Rhodobryum roseum</i>
Braref	<i>Brachythecium reflexum</i>	Fisspp	<i>Fissidens spp.</i>	Rhytri	<i>Rhytidiadelphus triquetrus</i>
Brariv	<i>Brachythecium rivulare</i>	Franig	<i>Fraxinus nigra</i>	Ribgla	<i>Ribes glandulosum</i>
Bratur	<i>Brachythecium turgidum</i>	Fraves	<i>Fragaria vesca</i>	Ribhir	<i>Ribes hirtellum</i>
Brocil	<i>Bromus ciliatus</i>	Fravir	<i>Fragaria virginiana</i>	Rosaci	<i>Rosa acicularis</i>
Brypse	<i>Bryum pseudotriquetrum</i>	Galasp	<i>Galium asprellum</i>	Rubaca	<i>Rubus acaulis</i>
Calcan	<i>Calamagrostis canadensis</i>	Galtri	<i>Galium trifidum</i>	Rubida	<i>Rubus idaeus</i>
Calspp	<i>Callicladium spp.</i>	Galtrifl	<i>Galium triflorum</i>	Rubpub	<i>Rubus pubescens</i>
Caraen	<i>Carex aenea</i>	Geuriv	<i>Geum rivale</i>	Salpet	<i>Salix petiolaris</i>
Caraqu	<i>Carex aquatilis</i>	Glybor	<i>Glyceria borealis</i>	Salspp	<i>Salix spp.</i>
Carcan	<i>Carex canescens</i>	Glycan	<i>Glyceria canadensis</i>	Sorame	<i>Sorbus americana</i>
Carcra	<i>Carex crawfordii</i>	Graspp	<i>Graminoide spp.</i>	Sordec	<i>Sorbus decora</i>
Carcri	<i>Carex crinita</i>	Gymdry	<i>Gymnocarpium dryopteris</i>	Sphang	<i>Sphagnum angustifolium</i>
Cardef	<i>Carex deflexa</i>	Hyprev	<i>Hypnum revolutum</i>	Sphspp	<i>Sphagnum spp.</i>
Cardis	<i>Carex disperma</i>	Lacbie	<i>Lactuca biennis</i>	Strros	<i>Streptopus roseus</i>
Carfla	<i>Carex flava</i>	Ledgro	<i>Ledum groenlandicum</i>	Thadas	<i>Thalictrum dasycarpum</i>
Cargra	<i>Carex gracillima</i>	Lonvil	<i>Lonicera villosa</i>	Thudel	<i>Thuidium delicatulum</i>
Carhou	<i>Carex houghtoniana</i>	Lycann	<i>Lycopodium annotinum</i>	Tribor	<i>Trientalis borealis</i>
Carint	<i>Carex interior</i>	Lycden	<i>Lycopodium dendroideum</i>	Tricer	<i>Trillium cernuum</i>
Carintu	<i>Carex intumescens</i>	Lycluc	<i>Lycopodium lucidulum</i>	Vacang	<i>Vaccinium angustifolium</i>
Carlas	<i>Carex lasiocarpum</i>	Lycuni	<i>Lycopus uniflorus</i>	Vibedu	<i>Viburnum edule</i>
Carlax	<i>Carex laxiflora</i>	Maican	<i>Maianthemum canadense</i>	Vioadu	<i>Viola adunca</i>
Carspp	<i>Carex spp.</i>	Matstr	<i>Matteuccia struthiopteris</i>	Viobla	<i>Viola blanda</i>
Cinlat	<i>Cinna latifolia</i>	Menarv	<i>Mentha arvensis</i>	Viocuc	<i>Viola cucullata</i>
Ciralp	<i>Circaea alpina</i>	Merpan	<i>Mertensia paniculata</i>	Viomac	<i>Viola macloskeyi</i>
Cirmut	<i>Cirsium muticum</i>	Mitnud	<i>Mitella nuda</i>	Vionep	<i>Viola nephrophylla</i>
Clibor	<i>Clintonia borealis</i>	Mnispp	<i>Mnium spp.</i>	Viopub	<i>Viola pubescens</i>
Cliden	<i>Climacium dendroides</i>	Oryasp	<i>Oryzopsis asperifolia</i>	Vioren	<i>Viola renifolia</i>
Coptri	<i>Coptis trifolia</i>	Osmcla	<i>Osmunda claytoniana</i>	Viosep	<i>Viola septentrionalis</i>

Appendix 6a: Changes in mean total cover of different life forms over time following harvesting disturbance at clearcut sites.



Note: T = tree; S = shrub; H = herb; F = fern; G = grass; M = moss.

Appendix 6b: Changes in mean total cover of different life forms over time following harvesting disturbance at buffer sites.



Note: T = tree; S = shrub; H = herb; F = fern; G = grass; M = moss.

Appendix 7: UTM co-ordinates and geo-ecological characteristics of the study site.

Stream No.	UTM X	UTM Y	Site Class	Ecosite	Av. Slope	Soil texture	Landform	Relief	Drainage
1	352208	5397648	2	NW21M	1.1	FS	MG	moderate	dry
2	349765	5398785	2	NW19D	5.5	FS	GE	low	mixed
3	350186	5399366	2	NW16	2.6	FS	RR	low	dry
4	350697	5396102	1	NW21M	4	FS	MG	moderate	dry
5	347246	5398424	2	NW19M	3.5	FS	RP	moderate	dry
6	346609	5397496	2	NW19M	4.6	FS	RP	moderate	dry
7	342680	5393816	2	NW19M	2.7	FS	RP	moderate	dry
8	355255	5396068	2	NW19D	2.4	FS	MG	moderate	dry
9	347555	5399930	3	NW19D	1.7	FS	MG	moderate	dry
10	354150	5394189	1	NW19D	3.2	FS	MG	moderate	dry
11	354110	5394628	2	NW22D	2.6	FS	MG	moderate	dry
12	364799	5386722	2	NW19D	1.3	MS	RN	moderate	dry
13	345769	5397367	2	NW21M	4.7	FS	RP	moderate	dry
14	345561	5399443	2	NW20S	2.8	FS	MG	moderate	dry
15	354734	5388638	2	NW21D	2.6	FS	RN	moderate	dry
16	356139	5390643	1	NW22D	1.8	FS	MG	moderate	dry
17	355776	5390264	1	NW22D	1.8	FS	MG	moderate	dry
18	357182	5390223	2	NW19M	5.2	FS	MG	moderate	dry
19	337132	5392304	2	NW31M	3.2	FS	RP	moderate	dry
20	366277	5407109	2	NW20M	3.1	FS	RP	low	mixed
21	369210	5409466	3	NW19D	2.1	FS	RP	low	mixed
22	369136	5409015	3	NW19D	2.1	FS	RP	low	mixed
23	325222	5411671	2	NW22M	2.5	FS	RN	moderate	dry
24	331767	5410824	1	NW12	2	FS	RR	moderate	dry
25	362546	5388719	3	NW19M	4	FS	RN	high	dry
26	362086	5387320	2	NW19D	4.3	FS	RN	high	dry
27	362099	5388152	3	NW19M	7.9	FS	RN	high	dry
28	349676	5397593	1	NW22D	2.1	FS	RR	low	dry
29	362854	5389839	1	NW22D	2.2	FS	RN	high	dry
30	363282	5388444	3	NW19M	7.9	FS	RN	high	dry

Note: Site class: 1= better, 2= good, 3=poor; Landform: MG=Ground moraine, GE= Esker, RR=Bedrock ridge, RP=Bedrock plain, RN=Bedrock knob; Soil texture: FS=Fine sand, MS=Medium sand.