INFLUENCE OF RIPARIAN HARVESTING ON BOREAL UNDERSTORY VEGETATION

By

Rebecca Louise MacDonald

A Dissertation Submitted in
Partial Fulfillment of the Requirements for the
Degree of Doctor of Philosophy in Forest Sciences

Faculty of Natural Resources Management
Lakehead University
September 2012

Abstract

MacDonald, R.L. 2012. Influence of riparian harvesting on boreal understory vegetation. 112 pp.

In the boreal forest, understory vegetation accounts for the majority of floristic diversity and affects overstory succession and productivity, nutrient cycling, and wildlife habitat. In riparian forests, understory vegetation also plays an important functional role by reducing erosion, stabilizing the stream channel, and regulating water quality and quantity. Despite this critical importance, effects of harvesting on understory plant communities in riparian forests are still poorly understood. This study uses data from two boreal ecozones in Canada to quantify how overstory harvesting affects understory vegetation communities and how disturbance-response relationships vary from stream edge to uplands.

Using data collected during the summer before harvesting (Yr 0), and three summers after harvesting (Yrs 1, 5 and 7) from headwater stream sites on the Boreal Plain study area (Central Alberta), compositional stability (i.e., the measure of change in community membership and abundance) was measured following disturbance. Non-metric multidimensional scaling was used to ordinate vegetation plots using species cover, and then measured vector length in the ordination space to quantify floristic dissimilarity (i.e., inverse of compositional stability) of each sample plot. Streamside understory plant communities were compositionally more stable relative to upland communities following clearcut harvesting. Compositional stability was positively related to pre-harvest species richness and negatively related to pre-harvest bryoid cover. Changes in species diversity, abundance and turnover following harvesting were also examined. Streamside communities harvested with or without a 30 m riparian buffer, were maintained to a condition similar to uncut forests. However, upland communities were less resistant to overstory harvest, relative to streamside communities, and subsequently colonized by grasses, forbs, and tall shrubs; many of which were present in pre-harvest riparian plots.

Mechanical site preparation (i.e., scarification) exacerbates environmental changes following overstory harvest by destroying above- and below-ground plant parts and coarse woody debris and removing more of the forest floor. The response of boreal understory plant communities to overstory harvesting with and without scarification was examined on 24 small stream sites on Boreal Shield (Northwestern Ontario) watersheds. Species composition was not strongly affected by harvesting when forest floor and soil disturbance is minimal; but it was following scarification. However, this effect varied with habitat. First, the riparian and upland plots that were harvested and scarified diverged from the uncut plant communities; however this effect was stronger in the upland communities. Second, changes within the community following scarification were not detectable in the transitional communities; these communities retain species of both riparian and upland communities and thus their flora has lower site fidelity and likely tolerates a wider range of environmental conditions. Scarification profoundly alters the substrate by breaking up coarse woody debris and decreasing the depth of organic matter, which destroys forest floor feathermosses and creates a habitat suitable for early colonizing species (i.e., grasses).

This study indicates that streamside understory plant communities are inherently more resilient to stand-replacing disturbance than upland assemblages. I attribute this to the higher moisture availability and shading from tall shrubs associated with riparian habitat that buffers the effect of harvesting on shade-tolerant species in streamside plots. Thus, the response to harvesting is not as marked as it is in the uplands. This study highlights that understory disturbance response relationships can differ within a small spatial scale (i.e., 30 m) based on habitat characteristics, imparted by hydrological processes and disturbance regimes that drive community composition.

Keywords: boreal forest; community ecology; compositional stability; disturbance; diversity; diversity-stability hypothesis; logging; riparian buffer; riparian forests; species composition; species richness; understory vegetation

CONTENTS

Figures

Tables

Acknowledgements

Many people have been instrumental throughout the development of this thesis, and I am extremely grateful to all of them. First and foremost, I would like to thank my Supervisors Drs. Ellie Prepas and Han Chen for their guidance, support and mentorship.

As a member of my committee, Dr. Brian Palik has taken an active role in my progression throughout this thesis, and guided me to a greater comprehension than I would have achieved on my own.

I am grateful to my external examiner, Dr. Daniel Kneeshaw, whose insight has undoubtedly strengthened my work.

Thank you to Janice Burke for improving my writing skills; Mark Serediak and Tim McCready for making my field seasons easier; and Virginia Antoniak for facilitating my dissertation in too many ways to list.

Scott Eberwein, Tom Butler, Mary Jane Moses, Lee Salmon and Marie LeRoux have my sincere gratitude for both their help in the field and for always maintaining a sense of humour.

I am tremendously appreciative for the funding provided by a Natural Sciences and Engineering Research Council of Canada (NSERC) Industrial (Millar Western Forest Products Ltd) Post-graduate Scholarship. Additional funding was gratefully received from the NSERC funded CRD project FORWARD and partners, as well as from Lakehead University.

Finally, I am indebted to those who have been exceptionally helpful on a personal level. Without the relentless support of my family and friends, especially my kind and generous Parents, none of this would have been possible. Thank you to my fellow graduate students (LUFGSA!) for camaraderie in good times and bad. Last but not least, I would like to thank David Nisker for all of his encouragement and moral support.

CHAPTER 1 : GENERAL INTRODUCTION

Riparian forests (Fig 1) are diverse, dynamic and complex systems, in which the flora plays an essential role in ecosystem functioning. In addition to providing critical habitat and corridors for terrestrial wildlife (Naiman et al. 1993), riparian vegetation affects surface water quality and quantity through the provision of a variety of ecological services**.** Sediment and nutrient pollution of streams may be decreased as water moving from upland areas to the stream channel interacts with riparian vegetation (Lee et al. 2003, Hefting et al. 2005, Luke et al. 2007, Sovik and Syversen 2008). The riparian forest canopy shades and controls the temperature of the stream, while the roots provide bank stability (Naiman and Décamps 1997, Naiman et al. 2005). The physiology of riparian plants influences fluvial processes through stream discharge, hydraulic lift and evapotranspiration (Brown and Krygier 1970, Norris 1993). Also, organic inputs to the stream ecosystem from riparian vegetation (including woody debris and leaf litter) create habitat and provide nutrients to stream organisms, dissipate energy and trap moving materials (Vannote et al. 1980, Naimen and Decamps 1997). Despite the critical importance of vegetation in riparian forest ecosystems and across the landscape, dynamics of riparian plant communities are still poorly understood, particularly in the context of anthropogenic perturbation.

With increased resource extraction over the last several decades, forest harvesting has become an important stand-replacing disturbance in the fire-driven North American boreal forest. Logging exerts strong controls on understory plant communities which, despite being small in stature in comparison with overstory trees, accounts for the majority of floristic diversity (Halpern and Spies 1995, Roberts and Gilliam 2003) and affects overstory

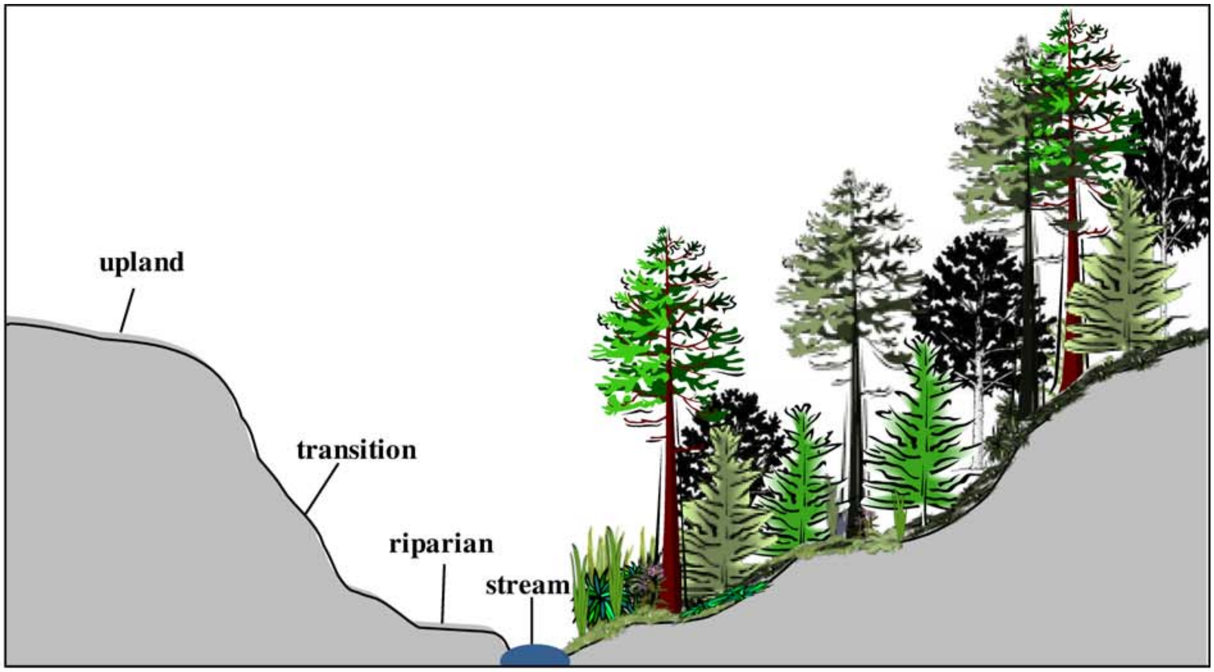


Figure 1.1 Example of cross section of stream valley across a boreal riparian ecotone, including stream channel, riparian, transition and upland areas.

succession and productivity (Connell and Slatyer 1977, Royo and Carson 2006, Ilisson and Chen 2009), nutrient cycling (Weber and Vancleve 1981, Johnson and Curtis 2001, Nilsson and Wardle 2005) and wildlife habitat (Johnson et al. 2003, Payer and Harrison 2003). A thorough review of the relationship between harvesting and boreal understory vegetation is available (see Hart and Chen 2006 for review); however, most of what is known regarding harvesting effects on understory vegetation are derived from studies in upland forests. In comparison to upland understory communities, riparian plant communities are characteristically of higher diversity of species and life-history strategies, resulting from higher resource quantity and heterogeneity of streamside habitats, imparted by hydrological processes and disturbance regimes of (Naiman et al. 1993). Furthermore, boreal upland understory communities are more commonly dominated by shade tolerant species (Nilsson and Wardle 2005, Hart and Chen 2008), which may be intolerant to overstory harvesting. The effect of disturbance on a community is a direct reflection of the traits of its members (Noble and Slatyer 1980), and thus understory plant communities in riparian forests may not respond to logging in the same manner as those in upland forests.

Inclusion of riparian buffers in forest management plans is a standard practice across North America, albeit with variations among provinces, states, and agencies. Although riparian buffers were devised initially to protect aquatic organisms and habitat, they have more recently been included as an element in terrestrial conservation initiatives. However, buffers may not be justified in the context of emulating fire disturbance (Buttle 2002, Macdonald et al. 2004, Braithwaite and Mallik 2012), which is the major driver of the boreal forest (Johnson 1992) and widely assumed to sustain forest dynamics and biodiversity (Palik et al. 2002, Fenton et al. 2009). Moreover, buffers, specifically those with a fixed width, may restrict the extent of habitat heterogeneity across managed forest landscapes (Darveau et al. 2001). Using intentional disturbance (e.g., harvesting) in riparian habitats may be an effective management tool to maintain ecosystem functioning and biodiversity (Sibley et al. 2012). The main objective of this thesis is to examine early successional dynamics of the diversity, abundance, and composition of understory flora following forest harvesting, with and without a streamside buffer, and to test whether these disturbance-response relationships differ with respect to distance from stream (i.e., streamside versus upland). I aim to elucidate the different mechanisms structuring plant communities along this latitudinal gradient from the stream channel and how they may contribute to the relative stability of understory flora to overstory harvesting. Data which contribute to our understanding of how forest harvesting affects understory plant communities in riparian forests is vital to address concerns for biodiversity conservation, and both surface water and forest management

1.1 Study area

Within this dissertation, each chapter is written as a discrete manuscript to facilitate publication. Therefore, study areas are described in-depth within each chapter. However, it is important to note that to improve pattern detection and widen the inference space, data were collected from two distinct boreal ecozones of Canada. Data from chapters two to four were collected on the relatively dry Boreal Plain (Central Alberta), while data from chapter five were collected on the moister Boreal Shield (Northwestern Ontario). Utilizing two ecozones with distinct moisture regimes enhances the contribution of this thesis as the contrast between streamside and uplands may be more pronounced in areas where moisture is a stronger limiting factor on understory vegetation. Although ecozones differ in both climate and geomorphology (for example, the Boreal Plain study area has fine-textured soils, whereas the Boreal Shield study area has coarse but shallow soils), all study streams were space-constrained headwater streams (i.e., 0.5 – 1 m wide) lacking distinct floodplains with narrow riparian zones usually constrained by the upslope and having nearly complete canopy closure. Since disturbance-response relationships are system dependent, the results from this dissertation should be most applicable to similar headwater, or small, stream forest ecosystems.

CHAPTER 2 : RELATIONSHIP BETWEEN ABOVEGROUND BIOMASS AND PERCENT COVER OF GROUND VEGETATION IN CANADIAN BOREAL PLAIN RIPARIAN FORESTS[1]

2.1 Abstract

Vegetation biomass is the ideal variable to estimate vegetation abundance and productivity, and is necessary for studies of community structure. However, biomass data are difficult and destructive to collect, unlike areal cover data. Currently, equations to predict biomass from percent cover have been developed for upland ground flora; however, these equations are lacking for riparian forests. I quantified relationships between aboveground biomass and percent cover of eight ground floristic growth forms (short forbs, tall forbs, ferns, clubmosses, horsetails, graminoids, dwarf shrubs and bryoids) in riparian forests of the Canadian Boreal Plain and tested whether relationships differ for ground plants growing in two different nutrient environments (early and late seral stage). Without exception, linear relationships were identified with percent cover ($P < 0.001$) that explained 61–93% of the variation in biomass. Slopes of these lines depended on growth form, but not on successional stage. When direct biomass measurements are not appropriate or possible, the relationships presented can be used to rapidly and non-destructively estimate biomass in the Boreal Plain riparian forests.

---

[1] This chapter is published. MacDonald, R.L., H.Y.H. Chen, J.M. Burke and E.E. Prepas. 2012. Relationship between aboveground biomass and percent cover of ground vegetation in Canadian Boreal Plain Forests. Forest Science: 58, 47-53.

2.2 Introduction

In forests, ground flora (the component of the understory that is < 1.5 m tall) affects tree regeneration and canopy succession (Kuusipalo 1983, Messier et al. 1998), nutrient cycling (Zavitkovski 1976, Weber and Vancleve 1981, Brumelis and Carleton 1989, Knops et al. 1996) and wildlife habitat (Johnson et al. 2003, Payer and Harrison 2003, Gunnarsson et al. 2004). In addition, ground flora is sensitive to environmental change, thus serving as a bioindicator of forest disturbance (Kern et al. 2006, Hart and Chen 2008). To estimate the aboveground abundance of ground flora, biomass is the ideal metric: it approximates productivity, is the basis to which other resources (e.g., soil nutrients) are related and is an important component of many hydrologic and ecosystem models (Kiniry et al. 2008). However, biomass data are difficult, time consuming and destructive to collect and thus may be inappropriate for temporal studies requiring repeated measures on the same plot. Rapid and non-destructive methods to estimate aboveground biomass of ground flora are needed to facilitate studies at the ecosystem level.

Studies in boreal forests in Alaska, Sweden and Finland have demonstrated that relationships exist between aboveground biomass and cover of many plant species growing in uplands (Alaback 1986, Jonasson 1988, Muukkonen et al. 2006). Percent cover analysis is typically used to estimate abundance of ground vegetation (Mueller-Dombois and Ellenberg 1974, Chiarucci et al. 1999) and is relatively simple to conduct. Since ground plant communities often exhibit high species richness (Zavitkovski 1976, Qian et al. 1998), modelling the biomass versus cover relationship of each species would be difficult and tedious. Species of a particular growth form (e.g., all species that are graminoids) should have similar biomass to cover ratios, given that this relationship is dependent on morphology and growth characteristics (Rottgermann et al. 2000, Muukkonen et al. 2006, Porté et al. 2009). Modelling ground flora biomass according to growth form simplifies model development and provides a sound link between physiological strategies and ecosystem processes (Chapin 1993).

Riparian zones represent a unique setting to examine the relationship between plant biomass and cover because they often exhibit a wide range of physical variability, including open and closed canopy conditions. The canopy is generally less dense than in the adjacent upland (Pabst and Spies 1999, Nierenberg and Hibbs 2000, Palik et al. 2003) and may exert less control on ground vegetation. Unlike upland vegetation, flora that grows in the active channel and floodplain is greatly influenced by hydrological disturbance events of varying frequencies and intensities (Naiman and Décamps 1997). This relationship is reciprocal as riparian vegetation affects surface water quality and quantity through the provision of ecological services including shading and controlling water temperature, stabilizing the bank, decreasing inputs of sediment and nutrient pollution and creating aquatic habitat through the input of organic matter (Brown and Krygier 1970, Vannote et al. 1980, Naiman and Décamps 1997, Hefting et al. 2005). Although relationships between biomass and percent cover have been developed for boreal uplands and peatlands (Alaback 1986, Muukkonen et al. 2006), there are no data documenting relationships between aboveground biomass and percent cover of understory vegetation in boreal riparian forests either in early or late seral stage forests. The objective of this study is to quantify relationships between aboveground biomass and percent cover of ground flora growing in early and late seral stage boreal riparian forests.

2.3 Materials and methods

2.3.1 Study Area

The Boreal Plain comprises approximately 20% of Canada's boreal forest and is located in central and northern Alberta, extending west into British Columbia and east through central Saskatchewan and southern Manitoba. The study area is located in the Lower Foothills sub-region of the Boreal Plain, approximately 20 km northwest of Whitecourt, Alberta. The climate is sub-humid and the precipitation is variable; long-term (1978 to 2009) mean annual precipitation recorded at a weather station at Whitecourt (elevation 782 m) ranged from 364 to 786 mm (Environment Canada 2010). The topography is undulating and occurs on moderately fine to fine-textured till or glaciolacustrine parent material. The typical canopy is dominated by lodgepole pine (Pinus contorta Dougl. ex Loud. var. latifolia Engelm), white spruce (Picea glauca (Moench) Voss), trembling aspen (Populus tremuloides Michx) and balsam poplar (Populus balsamifera L.) in well-drained sites, and black spruce (Picea mariana (Mill.) BSP) and tamarack (Larix laricina (DuRoi) K. Koch) in poorly drained sites. Common understory species on the Boreal Plain are low-bush cranberry (*Viburnum edule* Michx), green alder (*Alnus crispa* (Aiton) Pursh), prickly rose (Rosa acicularis Lindl), bunchberry (Cornus canadensis L.), wild sarsaparilla (Aralia nudicaulis L.), dewberry (Rubus pubescens RAF), big red stem moss (Pleurozium schreberi (Brid.) Mitt) and plume moss (Ptilium crista-castrensis (Hedw.) De Not.). In general, overstory and understory vegetation communities are less diverse relative to the central boreal forest in Canada (Qian et al. 1998). All sites originate from stand replacing fire circa 1940; early seral stage sites (> 80% canopy removal) were harvested during January to March 2004.

2.3.2 Vegetation Sampling

One hundred and fifty three - 1 m^2 ground vegetation sampling plots (64 and 89 from early and late seral stage, respectively) were established at 0, 5, 10, 15, 20, 25 and 30 m along randomly selected 30 m linear transects directly adjacent to the defined channels of streams draining seven headwater stream watersheds. Seven quadrats were placed along 21 transects, and six quadrats were placed along one transect due to the presence of a slash pile. Sampling was conducted during July 2010, when annual plant cover and biomass was at or near its maximum. Ocular estimations of cover were made in each sampling plot based on growth form — short forbs (< 50 cm), tall forbs (> 50 cm), ferns, clubmosses, horsetails, graminoids, dwarf shrubs and bryoids (bryophytes and lichens) — and then each plant was harvested by hand clipping at the root collar. If the cover of a particular growth form was > 10% in a sampling plot, then a random sub-sample (1 to 10%) of that growth form was taken, so that samples were manageable in the field. Harvested aboveground samples were stored in paper bags for up to 24 h at ambient temperature (5–33°C) until they could be processed in the laboratory. Plant material was then dried at 70°C for 48 h and weighed. For sub-samples, all biomass measurements were expressed as g m^{-2}. A total of 630 samples (269 and 361 samples from early and late seral stage sites, respectively) were used in this study.

2.3.3 Statistical Analyses

Data normality was tested using the Shapiro-Wilk test using SPSS version 18. Aboveground biomass and percent cover data for all growth forms were normally distributed; thus transformations were not required. Statistical significance was determined at $\alpha = 0.05$ for all tests. A one-way analysis of variance was used to compare mean percent cover and biomass data between the two seral stages for each of the eight growth forms. Simple linear regression analysis was performed on each of the eight growth forms to compare relationships between aboveground biomass and percent cover in early and late seral stages. Slopes were compared between the two seral stages with a two-tailed t-test (Zar 1996). If slopes did not differ, data for that particular growth form from both seral stages were pooled to fit the final regression. To evaluate the models, adjusted R-squared values were used. A two-tailed t-test was also used to compare among growth forms to determine if a coarser grouping could be used.

2.4 Results

In early seral stage plots, mean percent cover of graminoids was higher ($P < 0.001$) than in late seral stage plots, whereas mean percent cover of short forbs, ferns, clubmosses and bryoids was lower ($P = 0.028$, 0.008, 0.01 and < 0.001, respectively) than in late seral stage plots. By comparison, mean percent cover of tall forbs, horsetails and dwarf shrubs did not differ between the two seral stages ($P > 0.18$) (Table 1). Similarly, the mean biomass of graminoids was higher ($P = 0.01$) in the early than in late seral stage plots, and the mean biomass of ferns, clubmosses and bryoids was lower ($P = 0.022$, 0.007 and < 0.001, respectively) than in late seral stage plots (Table 2). However, the mean biomass of dwarf shrubs was higher ($P = 0.032$) in the early than late seral stage plots (Table 2), but percent cover of dwarf shrubs did not differ between early and late seral stages ($P = 0.18$) (Table 1). Mean biomass of short forbs, tall forbs and horsetails did not differ between the two seral stages ($P > 0.14$) (Table 2).

The slopes of regression lines describing biomass to percent cover relationships did not differ between the early and late seral stages for any of the growth forms (horsetails $P = 0.060$; graminoids $P = 0.112$; bryoids $P = 0.167$; clubmosses $P = 0.737$; ferns $P = 0.755$; short forbs and dwarf shrubs $P = 0.758$; tall forbs $P = 0.955$). Therefore early and late seral stage data were pooled for each growth form. Aboveground biomass was linearly related to percent cover for all eight growth forms (Table 3). Since the intercept did not differ from zero in the growth form data sets except for short forbs and horsetails (Table 3), and the regression function is known to pass through 0,0 (i.e., 0 g m^{-2} biomass will always equal 0% cover), all data sets were modelled with the intercept forced through the origin (Fig. 2). Percent cover explained 61% (ferns) to 93% (horsetails) of the variation in aboveground biomass ($P < 0.001$ in all cases). The pooled slopes of all growth forms differed ($P < 0.05$), including pteridophytes (ferns, clubmosses and horsetails) and therefore I retained eight growth forms.

Table 2.1 Mean (± 1 Standard Error) percent cover of eight understory growth forms in Canadian Boreal Plain riparian forests in early and late seral stages. (*$P < 0.05$, **$P < 0.01$, and ***$P < 0.001$).

Growth Form	**Early**	**S.E.**	**Late**	**S.E.**
Short forbs*	10.73	1.18	16.58	1.42
Tall forbs	5.25	1.16	6.69	7.61
Ferns**	4.67	1.76	6.59	0.76
Clubmosses**	3.00	1.00	10.00	1.24
Horsetails	5.45	1.32	10.51	2.79
Graminoids***	16.70	2.77	7.15	1.56
Dwarf shrubs	14.98	1.96	10.24	1.42
Bryoids***	7.46	2.09	32.50	4.42

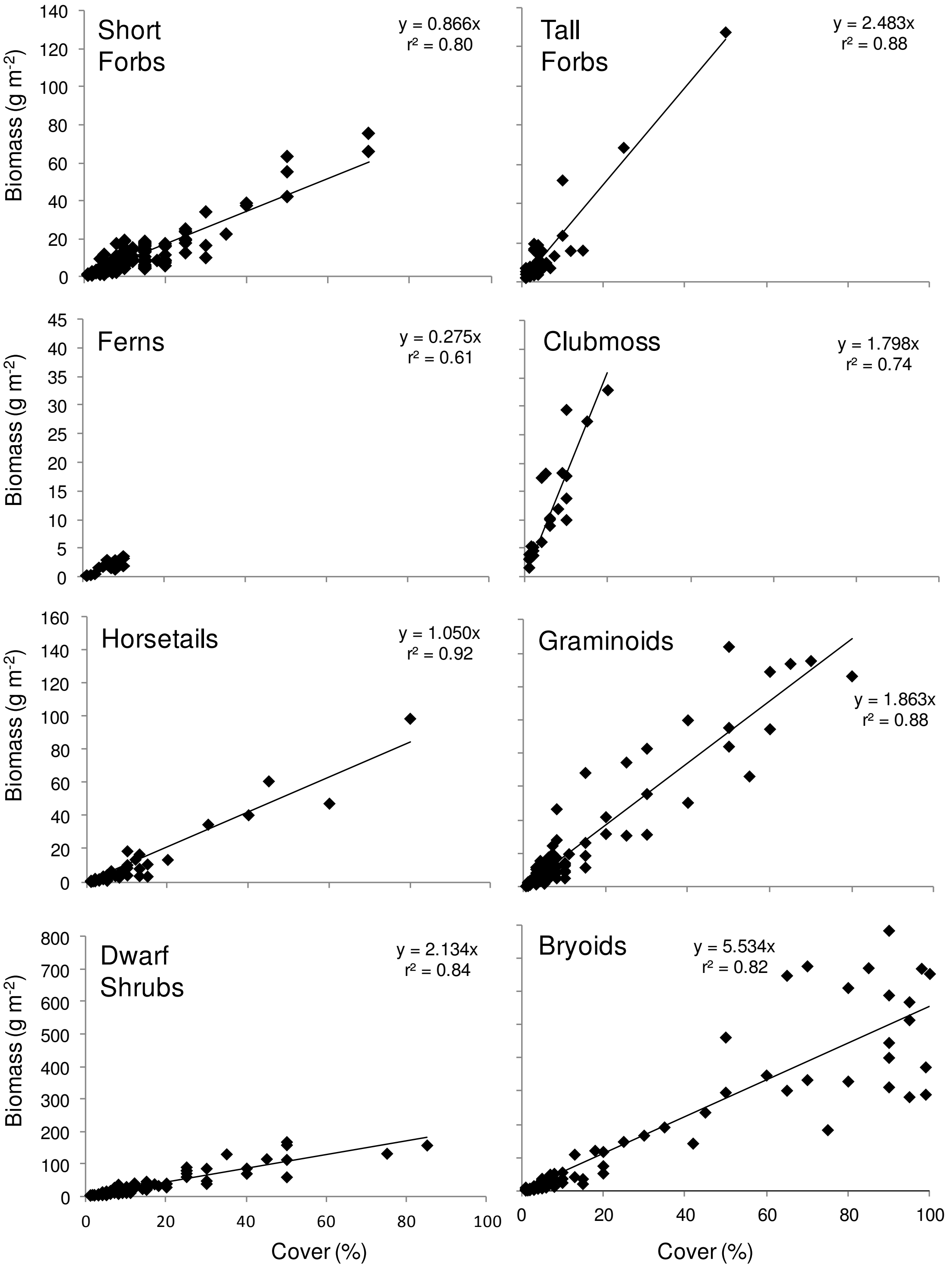


Figure 2.1 Simple linear regression of pooled early and late seral stage aboveground understory biomass versus percent cover based on eight growth forms in Canadian Boreal Plain riparian forests.

Table 2.2 Mean (± 1 Standard Error) aboveground biomass (g m^{-2}) of eight understory growth forms in Canadian Boreal Plain riparian forests in early and late seral stages. (*P < 0.05, **P < 0.01, and ***P <0.001).

Growth Form	**Early**	**S.E.**	**Late**	**S.E.**
Short forbs	9.50	1.23	13.46	1.51
Tall forbs	14.79	3.41	14.82	5.83
Ferns*	1.65	0.58	1.77	0.26
Clubmosses**	8.90	1.15	17.66	2.22
Horsetails	3.44	1.27	10.52	3.27
Graminoids***	33.24	5.93	13.72	3.67
Dwarf shrubs*	33.82	4.81	18.58	3.24
Bryoids***	29.61	9.97	175.83	27.7

Table 2.3 Outputs from simple linear regressions between aboveground biomass and percent cover for eight understory growth forms from early and late seral stage Canadian boreal riparian forests; where B_1 is the slope factor and B_0 is the intercept.

Growth Form	B_1	P_{B1}	B_0	P_{B0}	**n**	r^2
Short Forbs	0.926	<0.001	-1.393	0.048	136	0.81
Tall Forbs	2.463	<0.001	0.383	0.806	38	0.88
Ferns	0.265	<0.001	0.080	0.813	20	0.61
Clubmosses	1.574	<0.001	2.258	0.152	22	0.76
Horsetails	1.113	<0.001	-1.940	0.002	66	0.93
Graminoids	1.855	<0.001	0.268	0.857	97	0.88
Dwarf Shrubs	2.769	<0.001	-1.692	0.157	127	0.84
Bryoids	5.634	<0.001	-7.174	0.479	103	0.83

2.5 Discussion

In these Boreal Plain riparian ground flora samples, variation within growth forms coinciding with successional stage was reflected in the one-way analysis of variance. Total biomass of vascular plants was higher in early seral plots (105 g m^{-2}) than late seral plots (91 g m^{-2}). In contrast, total biomass of non-vascular plots was lower in early seral plots (27 g m^{-2}) than in late seral plots (176 g m^{-2}). The observed trends associated with succession are similar to previous reports (Zavitkovski 1976, MacLean and Wein 1977, Giese et al. 2003). Percent cover and biomass of graminoids were higher in early seral stage plots than late seral stage plots. Tall herbaceous plants like graminoids are expected to dominate in resource abundant environments, such as the sites in early seral stage, due to their greater competitive ability (rapid growth) to exploit light and nutrient resources (Tilman 1985, Caldwell 1987, Grime 2001). Mean biomass of dwarf shrubs was also higher in early than late seral plots; however their percent cover differed at lesser extent. This could be attributed to the tendency for low (~10–50 cm tall) spreading evergreen shrubs (e.g., Ledum groenlandicum, Vaccinium vitis-idaea) to be the most common dwarf shrubs in late seral stage plots. These spreading evergreen shrubs would have high percent cover per unit biomass. Conversely, the tall (~ 1 m tall) erect perennial shrubs (e.g., *V. edule*, Lonicera involucrata) common in early seral stage plots would have a low percent cover per unit biomass.

Mean percent cover and biomass of ferns, clubmosses and bryoids were lower in early than late seral stages. In addition, mean percent cover of short forbs was also lower in early plots. In an early seral stage forest, light levels, soil temperatures and organic debris are high relative to the period before canopy removal, which stimulates nutrient release (Gholz et al. 1985a, Hart and Chen 2006). This creates an environment favourable to ruderal species, or species specialized at exploiting productive habitats. Most ferns, clubmosses, bryoids and short forbs are able to tolerate stressful conditions, such as inhabiting resource poor environments, at the expense of being less competitive in productive habitats (Tilman 1985).

Allometric equations obtained from regression analysis clearly indicate a linear relationship between aboveground biomass and percent cover of ground plants in the riparian vegetation plots. Ferns had the smallest increase in biomass per unit cover, the lowest proportion of explained variance ($r^2 = 0.61$) and the smallest sample size ($n = 20$). The most commonly observed ferns in this study (i.e., Athyrium filix-femina, Dryopteris spp. and Gymnocarpium dryopteris) were morphologically highly variable and sparse thus contributing to the lower proportion of biomass explained by percent cover. A. filix-femina have rather large erect leaves, while Dryopteris spp. and G. dryopteris have small, fairly thin, horizontally oriented leaves. Short forbs (< 50 cm) had the second smallest increase in biomass with increasing percent cover, probably because the most common species observed in the plots (e.g., C. canadensis, A. nudicaulis and R. pubescens) tend to be relatively short with horizontal leaves. Although bryoids grow relatively low to the ground, they had the highest biomass to cover ratio. This relationship is likely due to the propensity of pleurocarpous mosses (e.g., P. schreberi, P. castris-canadensis and Hylocomium splendens) to form dense mats and thus often dominate the depauperate understory of late seral stage northern boreal forests (Carleton 1979, Alaback 1982, Nieppola and Carleton 1991). As expected, tall forbs (> 50 cm) had the second highest increase in aboveground biomass with increasing percent cover. Epilobium angustifolium, a tall plant with many stalkless, slightly vertically oriented leaves on the stem, was the most common species in this growth form. Surprisingly, dwarf shrubs had the third largest increase in biomass with increasing percent cover. Common dwarf shrub species used in this study (e.g., Vaccinium vitis-idaea, V. caespitosum, Gaultheria hispidula and L. groenlandicum) were fairly low spreading shrubs.

Linear regression models developed by Muukkonen et al. (2006) to predict biomass based on percent cover of upland dwarf shrubs in Finnish boreal pine forests had identical slopes as those developed for riparian dwarf shrubs in the present study ($B_1 = 2.1$). Muukkonen et al. (2006) found that the relationship between aboveground biomass and cover for bryoids was curvilinear, whereas I identified a linear relationship between the same variables. This divergence is most likely due to a distinct change in species composition with increasing cover in the input data used in the Finnish study. In contrast, the dominant species in my riparian bryoid samples remained constant throughout the entire range of my input data and included both pleurocarpous mosses (e.g., P. schreberi and H. splendens), as well as acrocarpous mosses (e.g., Plagiomnium spp. and Polytrichium commune). In upland conditions, only a few moss species form extensive mats (i.e., dominant pleurocarpous mosses), whereas in riparian conditions, many moss species can dominate. Therefore the bryoid composition and abundance of each riparian plot varied widely in the present study.

Canopy in upland communities has been shown to be a driver of understory species abundance and composition (Økland and Eilerston 1996, Hart and Chen 2008). Given that there is a lack of evidence for coupling of the canopy and understory strata in riparian flora (Korol 1996, Lyon and Sagers 1998, Decocq 2002) canopy type was not included in this study. For example, Korol (1996) compared 134 boreal riparian vegetation plots, under differing canopy types approximately 650 km east of my study area and reported a large amount of overlap and little differentiation between understory communities, likely because the riparian understory community is more driven by hydrological processes than canopy composition.

The strong allometric relationships between biomass and percent cover reported in this study present a way to approximate understory biomass when a large number of sample plots are needed. In most ground vegetation studies, hundreds to thousands of plots are sampled; harvesting biomass measurements at all of these plots can be incredibly difficult. Depending on the study objective, understory biomass may need to be harvested at maximum annual growth. In the boreal forest, this occurs between July and August, thus temporally constraining field sampling. From the present study, the time needed for one person to obtain biomass measurements for sampling a square meter plot was approximately 60 minutes in the field, as well as an additional 30 minutes in the laboratory. In contrast, sampling percent cover in the same plot took the same person approximately 20 minutes in the field and no time in the laboratory, and therefore required less than 25% of the time. A study in Finland that modelled understory biomass as a function of percent cover and height reported that the two factors accounted for 80% of the variation in biomass; however cover alone accounted for 70% of the variation in biomass (Kuusipalo 1983). Measuring heights of individual plants requires a large time investment and likely is not warranted as height data may not vastly improve the model.

2.6 Conclusion

This study developed allometric equations from destructively sampled biomass measurements for eight ground-layer growth forms (short forbs, tall forbs, ferns, clubmosses, horsetails, graminoids, dwarf shrubs and bryoids). While percent cover and biomass for each given life form generally differed between the early and late seral stages, allometric functions did not differ, resulting in common, linear relationships between biomass and cover. My models using percent cover as the predictor explained 61 to 93% of the variation in biomass, representing a promising approach to estimate biomass when large sample plots are studied simultaneously. If the level of accuracy is acceptable within a given study's design and when direct biomass measurements are not appropriate, the relationships presented here can be used to rapidly and non-destructively estimate ground vegetation aboveground biomass from percent cover.

CHAPTER 3 : COMPOSITIONAL STABILITY OF BOREAL RIPARIAN UNDERSTORY VEGETATION AFTER CLEARCUT HARVESTING

3.1 Abstract

Understanding factors that contribute to the compositional stability of a community following clearcut harvesting is central to predict how boreal forests respond to altered disturbance regimes in the Anthropocene. I hypothesized that streamside plant communities would have higher compositionally stability following disturbance than upland communities due to their inherently higher plant species richness and less abundant bryoid species. I sampled understory vegetation at eight Canadian boreal headwater stream sites: four were winter harvested to the stream and four were unharvested. Species cover were measured during the summer 2003 (Yr 0), 2004(Yr 1), 2008 (Yr 5) and 2010 (Yr 7) along the streams. Non-metric multidimensional scaling was used to ordinate vegetation plots using species cover, and then measured vector length in the ordination space to quantify floristic dissimilarity (FD) of each sample plot between Yr 0 and Yrs 1, 5, and 7, an inverse measure of compositional stability. FD increased with distance from stream in harvested sites, but not in unharvested sites. In harvested sites, FD was negatively related to pre-harvest species richness and positively related to pre-harvest bryoid cover, explaining 12% and 49% of the variation in FD, respectively. Results demonstrate that streamside understory plant communities were compositionally more stable relative to upland communities following clearcut harvesting. Although my results support the diversity-stability hypothesis, the strong predictive power of bryoid cover indicates that plant functional group composition prior to disturbance is a major factor determining plant compositional stability across boreal riparian ecotones.

3.2 Introduction

Species diversity is critical for maintaining ecosystem services (Isbell et al. 2011), and may also play an important role in the capacity of ecological communities to cope with environmental changes (Tilman and Downing 1994). Increased anthropogenic perturbation and continued loss of biodiversity have raised concerns regarding sustainability of ecosystem functioning worldwide (Goldberg and Barton 1992, Isbell et al. 2011). In the boreal forest, understory flora is an important driver of nutrient cycling and overstory succession (Nilsson and Wardle 2005), and accounts for the majority of plant diversity (Gilliam 2007). Understanding factors that contribute to the stability of understory flora following clearcut harvesting is a critical component in assessing how boreal forests respond to altered disturbance regimes in the Anthropocene (Paquette and Messier 2010).

For over half a century, ecologists have been ensnared by the concept that greater biodiversity leads to increased ecosystem stability (e.g., Elton 1958, May 1974, Pimm 1984, Frank and McNaughton 1991, Tilman et al. 2006). Prominent in these investigations is the ‘insurance hypothesis’ (Walker 1992, Naeem et al. 1994, Tilman and Downing 1994, Yachi and Loreau 1999), i.e., communities with higher biodiversity are more likely to contain species that can survive a given environmental perturbation. Thus, high biodiversity impedes or prevents the establishment of non-resident colonizing species and diverse communities are more able to resist community change. However, this theory has been widely debated, both theoretically (May 1974, King and Pimm 1983) and empirically (Macarthur 1955, McNaughton 1977, Frank and McNaughton 1991, Tilman 1996, Tilman et al. 2006). These divergent results are likely a result of the many definitions of stability, inherently different dynamics among systems, and perturbation types (Ives and Carpenter 2007). Positive stability and diversity relationships are common for aggregate ecosystem properties (i.e., biomass, productivity, and nutrient cycling) of grassland or herbaceous plant communities, in which diversity is directly manipulated (Ives and Carpenter 2007). Compositional stability, the measure of change in community membership and abundance following a disturbance, has also been studied under manipulated grassland experiments (e.g., McCann 2000, Foster et al. 2002, Wang et al. 2010) and in natural communities undergoing natural or man-made disturbances (e.g., O'Neil 1976, Frank and McNaughton 1991, De Grandpré and Bergeron 1997) with contrasting results. Positive relationships between diversity and compositional stability result if diversity reduces extinction and colonization rates, but this facilitation would likely be the result of extrinsic factors such as resource availability and disturbance regime. Thus, understanding compositional stability and diversity relationships remains elusive, particularly in the context of press perturbations (McCann 2000, Ives and Carpenter 2007).

Species or functional group composition within the vegetation community is also an important factor in predicting ecosystem responses to disturbance (Wardle et al. 2000, Lavorel and Garnier 2002, Haddad et al. 2008, Hart and Chen 2008). For example, herbaceous species in boreal forests may respond differently to stand replacing disturbances than many bryoid (bryophytes and lichens) species. Following canopy removal, light levels, air and soil temperatures and soil resource availability increase, creating an environment that is generally more favourable for vascular plants (Gholz et al. 1985b, Hart and Chen 2006). These conditions, as well as high pH and low moisture content in the thin organic layer following canopy removal, exceed the tolerance of many non-vascular plants (Fenton and Frego 2005, Hylander 2005, Åström et al. 2007). Therefore, bryoid cover typically declines following clearcut harvesting (Fenton and Frego 2005, Nelson and Halpern 2005, Frego 2007, Hart and Chen 2008). In systems like the boreal forest, where bryoid species contribute a major proportion to understory diversity and productivity, compositional stability may be strongly influenced by the abundance of bryoid species, irrespective of overall species diversity.

Headwater stream riparian ecosystems often represent a high to low diversity gradient (Naiman et al. 1993), as well as distinct shifts in species composition from stream edge to upland (Lamb and Mallik 2003, Dynesius et al. 2009). The diversity and compositional gradients reflect hydrological disturbance events, the ability of fluvial systems to act as conduits for the dispersal of propagules (Thebaud and Debussche 1991, Pysek and Prach 1993), and the decrease of understory resource availability (i.e., light and soil moisture) with lateral distance from the active channel (Gregory et al. 1990, Pabst and Spies 1999, Nierenberg and Hibbs 2000, Goebel et al. 2003). Ruderal species (adapted to high disturbance and low resource stress) like graminoids and tall forbs are more likely to dominate near the stream, whereas cover of stress tolerant species (adapted to low disturbance and high resource stress) like short forbs and bryophytes increase in dominance with distance from the stream. Thus understory plant assemblages growing further into the upland may be less tolerant to stand replacing disturbance events than streamside communities (Dynesius et al. 2009).

Here, I measure the compositional stability of understory plant communities across boreal riparian ecotones following clearcut harvesting. The objectives of this study are to (1) compare compositional stability following clearcut harvesting between streamside and upland understory communities; (2) test whether compositional stability is related to pre-harvest species diversity; and (3) determine whether pre-harvest total bryoid cover affects compositional stability. I hypothesize that compositional stability following clearcut harvesting decreases from stream edge to upland along the gradient of decreasing diversity and increasing bryoid cover.

3.3 Materials and methods

3.3.1 Study Areas

The study was conducted in the Lower Foothills sub-region of the Boreal Plain, approximately 20 km northwest of Whitecourt, Alberta, Canada. The climate is sub-humid and the precipitation is variable: long-term (1978 to 2009) total annual precipitation recorded at Whitecourt (elevation 782 m) ranged from 364 to 786 mm (Environment Canada 2011a). The rolling topography occurs on moderately fine to fine-textured till or glaciolacustrine parent material. The characteristic forest canopy is dominated by lodgepole pine (Pinus contorta Dougl. ex Loud. var. latifolia Engelm), white spruce (Picea glauca (Moench) Voss), trembling aspen (Populus tremuloides Michx) and balsam poplar (Populus balsamifera L.) on well-drained sites, and black spruce (Picea mariana (Mill.) BSP) and tamarack (Larix laricina (DuRoi) K. Koch) on poorly drained sites. Understory vegetation is depauperate relative to central Canadian boreal systems (Qian et al. 1998). Forest of the study area originated from stand replacing fire in 1940.

3.3.2 Experimental Design and Data Collection

Four headwater stream sites were clearcut to the stream during January to March 2004. Chemical site preparation consisted of aerial application of Vision® (Monsanto Co., St. Louis, Mo.) in August 2004, which was applied >30 m away from the stream, and thus did not directly influence my study plots. I also sampled four headwater stream reference sites that were not harvested to monitor temporal understory vegetation dynamics without disturbance.

At each site, three randomly located, 30-m long transects were established running perpendicular from the stream to the upland transition zone. Two 1-m^2 understory (the component of the understory < 1.5 m tall) vegetation plots were randomly located within each of the following distance ranges from the stream channel bank: 0 to 5 m, 5 to 10 m, 10 to15 m, 15 to 20 m, 20 to 25 m and 25 to 30 m, for a total of 12 plots per transect and 36 plots per site. Transects and permanent vegetation plots were marked with GPS, as well as physically marked with corner and center posts.

Vegetation sampling was conducted during the periods of peak vegetation cover in the summer (July through August) in 2003 (Yr 0) and the summers of 2004 (Yr 1), 2008 (Yr 5) and 2010 (Yr 7). I attempted to identify all plants to species in the field; however some plants, e.g., Carex spp., were identified only to genus due to the difficulty for their identification without flowers or fruits. Percent cover (0-100%) of each plant species or genus in each plot was estimated by eye following the procedure described by Mueller-Dombois and Ellenberg (1974).

3.3.3 Statistical Analyses

We quantified temporal compositional stability by measuring changes in species composition after disturbance relative to before disturbance (or Yr 0) (sensu Halpern 1988). Within each site, species-specific percent cover of the 6 1-m^2 plots within each distance range at each sampling time (Yr 0, 1, 5, or 7) were averaged to represent mean response of a sampling unit, i.e., a specific distance range within each site, prior to statistical analysis . Trends in the compositional data were examined using nonmetric multidimensional scaling (NMS). NMS is well suited for community data, because it uses non-metric rank ordering to perceptually map data; NMS avoids assumptions of normality and homogeneity of variance that are required in traditional ordination techniques (McCune and Grace 2002). NMS was carried out using PC-ORD version 5 (McCune and Grace 2002, McCune and Mefford 2005) set to the slow and thorough auto-pilot mode to select the optimal solution (i.e., dimensionality). Floristic dissimilarity (FD) from Yr 0 to Yrs 1, 5 and 7 of each sampling unit was measured as Euclidian distance in NMS ordination space. Compositional stability is inversely related to the Euclidian distance (sensu Halpern 1988): stability is at maximum when the sample unit maintains its initial position in ordination space (i.e., Euclidian distance = 0).

To test the effects of harvesting, distance from stream, and Yr 0 attributes (i.e., species richness and bryoid cover) on FD, I conducted two repeated measures general linear models (rGLM) with type III sums of squares. I used harvesting as a categorical fixed factor, distance from stream as a continuous fixed factor, one of the two Yr 0 attributes as a continuous fixed factor for each model, FD as the response variable, and sampling year as the repeated measure. Because of multicollinearity between distance from stream and Yr 0 attributes (i.e., species richness and bryoid cover) the full factorial model was modified to eliminate interaction terms between the correlated explanatory variables and thus enhance the reliability and interpretation of the rGLM (Odum and Pinkerton 1955). Each model was expressed as:

$$\begin{aligned} Y_{ijklmn} &= \mu + H_i + D_j + HD_{ij} + C_k + HC_{ik} + \varepsilon_{l(ijk)} \\ &\quad + T_m + HT_{im} + DT_{jm} + HDT_{ijm} + CT_{km} + HCT_{jkm} + \varepsilon_{n(ijkm)} \end{aligned} \tag{3.1}$$

where Y_{ijkl} is FD; μ is the overall mean; H_i ($i = 1, 2$) is harvesting; D_j is distance from stream; C_k is the Yr 0 attribute (species richness or bryoid cover); $\varepsilon_{l(ijk)}$ is the error term associated with between-subjects; T_m is sampling year; $\varepsilon_{n(ijklm)}$ is the error term associated with within-subjects. Species richness is a measurement of the total number of vascular and non-vascular species in each sample unit. Total bryoid cover was the summation of percent cover of all non-vascular species in each sampling unit.

Floristic dissimilarity was natural log-transformed to satisfy linear model assumptions of normality and homogenous variances. For each rGLM, I tested the sphericity (i.e., symmetry of the covariance matrix) with Mauchly's criterion test and applied the Huynh-Feldt correction to my results if the assumption was violated (Huynh and Feldt 1976). I calculated the effect size (η^2) to estimate the proportion of the total variance attributed to an effect (Reeves et al. 2006).

3.4 Results

NMS ordination identified a three-dimensional solution with a stress of 6.32. Axes 1, 2 and 3 had r^2 values of 0.40, 0.21 and 0.17, respectively, and therefore the resultant model accounted for 78% of the total variability of the understory flora species (see Appendix 1).

FD between Yr 0 and the following periods was greater in harvested than unharvested sites for all three sampling years ($P \leq 0.002$; Figs. 1a-c). In harvested sites, FD increased with distance from stream ($P \leq 0.02$; Figs. 1a-c), but not in the unharvested sites (Figs. 1a-c). Total species richness in Yr 0 communities decreased ($P = 0.007$; $r^2 = 0.15$), and bryoid cover increased ($P < 0.001$; $r^2 = 0.21$) with increasing distance from stream.

The effect of distance to stream was not detectable when Yr 0 attributes (species richness and bryoid cover) were added to the full models ($P \geq 0.07$; Tables 1 and 2). FD differed strongly with harvesting and Yr 0 species richness with the species richness related variables explaining approximately 12% of the variation in FD, but not with sampling year (Table 1). In harvested sites, FD was negatively related to Yr 0 species richness in all post-harvest years

(Table 1; Fig. 2a). However, there was no relationship between FD and Yr 0 species richness in unharvested communities (Fig 2b).

FD was strongly related to Yr 0 total bryoid cover with the bryoid cover related variables explaining 49% of the variation in FD (Table 2). In harvested sites, FD was positively related to Yr 0 bryoid cover (Fig. 2c). Conversely, FD was negatively related to bryoid cover in unharvested sites (Fig. 2d). Similar to the analysis using Yr 0 species richness as a predictor, there were no differences in FD among sampling years ($P = 0.11$, Table 2).

Table 3.1 Floristic dissimilarity (natural log transformed vector length between Yr 0 and Yrs 1, 5, and 7 in NMS ordination space) in relation to harvesting, distance from stream, species richness, and sampling year.

Source	df	F	P	η^2
Between subjects				
Harvesting (H_i)	1	11.61	0.001	0.22
Distance from stream (D_j)	1	2.45	0.13	0.06
Harvesting x distance from stream (HD_{ij})	1	1.80	0.19	0.04
Species richness (C_k)	1	0.13	0.73	<0.01
Harvesting x species richness (HC_{ik})	1	5.40	0.03	0.11
Error 1 ($\varepsilon_{l(ijk)}$)	42			
Within subjects				
Sampling year (T_m)	2	1.64	0.20‡	0.04
Harvesting x sampling year (HT_{im})	2	0.66	0.52‡	0.02
Distance from stream x sampling year (DT_{jm})	2	0.66	0.52‡	0.02
Harvesting x distance from stream x sampling year (HDT_{ijm})	2	0.04	0.96‡	<0.01
Species richness x sampling year (CT_{km})	2	3.36	0.06‡	0.07
Harvesting x species richness x sampling year (HCT_{ikm})	2	0.32	0.72‡	0.01
Error 2 ($\varepsilon_{n(ijklm)}$)	84			

‡ Huynh-Feldt correction was applied to correct for sphericity

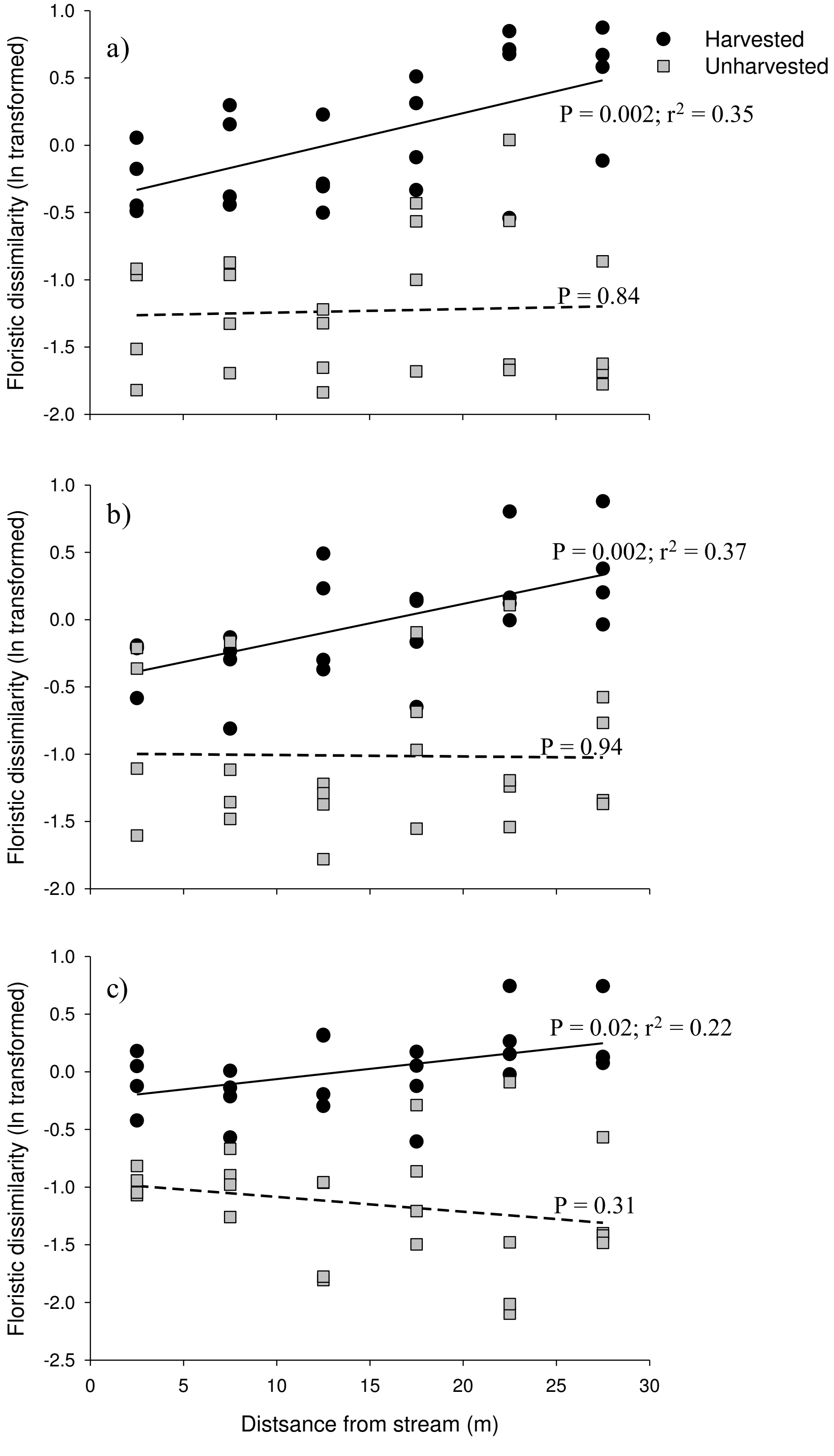


Figure 3.1 Floristic dissimilarity in relation to distance from stream in harvested and unharvested sites between Yr 0 and (a) Yr 1, (b) Yr 5, and (c) Yr 7.

Table 3.2 Floristic dissimilarity (natural log transformed vector length between Yr 0 and Yrs 1, 5, and 7 in NMS ordination space) in relation to harvesting, distance from stream, bryoid cover and sampling year.

Source	df	F	P	η^2
Between subjects				
Harvesting (H_i)	1	10.99	0.002	0.21
Distance from stream (D_j)	1	3.53	0.07	0.08
Harvesting x distance from stream (HD_{ij})	1	0.24	0.63	0.01
Bryoid cover (C_k)	1	3.53	0.07	0.08
Harvesting x bryoid cover (HC_{ik})	1	28.51	<0.001	0.41
Error 1 ($\varepsilon_{l(ijk)}$)	42			
Within subjects				
Sampling year (T_m)	2	2.31	0.11‡	0.05
Harvesting x sampling year (HT_{im})	2	0.96	0.38‡	0.02
Distance from stream x sampling year (DT_{jm})	2	0.66	0.52‡	0.02
Harvesting x distance from stream x sampling year (HDT_{ijm})	2	0.14	0.87‡	<0.01
Bryoid cover x sampling year (CT_{km})	2	2.36	0.10‡	0.05
Harvesting x bryoid cover x sampling year (HCT_{ikm})	2	0.08	0.92‡	<0.01
Error 2 ($\varepsilon_{n(ijklm)}$)	84			

‡ Huynh-Feldt correction was applied to correct for sphericity

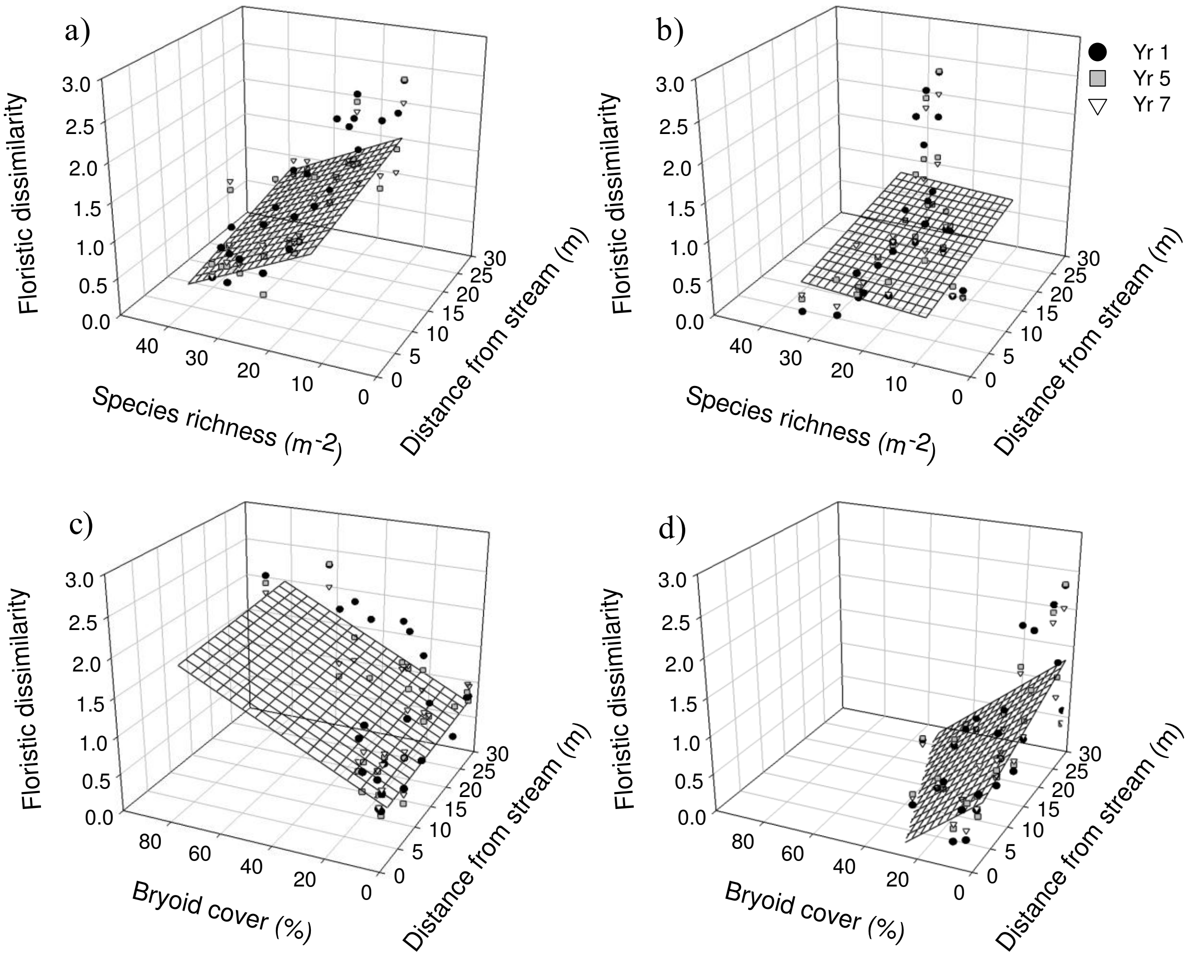


Figure 3.2 Floristic dissimilarity in relation to distance from stream and Yr 0 community attributes: understory species richness in (a) harvested and (b) unharvested sites; and bryoid cover in (c) harvested and (d) unharvested sites.

3.5 Discussion

Across boreal riparian ecotones, understory plant communities following harvesting tended to shift. The lower compositional stability after harvesting is consistent with previous understory vegetation studies in boreal and temperate forests (O'Neil 1976, Halpern 1988, De Grandpré and Bergeron 1997). Furthermore, my study represents one of the first to demonstrate that compositional stability after harvesting decreases from stream to upland in boreal forests (see Dynesius et al. 2009). My results provide direct evidence for a lateral pattern of compositional stability across riparian ecotones; however, mechanisms for the higher compositional stability near the stream are complex, involving multi-causalities.

First, compositional stability is positively correlated with pre-harvest species richness along the streams. This result generally supports the diversity-stability hypothesis (Elton 1958, Pimm 1984, Frank and McNaughton 1991, Tilman et al. 2006, Ives and Carpenter 2007), and it is consistent with the positive relationship between understory compositional stability following gap creation and initial species diversity observed in the eastern boreal forest of Canada (De Grandpré and Bergeron 1997). In contrast, empirical studies in both natural (McCann 2000) and experimentally manipulated grasslands (Foster et al. 2002, Wang et al. 2010) have reported negative relationships between compositional stability and diversity following disturbance events typical of their native environment. The contrasting diversity-stability relationships may be attributed to different mechanisms structuring communities in canopy versus understory systems. Competition exerts strong controls on the structure of communities in canopy systems (Goldberg and Barton 1992, Gurevitch et al. 1992). However, tolerating low resource availability (i.e., light), rather than competition, may have a stronger influence on the understory communities in the boreal forest (Hart and Chen 2008). It appears that compositional stability and diversity relationships remain open for further investigation.

Second, compositional stability following harvesting was strongly negatively related to total bryoid cover that increased from stream to upland. The most frequent and abundant upland bryophyte species (i.e., Pleurozium schreberi, Hylocomium splendens, and Ptilium crista-castrensis) in our study prior to disturbance are generally intolerant of the environmental conditions of early seral systems and declined in abundance, and in some sample plots, they were extirpated, following harvesting. Similar observations were made previously in boreal forests (Bock and Van Rees 2002, Fenton and Frego 2005). These results indicate that the difference in plant functional group composition along my boreal forest streams prior to disturbance is a strong driver for compositional stability when disturbed (McCann 2000).

Third, there are multiple causes for the gradients of diversity and dominance of bryoid species along the streams. The higher pre-harvest species richness and the lower bryoid cover near the streams are a result of higher resource availability and more frequent hydrological disturbances compared to upland (Naiman et al. 1993). Species closer to the stream are generally adapted to grow in a resource rich environment highly influenced by stream hydrology. In upland conditions, the forest canopy drives the composition of the understory strata by exerting strong controls on resource availability (e.g., light, nutrients and water) (Gurevitch et al. 1992, Hart and Chen 2008), as well as providing detritus inputs (Whitney and Foster 1988, Saetre et al. 1997). In contrast, there may not be as strong a coupling of the canopy and understory strata in streamside plant assemblages as there is in the upland (Lyon and Sagers 1998, Decocq 2002). This suggests that streamside communities may be primarily driven by stream hydrology rather than the canopy, and therefore may be better able to cope with canopy replacing perturbations. However, it is not my intent (nor possible) to partition the relative contributions of inherently correlated species richness or bryoid cover and resource availability, microclimate, and disturbance regime from stream to upland. Future work may consider decoupling these factors for a better understanding of the mechanisms driving understory compositional stability following harvesting.

3.6 Conclusions

I showed that compositional stability of understory vegetation, including vascular and bryoid species, after harvesting decreases from stream to upland in boreal forests. Compositional stability was related positively to pre-harvest species richness and negatively to bryoid cover, with the former decreasing and the latter increasing from stream to upland. While my results provide support for the diversity-stability hypothesis, the strong predictive power of bryoid cover indicates that plant functional group composition prior to disturbance is a major factor determining compositional stability of plant communities along boreal riparian ecosystems. However, the coupling influence of stream hydrology that drives community characteristics such as diversity and plant functional group composition from stream to upland makes it difficult to draw strong conclusions regarding relationships between compositional stability, diversity, and plant functional group composition.

CHAPTER 4 : INFLUENCE OF HARVESTING ON BOREAL RIPARIAN UNDERSTORY VEGETATION

4.1 Abstract

Harvesting has become a globally significant stand-replacing disturbance event. In the boreal forest, understory vegetation accounts for the majority of floristic diversity and affects overstory succession and productivity, nutrient cycling, and wildlife habitat. In riparian forests, understory vegetation also plays an important functional role by reducing erosion, stabilizing the stream channel, and regulating water quality and quantity. Despite this critical importance, effects of harvesting on understory plant communities in riparian forests are still poorly understood. Using pre- and post-harvest data, I quantified how riparian harvesting affects understory vegetation species diversity, abundance, turnover, and composition and how disturbance-response relationships vary from stream edge to uplands. I predicted that changes in the plant community following logging disturbance will be greater with increasing distance from the stream channel. I found that streamside communities harvested with or without a 30 m riparian buffer, were maintained to a condition similar to uncut forests. However, upland communities were less resistant to overstory harvest, relative to streamside communities, and subsequently colonized by grasses, forbs, and tall shrubs; many of which were present in pre-harvest riparian plots. My results indicate that streamside understory vegetation is inherently more resilient to stand-replacing disturbance than upland assemblages. Higher moisture availability and shading from tall shrubs associated with riparian habitat buffers the effect of harvesting on shade-tolerant species in streamside plots and thus the response to harvesting is not as marked as it is in the uplands. My results

highlight that understory disturbance response relationships can differ within a small spatial scale (i.e., 30 m) based on habitat characteristics, such as moisture regime, that drive community composition.

4.2 Introduction

Understanding mechanisms that control understory (i.e., ground and shrub strata) plant diversity and composition is important for sustainable forest management since understory vegetation, despite being small in stature in comparison with overstory trees, accounts for the majority of floristic diversity (Halpern and Spies 1995, Roberts and Gilliam 2003) and affects overstory succession and productivity(Connell and Slatyer 1977, Royo and Carson 2006, Ilisson and Chen 2009), nutrient cycling (Weber and Vancleve 1981, Johnson and Curtis 2001, Nilsson and Wardle 2005) and wildlife habitat (Johnson et al. 2003, Payer and Harrison 2003).In the fire-driven North American boreal forest, with increased resource extraction, forest harvesting has become an important stand-replacing disturbance for the past several decades. Overstory harvesting and associated ground disturbance may alter understory plant communities directly through increasing mortality of individuals, propagules, local populations or groups of species, or indirectly by varying environmental conditions, habitat heterogeneity, and resource availability(Halpern and Spies 1995, Roberts and Gilliam 1995, Bergeron and Harvey 1997, Scheller and Mladenoff 2002). Both direct and indirect processes result in well documented directional shifts in understory plant communities affecting both species diversity and composition (e.g., Halpern 1988, Reich et al. 2001, Hart and Chen 2008).Despite the critical importance of understory vegetation in boreal forest ecosystems, how forest harvesting affects understory species diversity, abundance, turnover and composition in riparian forests is still poorly understood.

The contribution of understory vegetation in riparian forests to overall diversity and productivity greatly exceeds their spatial extent across the landscape. Hydrological disturbance events (i.e., erosion of the soil surface and abrasion by suspended sediment and debris) and the ability of fluvial systems to acts as conduits for the dispersal of propagules result in dynamic streamside communities that are highly heterogeneous in space and time (Naiman and Décamps 1997). Laterally, frequency and severity of flood disturbance typically decline with increased distance from the active channel, paralleled by an increase in ground-water depth. Along this same gradient, understory light availability generally decreases as tree density increases (Nierenberg and Hibbs 2000, Lamb and Mallik 2003, Palik et al. 2003). Resource quantity and heterogeneity of streamside habitats, imparted by hydrological processes and disturbance regimes, is reflected in the life-history strategies, productivity, and diversity of the plant community (Naiman et al. 1993). In the boreal forest, streamside communities harbor a variety of species and functional groups, including generalist plant species (which also inhabit the uplands), specialized species adapted to streamside habitats (riparian obligates), and early successional species adapted to productive habitats at the trade-off of being less competitive in resource stressed environments (Lamb et al. 2003, Dynesius et al. 2009, Biswas and Mallik 2010); whereas, boreal upland understory communities are more commonly dominated by shade tolerant species (Nilsson and Wardle 2005, Hart and Chen 2008). Since a community's response to disturbance depends on the traits of its members (Noble and Slatyer 1980), understory plant communities in riparian forests may not respond to logging in the same manner as those in upland forests.

Through a carefully controlled field experiment using pre- and post-harvest data, I quantify how harvesting treatments (i.e., cut to shore, riparian buffers and uncut) affect understory species diversity, composition, and turnover over seven years. I also test if the treatment effects change with distance from the stream channel (i.e., from stream edge to uplands). Based on the different processes that drive understory communities among habitats, I predict that changes in the plant community following logging disturbance will be greater with increasing distance from the stream channel.

4.3 Methods and Materials

4.3.1 Study Area

The study is located in the Lower Foothills sub-region of the Boreal Plain, approximately 20 km northwest of Whitecourt, Alberta. The climate is sub-humid with a mean annual precipitation of 577 mm recorded at a weather station at Whitecourt (elevation 782 m) (Environment Canada 2010). Rolling topography is a common feature of the study area. Soils originated from moderately fine to fine-textured till or glaciolacustrine parent material. The characteristic canopy is dominated by lodgepole pine (Pinus contorta Dougl. ex Loud. var. latifolia Engelm), white spruce (Picea glauca (Moench) Voss), trembling aspen (Populus tremuloides Michx) and balsam poplar (Populus balsamifera L.) in well-drained sites, and black spruce (Picea mariana (Mill.) BSP) and tamarack (Larix laricina (DuRoi) K. Koch) in poorly drained sites (Ecological Stratification Working Group, 1996). Understory vegetation is depauperate relative to other areas of the Canadian boreal forest (Qian et al. 1998).

4.3.2 Experimental Design and Data Collection

Twelve headwater stream sites, ranging in 0.5 to 1 m in width, were randomly selected in the study region to receive the following treatments; uncut (reference), riparian buffer, and cut-to-shore, each with four replicates. All selected sites originated from stand replacing fire in

1940.Uncut sites were undisturbed (i.e., no forestry activity in the adjacent upland). Buffer sites were clearcut with a 30 m wide un-harvested forest strip adjacent to the stream channel. Cut-to-shore sites were clearcut to the edge of the stream channel. Tree-length harvesting, i.e., trees were felled, topped, and delimbed at the stump before being dragged to roadside, was conducted during January to March 2004.

At each site, three randomly located, 30-m long transects were established running perpendicular from the stream to the upland. Along each transect, two 1-m^2understory vegetation plots were randomly located within each of the following distance ranges from the stream bank: 0 to 5 m, 5 to 10 m, 10 to15 m, 15 to 20 m, 20 to 25 m and 25 to 30 m, for a total of 12 plots per transect and 36 plots per site. Percent cover (0-100%) of each vascular and non-vascular plant species in each plot was estimated by eye (Mueller-Dombois and Ellenberg 1974). All plants were identified to species with an exception of a few that were identified to genus, since it was not feasible to identify them to species in the field without flowers or fruits (e.g., Carex spp., Salix spp. and Viola spp.). Vegetation sampling was conducted during the periods of peak vegetation cover in the summer (July through August) prior to treatment, i.e., Yr 0 (2003) and the summers of Yrs 1 (2004), 5 (2008) and 7 (2010) after treatment. Within each site, species cover data of the 6 plots at each distance range were averaged to derive a mean.

4.3.3 Statistical Analyses

Species Richness, Abundance and Turnover

Species richness (S) was used as a measurement of diversity, which is the total number of species in each sample plot. Abundance was quantified through a summation of total species percent cover in each sample plot. To quantify species dynamics among multiple measurements, a species turnover rate index (T) for each sampling plot that includes both colonization and local extirpation from two successive measurements was calculated as Bakker et al. (2003):

$$T = 1 - (\text{number of species present at both } t \text{ and } t+1)/[(S_t+S_{t+1})/2] \qquad [4.1]$$

Where S_t and S_{t+1} are species richness at time t and t+1, respectively. T can range from 0 to 1, indicative of no species turnover to a complete change in community composition, between two successive measurements.

To test the effects of harvesting and distance from stream on total, vascular and non-vascular species richness, abundance and turnover, the following repeated measures general linear models (rGLM) with type III sums of squares:

$$Y_{ijklm} = \mu + H_i + D_j + H \times D_{ij} + \varepsilon_{(ij)k} + T_l + H \times T_{il} + D \times T_{jl} + H \times D \times T_{ijl} + \varepsilon_{(ijl)m} \qquad [4.2]$$

where Y_{ijklm} is species richness, total abundance or turnover; μ is the overall mean; H_i ($i = 1, 2, 3$) is the effect of harvesting, D_j is distance from stream; $\varepsilon_{(ij)k}$ is the error term associated with between-subjects; T_l is the effect of the sampling year; $\varepsilon_{(ijkl)m}$ is the error term associated with within-subjects. For each rGLM, in addition to testing data normality and homogeneity of variances, I assessed the sphericity (i.e., symmetry of the covariance matrix) with Mauchly's criterion test and applied the Huynh-Feldt correction to the results if the assumption was violated at $P = 0.05$ (Huynh and Feldt 1976). I calculated the effect size (η^2) to estimate the proportion of the total variance attributed to an effect (Tabachnick and Fidell 1989).

Species Composition

Trends in successional pathways of understory vegetation were evaluated using non-metric multidimensional scaling (NMS) ordination with Sørenson's distance measure. NMS was carried out using PC-ORD version 5 (McCune and Grace 2002, McCune and Mefford 2005) set to the slow and thorough auto-pilot mode to select the optimal solution (i.e., dimensionality). NMS is well suited for community data because it uses non-metric rank ordering to perceptually map data; NMS avoids assumptions of the underlying structure of the data (i.e., normality and homogeneity of variance) made by traditional ordination techniques (McCune and Grace 2002).The criterion for success is the measure of "stress", which is an inverse measure of fit to the data (McCune and Grace 2002), a lower stress value represents a better fit. An acceptable stress value for community ecology data is generally in the range of 10 to 20 (Clarke 1993). Data were first relativized by species maximum, to lessen, but not to eliminate the influence of dominant species on the patterns and trends identified by NMS ordination. This procedure reduces the skew and overall coefficient of variation of the data, and lessens sampling error in ocular estimations (McCune and Grace 2002). All plant species were used in the ordination analysis, with the exception of species occurring in < 5% of sampling units (McCune and Grace 2002). Successional vectors were created to connect sites through time.

I used a Multiple Response Permutation Procedure (MRPP) with Sørenson's distance measure (Bray and Curtis 1957) to test for differences in species composition and abundance among treatments and distance ranges. Pairwise comparison was used to assess differences among harvesting treatments. I ran separate MRPPs for Yrs 1, 0, 5 and 7 to examine if compositional differences among treatments were detected at each sampling period. MRPP is a non-parametric analog to discriminant function analysis and is thus not limited by assumptions of normally-distributed data or homogenous variances (Mielke and Berry 2001, McCune and Grace 2002). The procedure produces a P value as well as an agreement statistic (A) value. The latter describes within-group homogeneity compared to random expectation and has a range of -1 to 1. If all samples in a group are identical, $A = 1$. When agreement within group equals expectation by chance, $A = 0$. If there is more within-group heterogeneity than expected by chance, then $A < 0$ (McCune and Grace 2002).

Finally, I used indicator species analysis (ISA) (Dufrêne and Legendre 1997) with combinations of site group extension (De Caceres and Legendre 2009, De Caceres et al. 2010) to assess habitat associations (i.e., distance from the stream channel and harvesting treatment) of understory species and how these associations vary with time. I chose this extension method rather than the original ISA procedure because the latter fails at detecting species related to conditions prevailing in two or more a priori groups of sites and it is likely that species' habitat requirements are met in more than one group. Where the original ISA method looked for the group that the species was maximally associated, the extension method retains the combination of groups showing the strongest association with the target species (De Caceres et al. 2010).I used the point-biserial correlation coefficient (r_{pb}) association index, which is the Pearson correlation between species abundance data (quantitative variable) and site membership to a site-group combination (binary variable) (See De Caceres and Legendre 2009 for details).Statistical significance of the association was evaluated with a permutation test of 1000 iterations. Due to computation limitations, sites were grouped by riparian (0-10 m), transition (10-20 m) and upland (20-30 m) communities in addition to harvesting treatment (uncut, buffer, cut-to-shore). Species occurring at less than two sites were removed from the analyses to not confuse statistical artifact with a meaningful biological response. MRPP and ISA were run with R version 2.15 (R Development Core Team 2010) with packages vegan 2.0-2 (Oksanen et al. 2011) and indicspecies (De Caceres et al. 2010). For MRPP and ISA, P-values were corrected with the Holm test for multiple comparisons.

4.4 Results

Species Richness, Abundance and Turnover

One hundred and nine vascular and non-vascular species were identified in this study. The responses of species richness of total, vascular and non-vascular understory vegetation to treatment differed significantly among the distance ranges to stream and with year of measurement (Table 1). Total species richness decreased with distance to stream in Yrs 0, 1, and 5, but this overall trend changed for cut-to-shore treatment in Yr 7 (Fig. 1). Furthermore, total species richness was significantly higher for cut-to-shore treatment than uncut and buffer treatments on transition and upland sites at Yr 7, but not for other years or sample plots close to the stream (Fig. 1). Vascular species richness tracked similarly to total species richness across the distance ranges and over time (Table 1). Non-vascular species richness decreased in all distance ranges, except for the streamside plots, in Yr 1 following both buffer and cut-to-shore treatments, relative to pre-harvest (Yr 0) levels. In Yr 5, non-vascular richness was still lower in cut-to-shore treatments relative to Yr 0, but was similar in buffer and uncut treatments at all distance ranges. Finally, non-vascular richness did not differ with treatment in Yr 7. Distance related variables accounted for 57%, 58%, and 35% of the variation in total, vascular and non-vascular species richness (Table 1), respectively.

Percent cover of total understory vegetation strongly differed with sampling year that accounted for 66% of its variation, and with treatment and distance from stream (Table 2). Total understory cover strongly decreased at Yr 1 from Yr 0 for both buffer and cut-to-shore treatments, but not for the uncut treatment (Fig. 2). The cover, however, increased in Yrs 5 and 7. Among treatments, cut-to-shore had the lowest total cover at Yr 1; buffer had the highest total cover at Yr 5, whereas at Yr 7, total cover was higher for cut-to-shore on uplands (Fig. 2). Vascular species percent cover had similar patterns to those of total understory cover except a more pronounced difference among treatments at Yr 5 (Fig. 2). By contrast, non-vascular species cover was generally lower after cut-to-shore treatment; but the difference among treatments was far less in the streamside plots relative to further upland (Fig 2).

Total, vascular and non-vascular species turnover was strongly related to harvesting treatments across all distance ranges and sampling years (Table 3). Total species turnover was generally highest in the cut-to-shore sites, whereas similar species turnover occurred in the uncut and buffer sites (Fig 3). Vascular species turnover more or less followed the patterns in total species turnover, but the turnover did not differ among treatments in the riparian and transition plots (Fig 3). Non-vascular species turnover was considerably higher in the cut-to-shore treatment than uncut and buffer, particularly in Yrs 5 and 7.

Table 4.1 Repeated measures general linear model relating species richness (m^{-2}) of total, vascular and non-vascular understory vegetation to harvesting treatment and distance from stream over time in Central Alberta, Canada.

Source	d.f.	Total		Vascular		Non-vascular	
		P	η^2	P	η^2	P	η^2
Between subjects							
Harvest (H_i)	2	0.87	0.01	0.55	0.02	0.11	0.08
Distance (D_j)	5	**0.02**	**0.22**	**0.04**	**0.19**	0.65	0.06
Harvest x distance (HD_{ij})	10	0.99	0.05	0.98	0.05	0.99	0.03
Error ($\varepsilon_{k(ij)}$)	54						
Within subjects							
Year (T_l)	3	**<0.001**†	**0.28**	**<0.001**†	**0.25**	**<0.001**	**0.13**
Year x harvest (HT_{il})	6	**<0.001**†	**0.24**	**<0.001**†	**0.21**	**<0.001**	**0.29**
Year x distance (DT_{jl})	15	**0.03**†	**0.15**	**0.04**†	**0.16**	0.14	0.12
Year x harvest x distance (HDT_{ijl})	30	0.13†	0.20	**0.05**†	**0.23**	0.37	0.17
Error ($\varepsilon_{m(ijkl)}$)	162						

† Huynh-Feldt epsilon was applied to correct for sphericity. Significant effects are shown in boldface type.

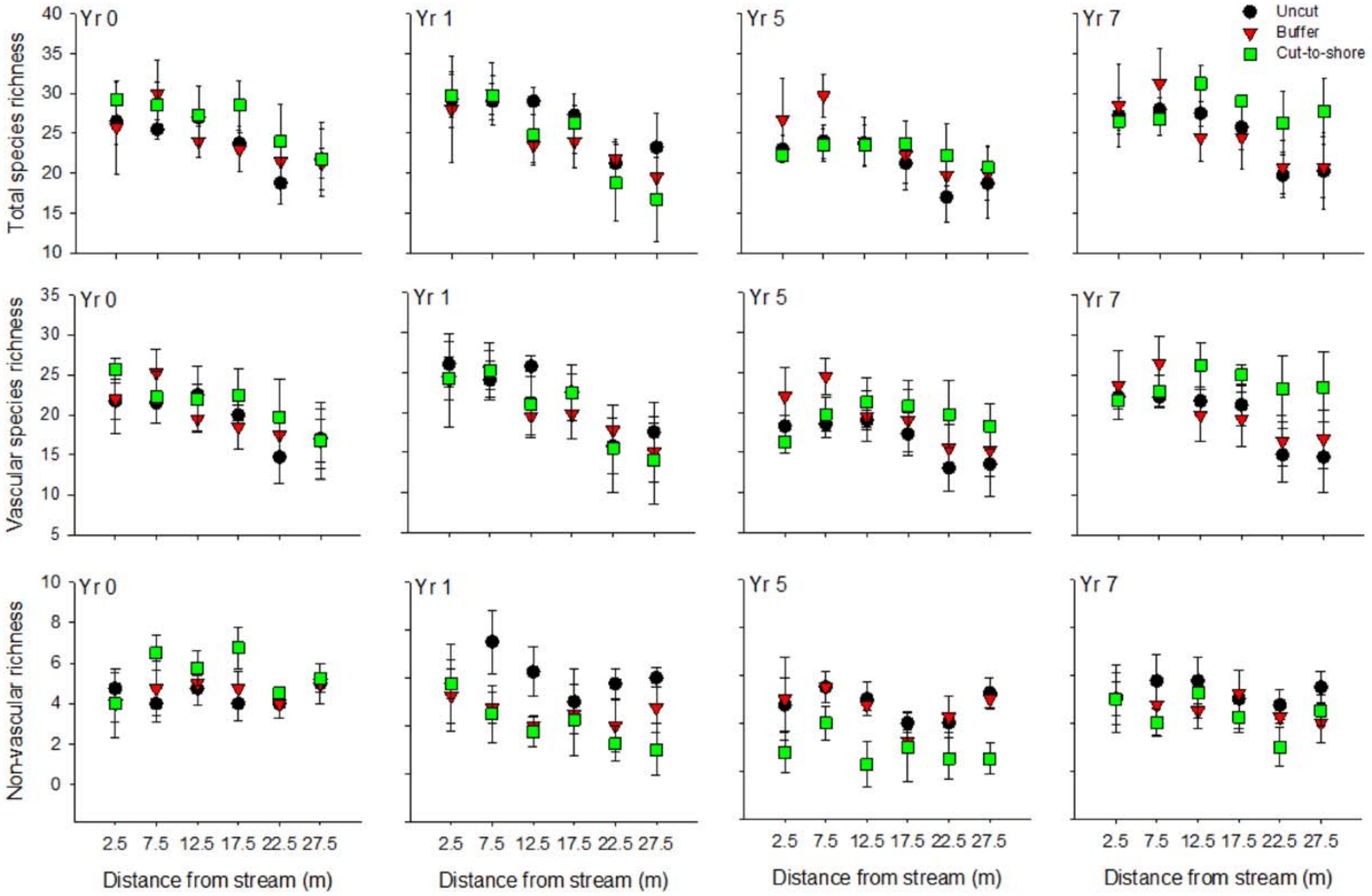


Figure 4.1 Mean (± 1 Standard Error) species richness (m^{-2}) of total, vascular and non-vascular understory plant species over a seven year sampling period in relation to distance from stream in uncut, buffer, and cut-to-shore boreal watersheds.

Table 4.2 Repeated measures general linear model relating abundance (i.e., percent cover) of total, vascular and non-vascular understory vegetation to riparian harvesting treatment and distance from stream over time in Central Alberta, Canada.

Source	d.f.	Total		Vascular		Non-vascular[‡]	
		P	η^2	P	η^2	P	η^2
Between subjects							
Harvest (H_i)	2	**0.01**	**0.15**	0.09	0.09	**0.01**	**0.16**
Distance (D_j)	5	0.12	0.15	**0.001**	**0.32**	0.25	0.11
Harvest x distance (HD_{ij})	10	0.52	0.15	0.87	0.09	0.98	0.03
Error ($\varepsilon_{k(ij)}$)	54						
Within subjects							
Year (T_l)	3	**<0.001**[†]	**0.66**	**<0.001**[†]	**0.65**	**<0.001**[†]	**0.38**
Year x harvest (HT_{il})	6	**<0.001**[†]	**0.26**	**<0.001**[†]	**0.30**	**<0.001**[†]	**0.27**
Year x distance (DT_{jl})	15	0.53[†]	0.08	0.57[†]	0.08	**0.003**[†]	**0.18**
Year x harvest x distance (HDT_{ijl})	30	0.91[†]	0.10	0.99[†]	0.07	0.61[†]	0.14
Error ($\varepsilon_{m(ijkl)}$)	162						

[†] Huynh-Feldt epsilon was applied to correct for sphericity. Significant effects are shown in boldface type.

[‡] Variable was square-root transformed.

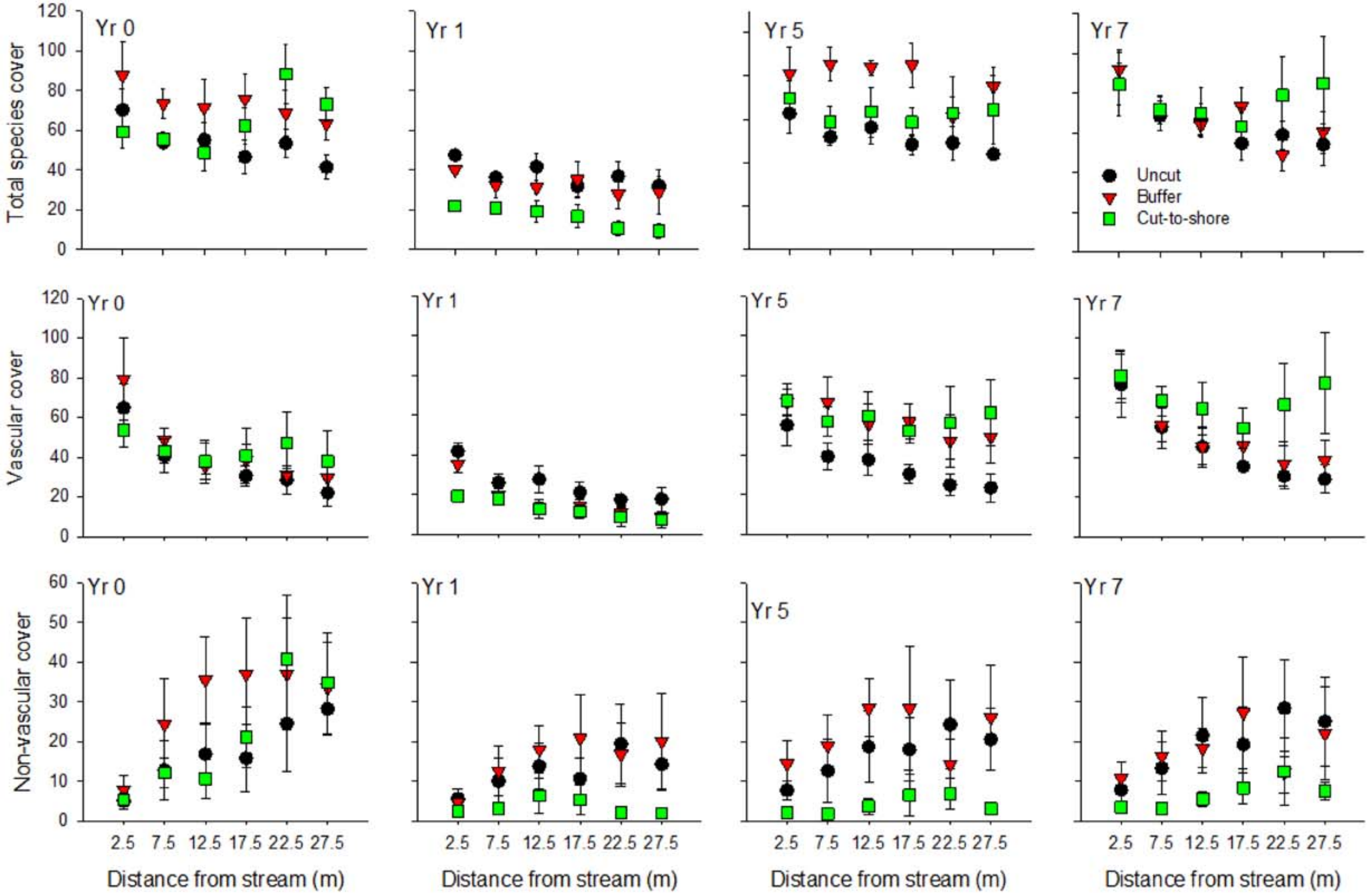


Figure 4.2 Mean (± 1 Standard Error) abundance (i.e., percent cover) of total, vascular and non-vascular understory plant species over a seven year sampling period in relation to distance from stream in uncut, buffer, and cut-to-shore boreal watersheds.

Species Composition

NMS ordination identified a 3-dimensional solution with a final stress of 8. 45. Although only ordination was performed, sites were separated by treatment to aid interpretation (Fig 4). Axes 1, 2, and 3 correspond to 39%, 39%, and 17% of understory floristic variability, respectively (Fig 4). Axis 1 represented a gradient of common boreal riparian species (e.g., the leafy mosses Plagiomnium cuspidatum and Climacium dendroides) to common upland species (e.g., the ericaceous shrubs Vaccinium myrtilloides and Rhododendron groenlandicum, and the feather mosses Ptilium crista-castrensis and Pleurozium schreberi). Axis 2 represented a gradient of shade-tolerant feather mosses (P. crista-castrensis, P. schreberi, and Hylocomium splendens) to shade-intolerant vascular species (e.g., Calamagrostis canadensis and Salix spp.). Axis 3 was positively correlated to tall shrubs (e.g., Alnus rugosa and Vibernum edule). Study sites lined up along Axis 1 according to distance from stream, but compositionally shifted over time depending on harvesting treatment. Uncut sites remained relatively stable in each sampling year, particularly in the 20 to 30 m from shore range. Upland sites in the cut-to-shore treatment experienced the most drastic changes in position in the ordination space relative to Yr 0, through an increase in grasses, forbs and willows, and decrease in feathermosses.

Table 4.3 Repeated measures general linear model relating species turnover (i.e., colonization and extirpation) of total, vascular and non-vascular understory vegetation to riparian harvesting treatment and distance from stream over time in Central Alberta, Canada.

Source	d.f.	Total		Vascular		Non-vascular[‡]	
		P	η^2	P	η^2	P	η^2
Between subjects							
Harvest (H_i)	2	**<0.001**	**0.37**	**<0.001**[†]	**0.25**	**<0.001**	**0.48**
Distance (D_j)	5	0.16	0.13	0.11	0.15	0.43	0.13
Harvest x distance (HD_{ij})	10	0.54	0.14	0.19	0.21	0.97	0.09
Error ($\varepsilon_{k(ij)}$)	54						
Within subjects							
Year (T_l)	**3**	**<0.001**	**0.56**	**<0.001**[†]	**0.38**	**0.001**[†]	**0.19**
Year x harvest (HT_{il})	6	**<0.001**	**0.24**	**0.002**[†]	**0.15**	0.22[†]	0.08
Year x distance (DT_{jl})	15	0.43	0.09	0.88[†]	0.04	0.89[†]	0.07
Year x harvest x distance (HDT_{ijl})	30	0.08	0.22	0.51[†]	0.15	0.38[†]	0.25
Error ($\varepsilon_{m(ijkl)}$)	162						

[†] Huynh-Feldt epsilon was applied to correct for sphericity. Significant effects are shown in boldface type.
[‡] Variables were ln-transformed.

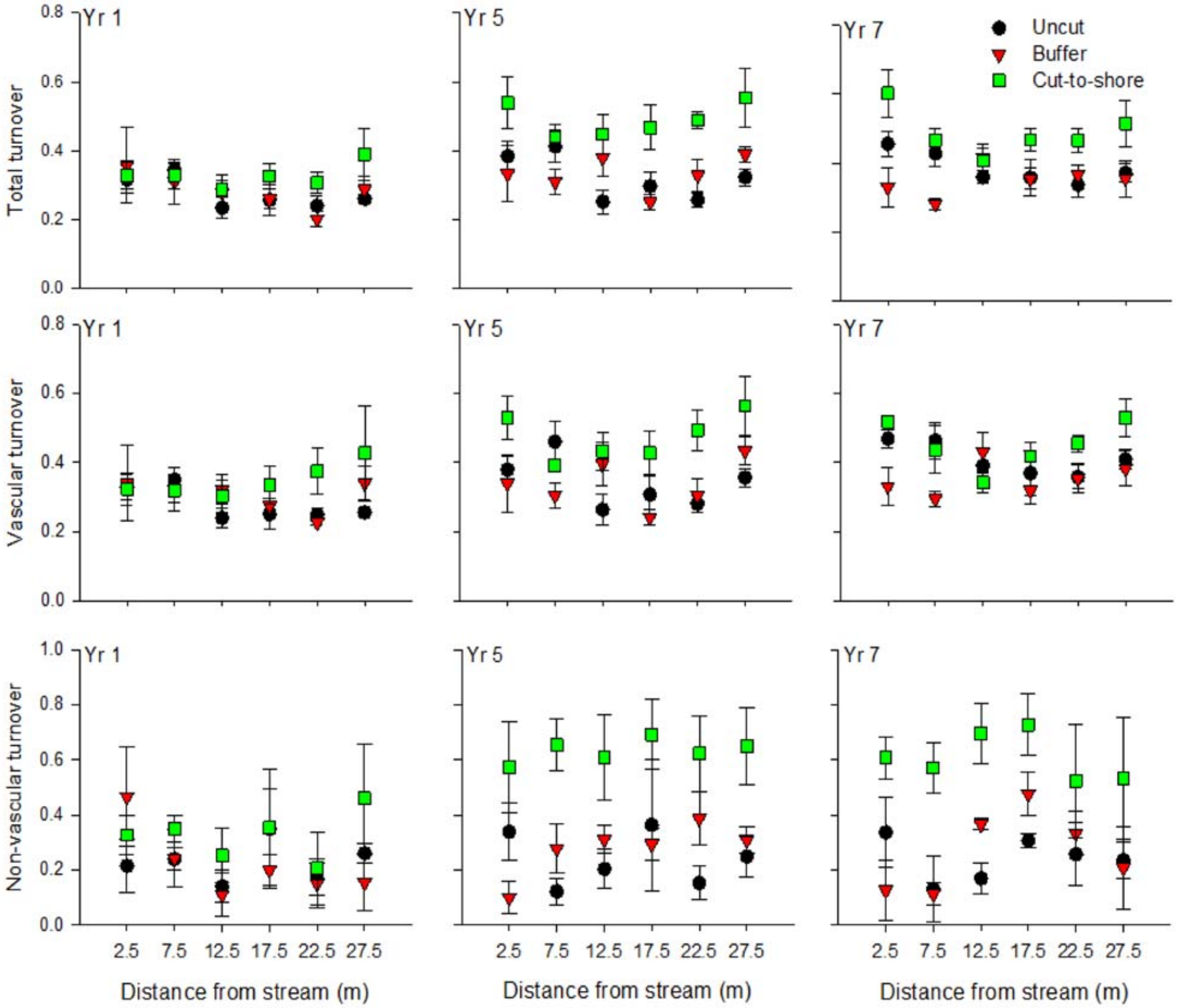


Figure 4.3 Mean (± 1 Standard Error) species turnover of total, vascular and non-vascular understory plant species over a seven year sampling period in relation to distance from stream in uncut, buffer, and cut-to-shore boreal watersheds.

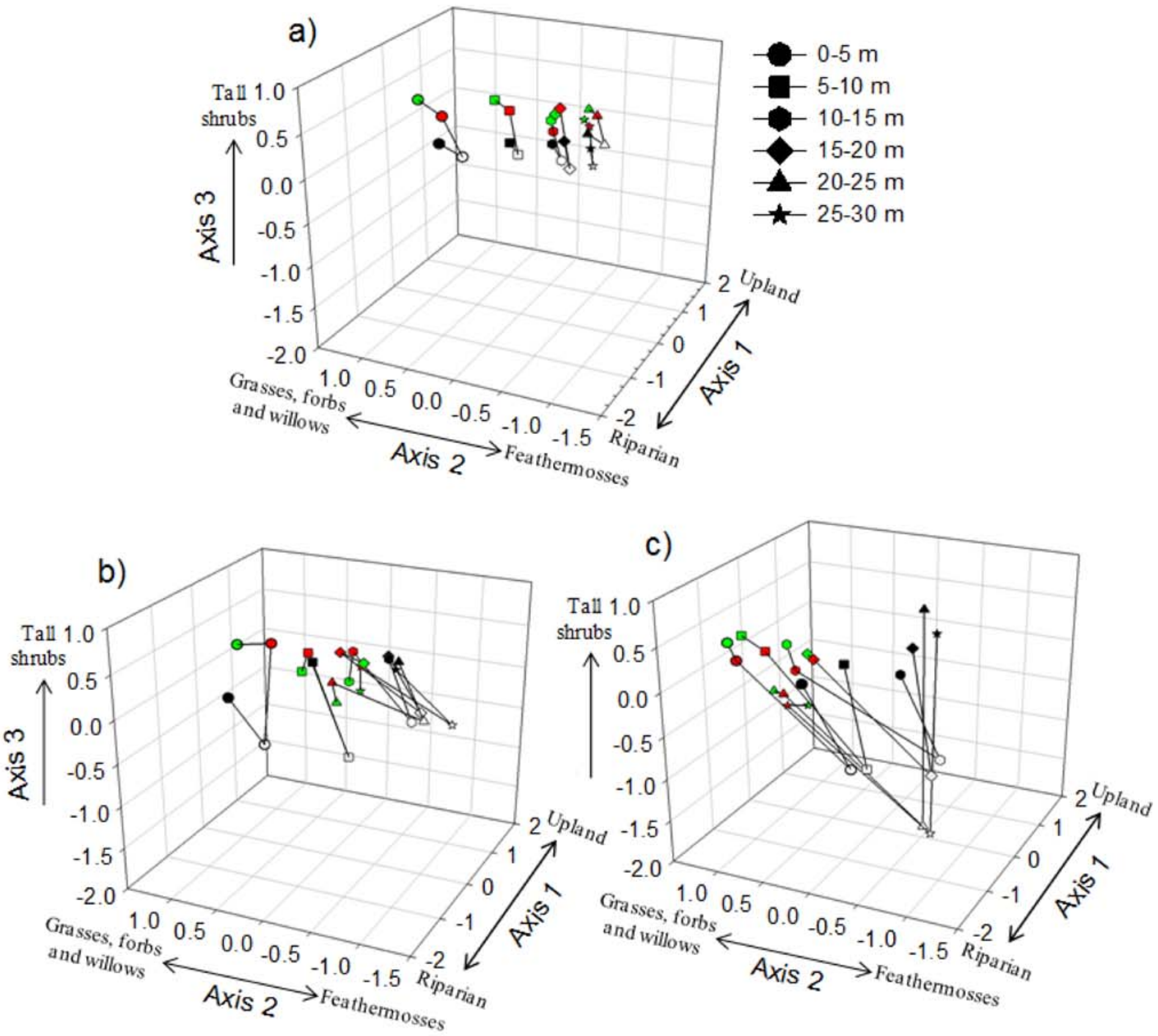


Figure 4.4 NMS ordination of average site data from a) uncut, b) buffer, and c) cut-to-shore sites over time in species space. Successional vectors connect Yr 0 (black), Yr 1 (white), Yr 5 (red), and Yr 7 (green). Axes 1, 2, and 3 account for 39%, 39%, and 17% of the understory variability, respectively.

Table 4.4 MRPP comparing understory composition among harvesting treatment over time. The value of the Agreement within group (A) and the significance of the association (P-value) after Holm correction are presented. Significant effects are shown in boldface type.

Site Classification			**Yr 0**		**Yr 1**		**Yr 5**		**Yr 7**	
			A	P	A	P	A	P	A	P
0 to 5 m										
Uncut	vs.	Buffer	-0.03	0.70	-0.01	0.60	0.01	0.32	0.00	0.38
Buffer	vs.	Cut-to-shore	-0.03	0.85	-0.01	0.58	0.02	0.23	0.03	0.10
Uncut	vs.	Cut-to-shore	0.01	0.36	**0.05**	**<0.01**	0.05	0.08	0.03	0.16
5 to 10 m										
Uncut	vs.	Buffer	-0.03	0.75	0.01	0.32	-0.01	0.63	0.00	0.37
Buffer	vs.	Cut-to-shore	-0.02	0.63	-0.01	0.60	0.02	0.19	0.07	0.09
Uncut	vs.	Cut-to-shore	-0.04	0.84	0.03	0.08	0.01	0.25	0.08	0.11
10 to 15 m										
Uncut	vs.	Buffer	0.01	0.32	0.00	0.45	0.01	0.37	-0.01	0.54
Buffer	vs.	Cut-to-shore	0.01	0.32	-0.03	0.70	**0.04**	**0.05**	**0.05**	**0.03**
Uncut	vs.	Cut-to-shore	-0.04	0.84	0.01	0.32	**0.08**	**0.02**	**0.05**	**0.04**
15 to 20 m										
Uncut	vs.	Buffer	0.00	0.49	0.00	0.41	0.06	0.07	-0.02	0.73
Buffer	vs.	Cut-to-shore	-0.04	0.90	0.02	0.25	0.01	0.30	0.02	0.23
Uncut	vs.	Cut-to-shore	-0.04	0.86	0.01	0.32	**0.07**	**0.02**	**0.06**	**0.01**
20 to 25 m										
Uncut	vs.	Buffer	-0.05	0.77	-0.02	0.58	0.01	0.35	0.01	0.33
Buffer	vs.	Cut-to-shore	-0.04	0.75	0.07	0.06	0.01	0.37	0.01	0.34
Uncut	vs.	Cut-to-shore	-0.04	0.74	**0.10**	**0.01**	**0.08**	**0.04**	**0.08**	**0.03**
25 to 30 m										
Uncut	vs.	Buffer	-0.03	0.66	0.01	0.31	0.00	0.49	0.00	0.48
Buffer	vs.	Cut-to-shore	-0.07	0.89	0.01	0.37	0.05	0.04	0.03	0.16
Uncut	vs.	Cut-to-shore	0.00	0.45	**0.10**	**0.02**	**0.08**	**0.02**	**0.08**	**0.02**

As expected, compositional differences among harvesting treatments were not detected using MRPP for Yr 0 at any of the distance ranges (Table 4). At streamside (0-5 m), composition only differed between uncut and cut-to-shore treatment at Yr 1, but it became similar for all treatments at Yrs 5 and 7. At the distance range of 5-10 m, composition was similar among all treatments during each sampling period. Composition consistently differed between uncut and cut-to-shore treatments at Yrs 1, 5, and 7 for uplands (20-25 m and 25-30 m), whereas this difference was only observed at Yrs 5 and 7 for the transitional zone.

Forty-six indicator species (IS) were identified as having an affinity for one or more habitat group in at least one sampling year (Table 5). Twenty-two IS were identified in Yr 0, of which two-thirds were associated with riparian (0 to10 m) habitat. Many of these riparian species (i.e., Calamagrostis canadensis, Equisetum spp., Galium triflorum, Lonicera involucrata, Mitella nuda, Plagiomnium spp., and Rubus pubescens) had fidelity for the riparian habitat regardless of the sampling year or treatment. However, all IS associated with upland (20 to 30 m) communities in Yr 0 (i.e., Cornus canadensis, Lathyrus ochroleucus, Pleurozium schreberi, Ptilium crista-castrensis, and Vaccinium vitis-ideae) were no longer associated with the cut-to-shore treatment in Yrs 1, 5 or 7. Similar to Yr 0, most of the Yr 1 IS were associated with riparian habitat; however, none of the 31 indicator species identified in Yr 1 were associated with the upland community in the cut-to-shore treatment. The trends in Yrs 5 and 7 were similar. Species associations increased in the transition and upland communities in Yrs 5 and 7, relative to Yrs 0 and 1. As expected, most of these IS (e.g., Epilobium angustifolium, Salix spp., and Polytrichium juniper) have ruderal characteristics, such as highly dispersive propagules.

Table 4.5 Species-habitat association patterns of understory vegetation on managed boreal watersheds over 7 sampling years based on indicator species analysis. For each indicator species, the site-group combination that obtained the highest correlation and the value of the correlation (r_{pb}) are presented. Significance at *P< 0.05, ** P< 0.01, *** P<0.001

Species	**Life-form**	**Reproductive strategy**	**Yr 0**		**Yr 1**		**Yr 5**		**Yr 7**	
			Habitat	r_{pb}	**Habitat**	r_{pb}	**Habitat**	r_{pb}	**Habitat**	r_{pb}
Achillea millefolium	FORB	INV	-	-	-	-	CT/U	0.42*	CU	0.57*
Arnica cordifolia	FORB	INV	-	-	-	-	BT/U CU	0.46**	-	-
Aster ciliolatus	FORB	INV	-	-	-	-	-	-	CU	0.57***
Brachythecium spp.	BRYO	AVO	-	-	UR/T/U	0.64***	UR BR	0.47**	UR BR CR	0.43*
Calamagrostis canadensis	GRAM	INV/END	UR BR CR	0.49**	CR	0.48**	CR	0.57***	CR	0.51*
Carex spp.	GRAM	INV	CR	0.51*	-	-	-	-	CR/T/U	0.42*
Climacium dendroides	BRYO	AVO	-	-	UR	0.38*	BR	0.38*	-	-
Delphinium glaucum	FORB	INV	-	-	-	-	UR	0.53*	UR	0.50*
Cornus candensis	FORB	END	UT/U BT/U CT/U	0.56***	UT UU	0.76***	UT/U BT/U	0.56***	UT/U BT	0.59***
Dicranum polysetum.	BRYO	AVO	-	-	UTUU	0.53**	UT/U BU	0.43*	UT/U	0.44*
Epilobium angustifolium	FORB	INV/END	-	-	-	-	BT/U CT/U	0.49**	CT CU	0.56***
Equisetum spp.	PTER	END	BR CR	0.46**	UR BR	0.51**	UR BR CR	0.55***	UR BR CR	0.46*
Erysimum cheiranthoides	FORB	INV	-	-	BR CR	0.45*	-	-	-	-
Fragaria vesca	FORB	INV	-	-	-	-	UT BR CU	0.43*	UT CU	0.41*
Galium triflorum	FORB	END/INV	UR BR CR	0.59***	BR	0.51**	-	-	UR BR CR	0.43*

Table 4.5 con’t

Geum rivale	FORB	END	-	-	UR BR CR	0.53**	-	-	UR BR CR	0.48**
Gymnocarpium dryopteris	PTER	END	-	-	UR	0.64***	UR	0.64***	UR	0.62***
Heracleum lanatum	FORB	END/INV	UR/T	0.48**	UR/T	0.51**	-	-	-	-
Hylocomium splendens	BRYO	AVO	-	-	-	-	UT/U BT/U	0.40*	UT/U BT/U	0.50*
Impatiens capensis	FORB	INV	UR	0.53*	UR	0.49**	-	-	-	-
Lathyrus ochroleucus	FORB	END	BR/T CT/U	0.45*	BR/T /U CR/T	0.42*	BT	0.52**	BR/T/U CT	0.41*
Linnea borealis	DWSH	AVO	BT	0.47*	UTUU BT	0.62***	UU BT	0.43*	BT	0.43*
Lonicera involucrata	SHRU	AVO	CR	0.59**	UR	0.51**	URBR CR	0.42*	UR CR	0.53**
Lycopodium annotinum	PTER	END	-	-	-	-	-	-	UTUU BT	0.41*
Lycopodium complanatum	PTER	END	-	-	BT/U CT	0.45*	BT BU	0.54**	-	-
Maianthemum canadense	FORB	END	-	-	-	-	UR BT	0.46**	-	-
Mertensia paniculata	FORB	END	UR	0.42*	UR/T	0.56**	UR/T BR CU	0.46*	UR	0.60***
Mitella nuda	FORB	AVO	UR BR CR	0.56**	UR BR CR	0.61***	UR BR CT	0.45*	UR BR CR	0.45*
Petasites palmatus	FORB	END	-	-	-	-	BR BU CT	0.56***	-	-
Plagiomnium spp.	BRYO	AVO	UR BR CR	0.55**	UR BR	0.46**	UR BR	0.61**	UR BR CR	0.45*
Pleurozium schreberi	BRYO	AVO	UT/U BT/U CT/U	0.42*	UT/U BT/U	0.45*	UTUUBT BU	0.41*	UT/U BT/U	0.45*
Polytrichium juniper	BRYO	INV	-	-	-	-	CU	0.39*	CU	0.41**
Ptilium crista-castrensis	BRYO	AVO	BT BU CU	0.50**	UU BR BT	0.42*	BT	0.48**	UU BT	0.46*
Ribes oxyacanthoides	SHRU	EVA/INV	UR/T BR CR/T	0.44*	-	-	URUT BR	0.50**	UT BR	0.50**
Ribes triste	SHRU	EVA	UR	0.54**	UR BR	0.68***	-	-	-	-

Table 4.5 con't

Rosa acicularis	SHRU	END/INV	-	-	UT BT	0.40*	-	-	-	-
Rubus pubescens	FORB	END	UR CR	0.52**	UR	0.44*	-	-	UR CR	0.48**
Rubus pedatus	FORB	END	-	-	-	-	-	-	UTUU	0.44*
Salix spp.	SHRU	INV/END	-	-	-	-	CR CU	0.51**	CR	0.66***
Streptopus amplexifolius	FORB	EVA	UR	0.48**	UR BR	0.42*	-	-	-	-
Thalictrum venulosum	FORB	END	UR CR	0.49*	UR	0.55**	UR	0.45*	-	-
Urtica diocia	FORB	INV	UR	0.41*	URUT	0.43*	URUT	0.41*	URUT	0.43*
Vaccinium caespitosum	DWSH	END	UR BT/U CT/U	0.49**	UT/U BT/U	0.52**	B/U CT	0.63***	B/U CT	0.57***
Vaccinium vitis-ideae	DWSH	END	CU	0.45*	UT/U BT/U	0.52*	BT/U	0.44*	-	-
Vicea americana	FORB	INV	-	-	-	-	-	-	BR	0.54*
Viola spp.	FORB	END	-	-	UR/T BR CR	0.49**	-	-	-	-

Life-forms are: bryoids (BRYO), dwarf shrubs (DWSH), forbs (FORB), graminoids (GRAM), pteridophytes (PTER), and shrubs (SHRU).

Reproductive strategies are based on Rowe's(1983) classification; invaders (INV) and evaders (EVA) are both pioneer species; however the former has highly dispersive, short-lived propagules, whereas the latter regenerates through soil or canopy seed banks. Avoiders (AVO) are late-successional species that also colonize through seed dispersal. Resistors (RES) and endurers (END) withstand disturbance through the survival of above-ground and below-ground plant parts, respectively.

Habitat classes are defined by disturbance treatment (U uncut, B buffer and C cut-to-shore) and community type based on distance from stream (R riparian; 0 to 10 m, T transition; 10 to 20 m, and U upland; 20 to 30 m). First letter in habitat class indicates disturbance; second letter in habitat class indicates community.

4.5 Discussion

Disturbance severity from harvesting exerted strong controls on the dynamics of understory vegetation in boreal riparian forests, which was still evident seven years after the disturbance event. However, the dynamic responses strongly differed with the distance from the stream channel. Furthermore, vascular and non-vascular plants exhibited contrasting responses in their richness, abundance, turnover, and composition.

After an initial decrease, vascular species richness and abundance of understory vegetation was highest in the cut-to-shores sites, relative to the less disturbed treatments (i.e., buffer and uncut), but only in the transition and upland sites (10 to 30 m from shore). Along disturbance gradients, plant diversity is predicted to peak at intermediate levels of disturbance (sensu intermediate disturbance hypothesis; IDH) because competitive exclusion is slowed through physical alteration of the environment and the requirements of more species are liable to be met (Connell 1978). Cut-to-shore treatment was clearcut without site preparation, which has been defined as an intermediate disturbance in other Canadian boreal studies (Haeussler et al. 2002, Biswas and Mallik 2010). Vascular richness conformed to the IDH in upland plots, but did not in the streamside communities. It is generally accepted that resource availability is higher in riparian than upland forests and there is some evidence that vascular species growing in sites with higher resource availability are more resilient to disturbance (Hamilton and Haeussler 2008, Slocum and Mendelssohn 2008). However, I attribute the diverging disturbance-diversity relationships, to differing processes driving the communities from streamside to upland. In upland forests, the canopy exerts strong controls on the understory community composition, predominantly by limiting resource quantity (Hart and Chen 2008). However, there is a lack of evidence for as strong a coupling of the canopy and understory in streamside communities relative to upland plant assemblages (Lyon and Sagers 1998, Decocq 2002), suggesting that hydrology, rather than the canopy drives understory riparian communities, and thus may be able to better cope with stand-replacing disturbances as long as hydrological processes are not significantly altered.

Specific microclimatic conditions are vital for growth and reproduction of non-vascular species (Rydgren et al. 2006). For the dominant boreal upland bryophytes (i.e., Pleurozium schreberi, Hylocomium splendens and Ptilium crista-castrensis), the altered environment following stand-replacing disturbance, such as increased soil temperatures and decreased soil moisture, exceeds their tolerance, resulting in a decrease in their cover (Fenton and Frego 2005, Hylander 2005, Åström et al. 2007). In my study, richness and abundance of non-vascular species did decrease following cut-to-shore treatment. Similar to studies from the Swedish boreal forest (Dynesius and Hylander 2007, Dynesius et al. 2009), this response was, however, much less pronounced in the streamside communities. I speculate that high moisture availability and shading from tall shrubs associated with riparian habitat (Table 5) buffers the effect of harvesting on bryophytes in streamside plots, and thus their response to harvesting is not as marked as it is in the uplands.

Species turnover was consistently higher in the cut-to-shore treatment than both buffer and uncut plots, and the disturbance effect on turnover was greater in non-vascular than vascular species. Although shifts in richness and abundance following cut-to-shore treatment were greater in the upland than the streamside plots, I found that neither vascular nor non-vascular species turnover was mediated by distance from the stream channel. Immigration processes in streamside communities are enhanced because of hydrochory (i.e., flow facilitated propagules distribution) and better conditions for establishment, such as abundance of bare substrate

(Planty-Tabacchi et al. 1996, Brown and Peet 2003, Dynesius et al. 2009). However, lateral colonization from streamside into the upland is also highly probable as species associated with upland habitat are able to tolerate low resource levels (i.e., light) at the trade-off of being less competitive in more productive habitats (Tilman 1985). For example, sedges (Carex spp.) were only associated with riparian habitat in Yr 0, but seven years after cut-to-shore they were associated with all distance ranges. Therefore, it is not surprising that turnover was similar among habitats.

Clear patterns emerged in understory species composition along the riparian ecotone and over time. After five years following the disturbance event, and still evident in Yr 7, cut-to-shore plots in the 10 to 30 m from stream diverged from a feathermoss and ericaceous shrub dominated community to one characterized by grasses, forbs and tall shrubs. However, all three treatments (uncut, buffer and cut-to-shore) had similar understory vegetation communities in the streamside plots (0 to 10 m from stream). Many of the species that increased in abundance in the cut-to-shore treatment were present before harvesting in the streamside plots. For example, Calamagrostis canadensis, is a widely distributed perennial rhizomatous grass common in Canadian boreal riparian forests (Lamb and Mallik 2003), which may impede the colonization of invading species. Through both seed dispersal and clonal expansion, C. canadensis rapidly expands following timber harvesting (Lieffers et al. 1993). Most indicator species of the cut-to-shore riparian habitat in Yr 0 were still positively associated with the same habitat over time, whereas no species associated with cut-to-shore upland habitat in Yr 0, were associated with that habitat after harvesting. The alteration on the environment following timber harvesting disturbance had greater consequences on the growth and mortality of species associated with the upland plots relative to those growing streamside.

These results were similar to a study comparing bryophyte communities before and after clearcutting in riparian and upland communities. However, there are no studies, in any forest system, comparing the entire understory community before and after forest harvesting along a riparian ecotone.

Despite the difference in community composition in uncut and cut-to-shore plots, they were both similar to buffer plots in the 15 to 30 m range; indicating that these buffer plots contained both early and late seral species that characterize the cut-to-shore and uncut plots, respectively. My results were comparable to a study in the central portion of the Canadian boreal forest that reported an increase in early seral vascular species into 15 m of the riparian buffer (Braithwaite and Mallik 2012). These edge effects (i.e., detectable changes in the community reflective of abiotic and biotic processes at forest edges) from the adjacent clearcut may be related to microclimatic (i.e., canopy gap size, light transmittance, vapour pressure deficit, air temperature and soil temperature) changes within the buffer (Chen et al. 1995, Brosofske et al. 1997, Dong et al. 1998, Dignan and Bren 2003); which have been reported to have negative effects on boreal upland bryophytes (Stewart and Mallik 2006, Braithwaite and Mallik 2012), facilitating colonization of vascular species.

An inherent difficulty with field studies is untangling confounding effects caused by abiotic factors (Lawton et al. 1998, Gilliam and Roberts 2003). My study area suffered from a severe drought from 2002 to 03 (Government of Alberta 2003), which was the pre-harvest (i.e., Yr 0) sample period and may have affected the growth and resilience of post-harvest plant communities. Increased moisture availability to streamside plants, relative to those growing in the upland, may have buffered this effect. However, I used both pre-harvest and uncut sites as a control to compensate for abiotic fluctuations, and so it is unlikely that this limited my ability to interpret effects of harvesting across the riparian ecotone.

4.6 Conclusion

Overstory harvesting exerted stronger controls on non-vascular species than vascular species, as abundance and species turnover of non-vascular species shifted considerably. My prediction that shifts in the plant community following logging disturbance will be greater with increasing distance from the stream channel was supported. Overall my results suggest that riparian vegetation is not strongly affected by overstory harvesting, with or without a 30 m streamside buffer. Considering what is known about riparian ecology, these results aren't entirely unexpected. Hydrological processes and disturbance regimes that drive riparian ecosystems impede competitive exclusion, enhance vascular diversity, and create an environment liable to meet the competitive and resource requirements of more species; including robust perennials able to tolerate disturbance through the survival of belowground plant parts (Hughes and Fahey 1991, Økland 1995, Schimmel and Granstrom 1996).

CHAPTER 5 : EFFECT OF DISTURBANCE SEVERITY ON RIPARIAN AND UPLAND BOREAL UNDERSTORY PLANT COMMUNITIES

5.1Abstract

Overstory harvesting and associated ground disturbance affects understory plant communities through increasing mortality of individuals or propagules, or by varying environmental conditions and resource availability. Mechanical site preparation (i.e., scarification) exacerbates environmental changes following overstory harvest by destroying above- and below-ground plant parts and coarse woody debris and removing more of the forest floor. However, the capacity to absorb a disturbance event should also vary depending on habitat type. Here, I compare the response of boreal understory plant communities to overstory harvesting with and without scarification on 24 small stream sites on Boreal Shield watersheds. The disturbance-response relationship was also tested among habitats (i.e., riparian, transition and upland). The effects of forest harvesting, with or without scarification, on boreal understory species diversity were not detectable nine years following harvesting. Species composition was not strongly affected by harvesting when forest floor and soil disturbance is minimal; but it was following scarification. However, this effect varied with habitat. The riparian and upland plots that were harvested and scarified diverged from the uncut plant communities, but the transitional communities did not. Transitional communities retain species of both riparian and upland communities and thus the constitute flora has lesser site fidelity, and likely tolerates a wider range of environmental conditions. Overall, scarification profoundly altered the substrate by breaking up coarse woody debris and

decreasing the depth of organic matter, which destroyed forest floor feathermosses and created a habitat suitable for early colonizing species (i.e., grasses).

5.2 Introduction

In the boreal forest, harvesting is an important stand-replacing disturbance shaping the forest landscape with biotic responses to harvesting depending on size, frequency and severity of the event (Halpern 1988, Roberts and Gilliam 1995, Seymour et al. 2002, Roberts 2007, Hart and Chen 2008). Severity of overstory harvesting and associated ground-disturbance is generally defined as the amount of vegetation removed and the degree to which the forest floor and soils are disrupted (Oliver and Larson 1996). Harvesting and ground disturbance affects understory plant communities through increasing mortality of individuals or propagules (i.e., seed sources or vegetative plant parts), or by varying environmental conditions and resource availability (Halpern and Spies 1995, Roberts and Gilliam 1995, Bergeron and Harvey 1997, Scheller and Mladenoff 2002, Bartels and Chen 2010). For example, following canopy removal, light levels, soil temperatures and soil resource availability may increase (Gholz et al. 1985c, Hart and Chen 2006). These conditions are favourable for some understory vascular plants, specifically species with ruderal characteristics, such as rapid growth. Conversely, high light levels and soil temperatures, and low soil moisture content and pH levels following canopy removal (Bormann and Likens, 1979) exceed the tolerance of many bryophytes. Mechanical site preparation (i.e., scarification) exacerbates environmental changes following overstory harvest by destroying above- and below-ground plant parts and coarse woody debris and removing more of the forest floor (Vanha-Majamaa and Jalonen 2001, Roberts and Zhu 2002).

The capacity to cope with disturbance should vary depending on specific habitat characteristics. Habitat variability has historically been treated as background noise, but it is now well established that environmental variation among communities affects mechanisms of species diversity (Shea et al. 2004). Therefore, an interaction between habitat variability and the disturbance-response relationship is anticipated. For example, riparian communities may be more resistant to disturbance events than upland communities based on different characteristics that define the two habitats. Life-history strategies, productivity, and diversity of riparian plant communities are a reflection of the hydrological processes and disturbance regimes that shape riparian forests (Naiman et al. 1993). In the boreal forest, streamside communities are comprised of variety of species including generalist plant species (which may inhabit the uplands), riparian obligates specialized to survive in streamside habitats, and early successional species adapted to productive habitats (Lamb et al. 2002, Dynesius et al. 2009, Biswas and Mallik 2010); whereas, boreal upland understory communities are more commonly dominated by shade tolerant species (Nilsson and Wardle 2005, Hart and Chen 2008). Thus, understory plant communities in riparian forests may be able to better tolerate overstory harvesting than communities growing in upland forests.

Many boreal understory plants (i.e., herbaceous species) are robust perennials adapted to survive moderate disturbance through the survival of above- or belowground plants parts (Økland 1995), however, species that reproduce through the soil seed bank are most likely to colonize following severe ground disturbance (Nguyen-Xuan et al. 2000). Understory species most commonly found in the seed bank are ruderal and often not present in the extant vegetation community (Fyles 1989, Qi and Scarratt 1998), and there is some evidence that soil seed banks are even less developed in riparian ecosystems with respect to uplands

(Schneider and Sharitz 1988, Manders 1990). This is not surprising in the context of natural disturbance regimes, as wildfires in riparian areas often do not disturb the forest floor or remove the ground vegetation (Swanson 1994, Petit and Naimen 2007) as they may in uplands. Therefore, it is difficult to predict if the effects of overstory harvesting in conjunction with ground disturbance will be mediated by habitat. With this uncertainty in mind, the objective of this study is to compare the recovery of understory vegetation following contrasting soil disturbance due to harvesting impacts on the forest floor and soil in relation to habitat (i.e., from stream channel to upland). I also test if environmental variables (i.e., soil moisture content, coarse woody debris and depth of organic matter) are related to harvesting, with and without ground disturbance, and how they vary with respect to habitat. I hypothesize that shifts in species diversity and composition will be greater, relative to uncut condition, in harvested sites with more severe ground disturbance.

5.3 Materials and Methods

5.3.1 Study Area

I conducted this study in two watersheds on the Boreal Shield ecozone of Canada. The Mackenzie (MK) and Dog river (DR) watersheds are approximately 30 km northeast and 60 km northwest of the city of Thunder Bay, Canada, respectively. This area is characterized by low to moderate relief and podzol/spodosol soils over discontinuous till, glaciofluvial or aeolian deposits (Soil Classification Working 1998). The mean annual temperature is 2.4˚C, annual precipitation is 547 mm and the annual snowfall is 196 cm (Environment Canada 2011b). The canopy is dominated by boreal conifers (i.e. Picea mariana, Pinus banksiana, Abies balsamea and Picea glauca) or boreal mixedwoods (i.e., conifers mixed with Populus tremuloides, Populus balsamea and/or Betula papyrifera). The understory vegetation is rich relative to other parts of the Canadian boreal forest (Qian et al. 1998).

5.3.2 Experimental Design and Data Collection

Harvesting in the DR watershed was during the winter months of 2001 (i.e., when the ground was frozen) and the area did not receive any subsequent site preparation following canopy removal. Harvesting in the MK watershed was conducted during 2002 when the ground was not frozen and the sites were scarified following canopy removal. Therefore the harvesting treatment in DR represents overstory harvesting without ground disturbance, whereas the treatment in MK represents overstory harvesting with ground disturbance. Eight headwater stream sites were located in each watershed, for a total of sixteen sites that represented the following treatments; uncut (reference), and cut-to-shore, each with four replicates per watershed. Uncut sites were undisturbed (i.e., no forestry activity in the riparian or adjacent upland area). Cut-to-shore sites were clearcut to the edge of the stream channel. At each site, two randomly located ~50 m long transects were established running perpendicular from either side of the stream channel to the upland. Length of riparian, transition and upland habitats were determined along each transect based on compositional shifts (i.e., riparian and upland obligates) and topographical features (i.e., slope). Along each transect, 1-m^2 understory (i.e., ground and shrub strata) vegetation plots were placed consecutively within the riparian area (i.e., at every meter), and five were randomly located within both the transition and upland areas (Fig 5.1). Percent cover (0-100%) of vascular and non-vascular plant species in each plot was visually estimated (Mueller-Dombois and Ellenberg 1974). Vegetation sampling was conducted during the periods of peak vegetation cover in the summer (July through August) of 2009. Within each site, species cover data of the all plots in each habitat (i.e., riparian, transition and upland) were averaged to derive a mean.

Soil moisture content (using a moisture meter; HH2-Wet Sensor, type WET-2; Delta-T Devices, Cambridge, UK) and depth of organic matter (using a soil auger) was measured three times in each plot to derive a mean. Cover of coarse woody debris (CWD) was visually estimated in each plot.

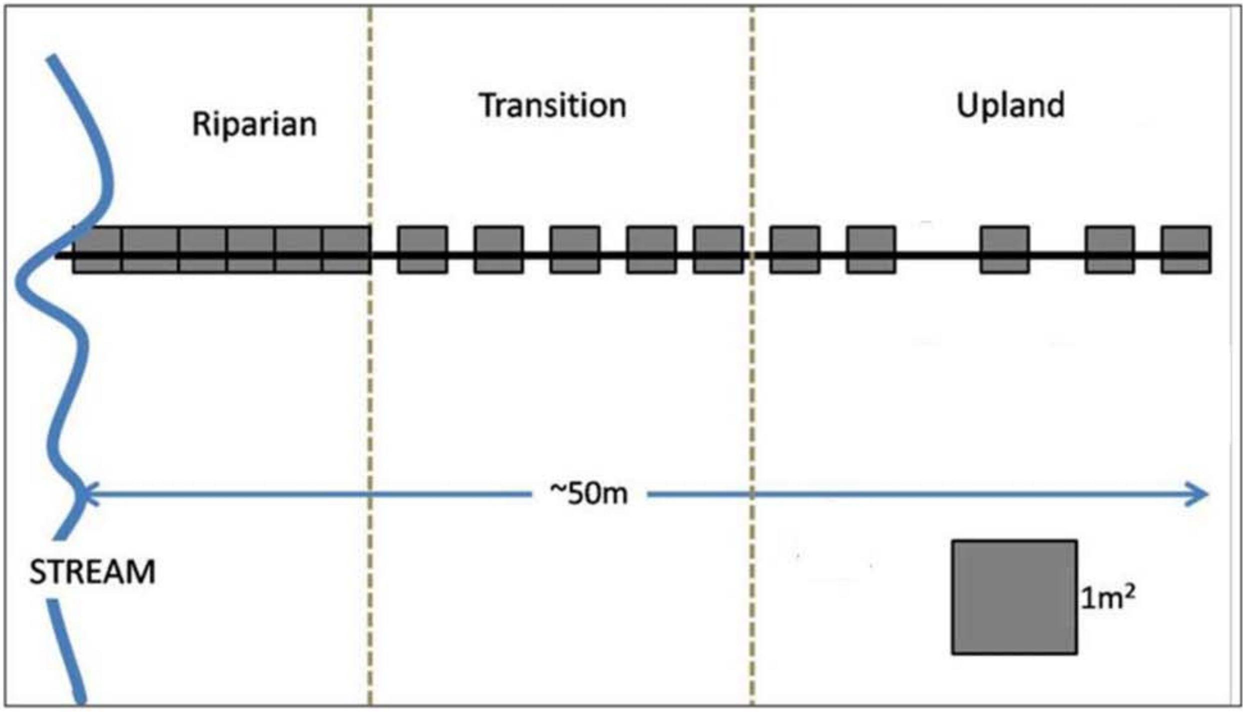


Figure 5.1 Example layout of transect running perpendicular from stream channel to the upland.

5.3.3 Statistical Analyses

Species diversity

Species richness (S) and evenness (J') were used as measurements of diversity. Species richness (S) is the total number of species in each sample plot. To calculate evenness, we used the (Pielou 1969) index (*J'*):

$$J' = H' \bullet \ln(S)^{-1} \quad [5.1]$$

Where S is species richness of the sample unit and *H'* is the Shannon-Weiner diversity, defined as:

$$H' = - \Sigma P_i \bullet \ln P_i \quad [5.2]$$

Where Pi is the proportion made up by the ith species.

A general linear model was run for each watershed to test the effects of habitat and disturbance on total, vascular and non-vascular species richness and evenness:

$$Y_{ijk} = \mu + H_i + D_j + H \times D_{ij} + \varepsilon_{(ij)k} \quad [5.3]$$

where Y_{ijk} is species diversity (richness or evenness); μ is the overall mean; H_i ($i = 1, 2, 3$) is the effect of habitat (i.e., riparian, transition or upland), D_j ($j = 1, 2$) is the effect of harvesting; $\varepsilon_{(ij)k}$ is the error term.

Species composition

Trends in successional pathways of understory vegetation were evaluated using non-metric multidimensional scaling (NMS) ordination with Sørenson's distance measure. NMS was carried out using PC-ORD version 5 (McCune and Grace 2002, McCune and Mefford 2005) set to the slow and thorough auto-pilot mode to select the optimal solution (i.e., dimensionality). NMS is uses non-metric rank ordering to map data, thus relaxing assumptions regarding the structure of the data (i.e., normality and homogeneity of variance) made by traditional ordination techniques (McCune and Grace 2002). All plant species were used in the ordination analysis, with the exception of species occurring in < 5% of sampling units (McCune and Grace 2002). The association of ordination axes with dominant species was evaluated with Kendall's rank correlation (tau); associations of ± 0.4 were considered strong. A Multiple Response Permutation Procedure (MRPP) with Sørenson's distance measure (Bray and Curtis 1957) was used to test for differences in species composition and abundance among habitats, disturbance levels, and watersheds. MRPP is a non-parametric analog to discriminant function analysis and is thus not limited by assumptions of normally-distributed data or homogenous variances (Mielke and Berry 2001, McCune and Grace 2002). In addition to a P value, the procedure produces a test statistic (T) as well as an agreement statistic (A) value. The former (i.e., T) describes the separation among groups (the more negative the value, the greater the separation among groups), and the latter (i.e., A) describes within-group homogeneity compared to random expectation and has a range of -1 to 1. If all samples in a group are identical, $A = 1$. When agreement within group equals expectation by chance, $A = 0$. If there is more within-group heterogeneity than expected by chance, then $A < 0$ (McCune and Grace 2002).

Environmental variables

To correlate vegetation patterns with environmental variables (i.e., soil moisture content, CWD and depth of organic matter), an NMS biplot with a secondary data matrix containing the environmental variables was produced and Pearson's correlation of each variable to the three ordination axes was calculated. Additionally, equation [5.2] was used to test for effects of harvesting and habitat on environmental variables, where Y_{ijk} is soil moisture content, coarse woody debris, or depth of organic material. Tukey's post-hoc test was used to evaluate differences among habitats.

5.4 Results

I identified 223 understory species in this study, including 176 and 47 vascular and non-vascular species, respectively. In the watershed that was not scarified, total, vascular and non-vascular species richness was not related to treatment or habitat (Table 5.1). In the scarified watershed, species richness was also not related to harvesting, but total and vascular species richness were higher in the riparian plots, in both uncut and cut-to-shore treatments, relative to transition and upland communities, but non-vascular richness was similar in all habitats (Table 5.1, Figure 5.2).

Habitat accounted for 38% of the variation in vascular species evenness in non-scarified sites, and 43% of the variation in scarified sites (Table 5.2). In both watersheds, evenness was not related to harvesting treatment (Table 5.2). Vascular evenness increased from the stream channel into the uplands (Fig 5.3c-d), and non-vascular species richness decreased along that same gradient but only in the non-scarified sites (Fig 5.3e).

Soil moisture content was higher in riparian sites than transition and upland communities ($P \leq 0.04$) in both watersheds and harvesting treatments (Fig. 5.4a-b). In the non-scarified watershed, soil moisture content was higher following harvesting in all habitats than in uncut sites (Fig. 5.4a). However, harvesting did not affect soil moisture content in the scarified watershed ($P = 0.3$). Coarse woody debris (Fig 5.4c) and depth of organic matter (Fig 5.4e) was neither related to habitat nor harvesting in the non-scarified sites ($P \geq 0.1$). Both coarse woody debris and depth of organic matter decreased following harvesting in the scarified sites (Fig 5.4d-f; $P \leq 0.02$). Habitats x disturbance interaction terms were not significant for any variable in either watershed (see Appendix 2 and 3 for complete GLM tables for scarified and non-scarified watersheds, respectively).

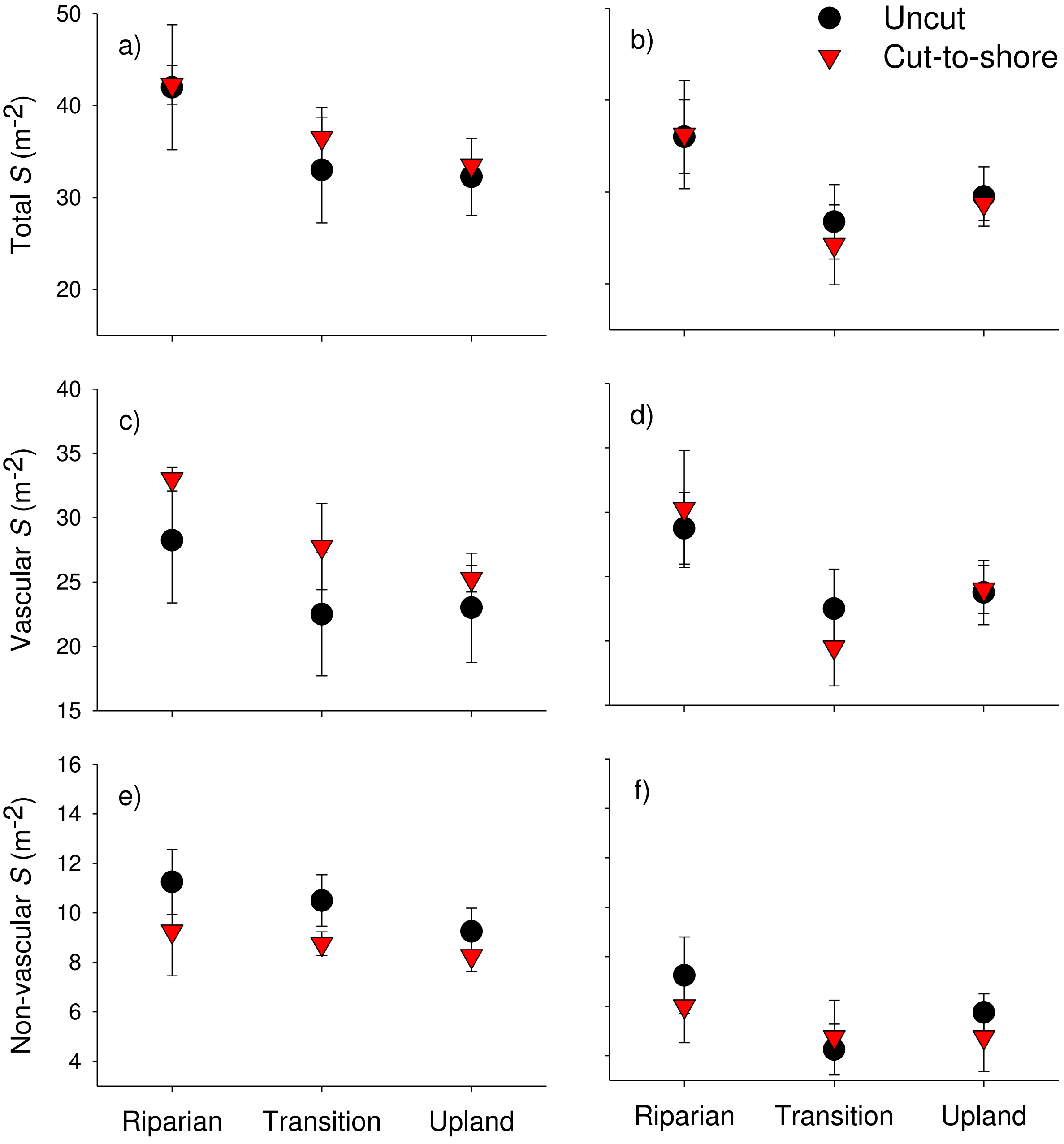


Figure 5.2 Mean (± 1 Standard Error) species richness (S) of total, vascular and non-vascular plant species in relation to riparian, transition, and upland habitat and harvesting treatment (uncut and cut-to-shore boreal) in non-scarified (left panels) and scarified (right panels) Boreal Shield watersheds.

Table 5.1 Total, vascular and non-vascular species richness in relation to habitat and harvesting on Boreal Shield watersheds.

Source	d.f.	F	P	η^2
Non-scarified				
Total Species richness† ($r^2 = 0.22$)				
Habitat (H_i)	2	2.06	0.16	0.19
Disturbance (D_j)	1	0.65	0.43	0.04
Habitat x disturbance (HD_{ij})	2	0.09	0.92	0.01
Error ($\varepsilon_{(ij)k}$)	18			
Vascular Species richness† ($r^2 = 0.24$)				
Habitat (H_i)	2	1.46	0.26	0.14
Disturbance (D_j)	1	2.53	0.13	0.12
Habitat x disturbance (HD_{ij})	2	0.09	0.92	0.01
Error ($\varepsilon_{(ij)k}$)	18			
Non-vascular Species richness† ($r^2 = 0.39$)				
Habitat (H_i)	2	1.17	0.33	0.12
Disturbance (D_j)	1	4.00	0.06	0.18
Habitat x disturbance (HD_{ij})	2	0.19	0.83	0.02
Error ($\varepsilon_{(ij)k}$)	18			
Scarified				
Total Species richness ($r^2 = 0.29$)				
Habitat (H_i)	2	3.5	0.05	0.28
Disturbance (D_j)	1	0.9	0.77	<0.01
Habitat x disturbance (HD_{ij})	2	0.06	0.94	<0.01
Error ($\varepsilon_{(ij)k}$)	18			
Vascular Species richness ($r^2 = 0.32$)				
Habitat (H_i)	2	3.96	0.04	0.31
Disturbance (D_j)	1	0.0.	0.87	0.01
Habitat X disturbance (HD_{ij})	2	0.29	0.76	0.03
Error ($\varepsilon_{(ij)k}$)	18			
Non-vascular Species richness ($r^2 = 0.16$)				
Habitat (H_i)	2	1.35	0.28	0.13
Disturbance (D_j)	1	0.28	0.59	0.02
Habitat x disturbance (HD_{ij})	2	0.26	0.77	0.03
Error ($\varepsilon_{(ij)k}$)	18			

† Variables are ln-transformed

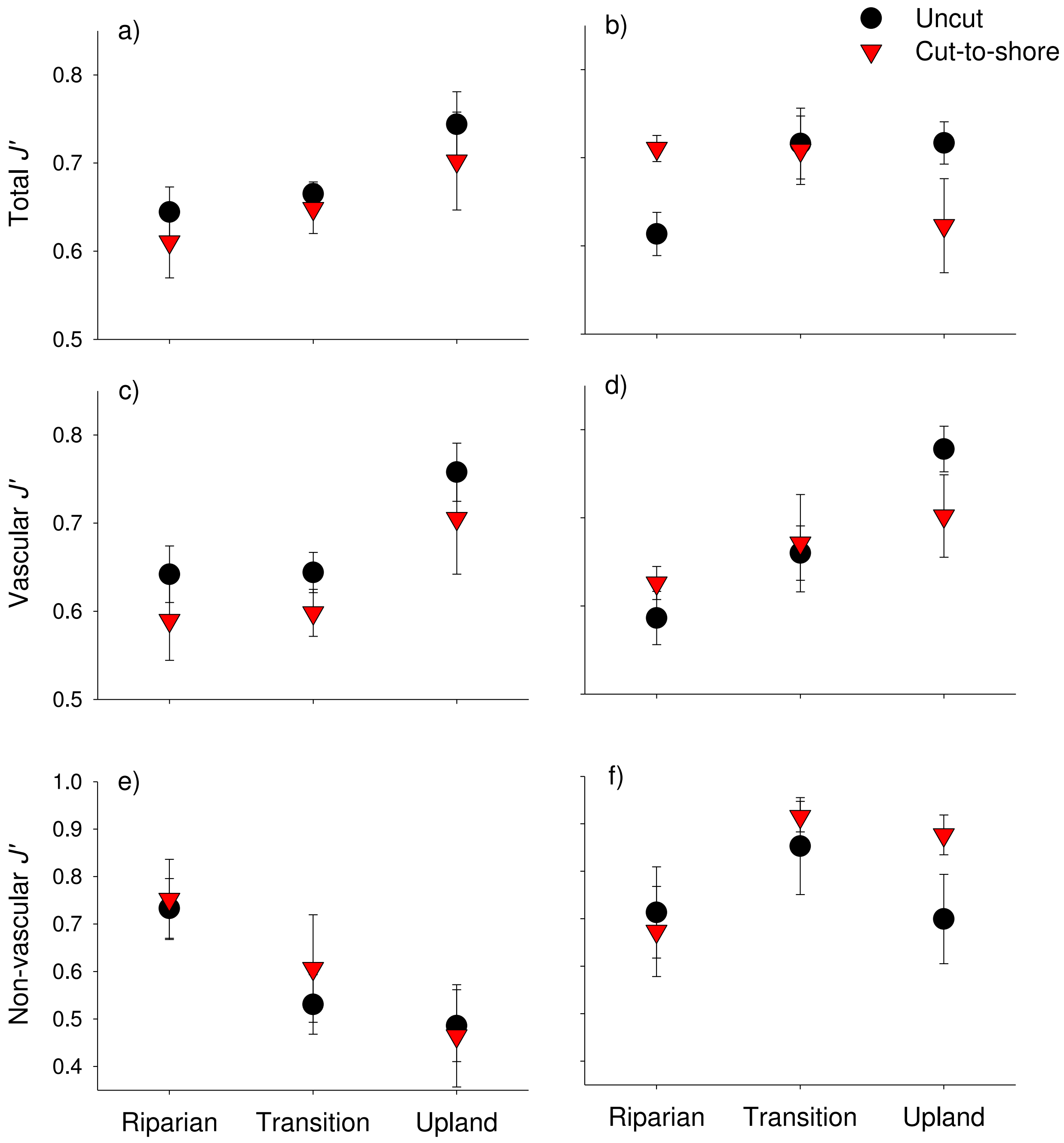


Figure 5.3 Mean (± 1 Standard Error) species evenness (*J'*) of total, vascular and non-vascular plant species in relation to riparian, transition, and upland habitat and harvesting treatment (uncut and cut-to-shore boreal) in non-scarified (left panels) and scarified (right panels) Boreal Shield watersheds.

Table 5.2 Total, vascular and non-vascular species evenness in relation to habitat and harvesting on Boreal Shield watersheds.

Source	d.f.	F	P	η^2
Non-scarified				
Total evenness ($r^2 = 0.13$)				
Habitat (H_i)	2	0.68	0.52	0.07
Disturbance (D_j)	1	0.89	0.36	0.05
Habitat x disturbance (HD_{ij})	2	0.19	0.83	0.02
Error ($\varepsilon_{(ij)k}$)	18			
Vascular evenness ($r^2 = 0.43$)				
Habitat (H_i)	2	5.47	0.01	0.38
Disturbance (D_j)	1	2.43	0.13	0.12
Habitat x disturbance (HD_{ij})	2	0.01	0.99	<0.01
Error ($\varepsilon_{(ij)k}$)	18			
Non-vascular evenness ($r^2 = 0.36$)				
Habitat (H_i)	2	4.89	0.02	0.35
Disturbance (D_j)	1	0.12	0.74	0.01
Habitat x disturbance (HD_{ij})	2	0.16	0.86	0.02
Error ($\varepsilon_{(ij)k}$)	18			
Scarified				
Total evenness ($r^2 = 0.10$)				
Habitat (H_i)	2	0.25	0.79	0.03
Disturbance (D_j)	1	1.29	0.27	0.07
Habitat x disturbance (HD_{ij})	2	0.14	0.87	0.02
Error ($\varepsilon_{(ij)k}$)	18			
Vascular evenness ($r^2 = 0.47$)				
Habitat (H_i)	2	6.65	0.01	0.43
Disturbance (D_j)	1	0.08	0.79	<0.01
Habitat x disturbance (HD_{ij})	2	1.35	0.29	0.13
Error ($\varepsilon_{(ij)k}$)	18			
Non-vascular evenness ($r^2 = 0.31$)				
Habitat (H_i)	2	2.71	0.09	0.23
Disturbance (D_j)	1	0.99	0.33	0.05
Habitat x disturbance (HD_{ij})	2	0.88	0.43	0.09
Error ($\varepsilon_{(ij)k}$)	18			

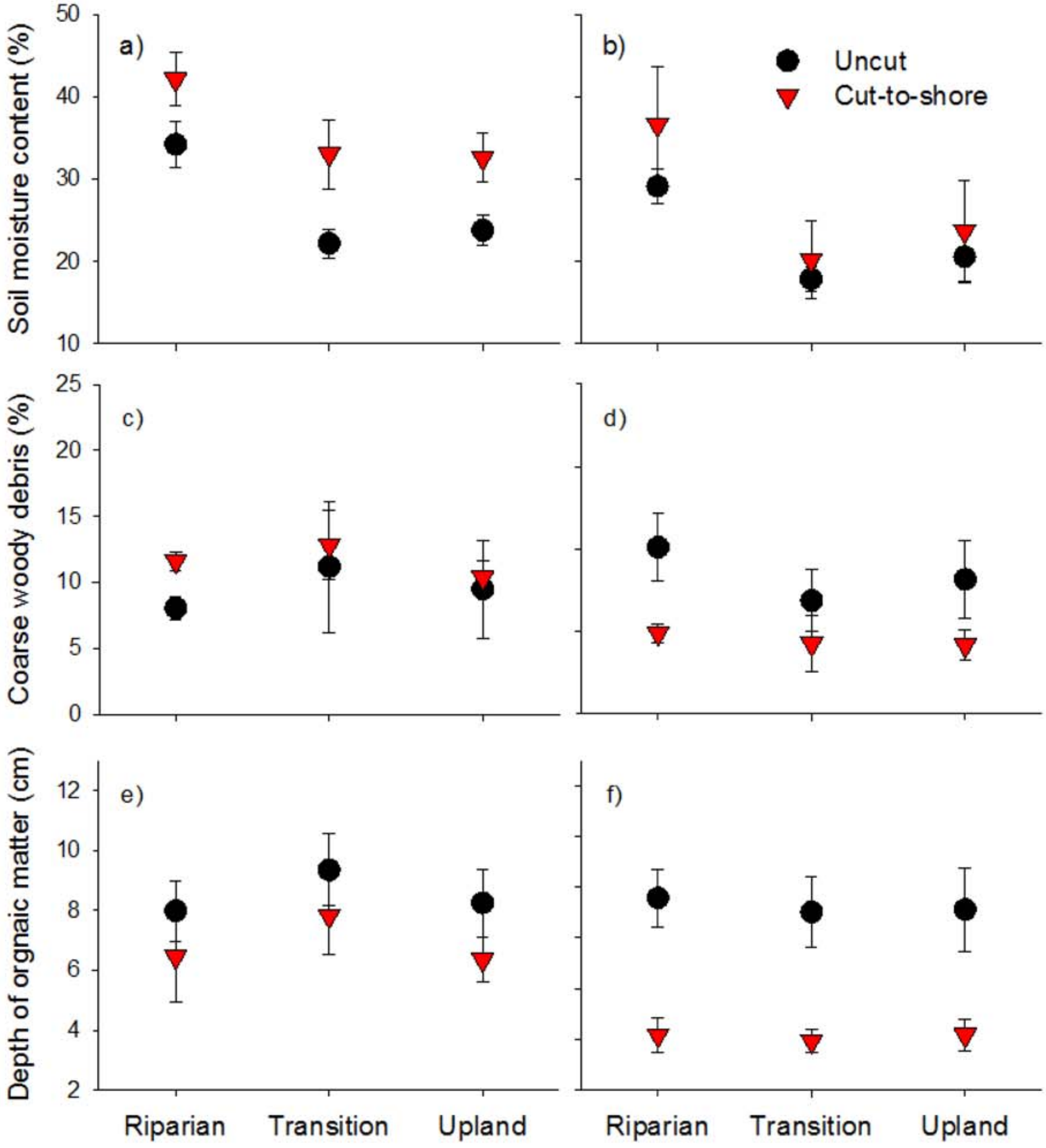


Figure 5.4 Average site data (± 1 SE) of soil moisture (a-b), coarse woody debris (c-d), and depth of organic matter (e-f) in non-scarified (left panels) and scarified (right panels) boreal watersheds.

A three-dimensional NMS ordination was identified with a final stress of 11.87 (Fig 5.5). Although the ordination was only done once, both watersheds were separated in the graph to aid interpretation. Axes 1, 2 and 3 account for 23%, 32%, and 29% of the understory variability, respectively. The first axis was positively associated with fire weed (Epilobium angustifolium), and other species associated with open canopies (Rubus idaeus, Solidago canadensis, Calamagrostis canadensis) and moist ground, including rushes (Juncus spp.) and sedges (Carex spp.); and negatively associated with tall shrubs, including mountain maple (Acer spicatum) and beaked hazelnut (Corylus cornuta), and the forbs wild sarsaparilla (Aralia nudicaulis) and blue bead lily (Clintonia borealis). The second axis is positively associated with grasses such as bluejoint (Calamagrostis canadensis) and false melic (Schizachne purpurascens) and pin cherry (Prunus pensylvanica); and negatively associated with feathermosses (i.e., Pleurozium schreberi, Ptilium crista-castrensis, and Hylocomium splendens). The third axis represents a gradient of riparian species, including speckled alder (Alnus rugosa) and ferns (i.e., Athyrium filix-femina and Thelypteris phegopteris) to common upland species including ericaceous shrubs, such as Labrador tea (Rhododendron groenlandicum), forbs, such as bunchberry (Cornus canadensis), and forest floor mosses (i.e., P. schreberi and Dicranum polysetum). Axis 1 of the NMS ordination was positively correlated with soil moisture content ($r^2 = 0.05$), and axis 2 was negatively correlated with coarse woody debris ($r^2 = 0.15$) and depth of organic matter ($r^2 = 0.60$) (Figure 5.5b).

Sites in the non-scarified watershed are ordinated in species space based on habitat, but not disturbance; sites are grouped from riparian to upland along the third axis. Conversely, sites in the scarified watershed are strongly grouped by harvesting disturbance (i.e., cut or uncut) along the second axis; from grasses to feathermosses. The MRPP supports the results of the ordination; there was not a detectable difference in the understory vegetation among harvesting treatments in the non-scarified watershed, but there was in the scarified riparian and upland sites (Table 5.3). However, separation among harvested and uncut sites was greater in the upland than the riparian sites, as indicated by the T value.

Table 5.3 MRPP comparing understory composition among uncut and harvested treatments in riparian, transition and upland habitats in two Boreal Shield watersheds. The value of the test statistic (T), agreement within group (A) and the significance of the association (P-value) are presented. Significant effects are in boldface.

Site Classification	T	A	P
Scarified			
Riparian	**-1.85**	**0.07**	**0.04**
Transition	-1.12	0.05	0.10
Upland	**-2.20**	**0.09**	**0.03**
Non-scarified			
Riparian	-0.69	0.02	0.24
Transition	-0.31	0.02	0.29
Upland	-0.70	0.02	0.22

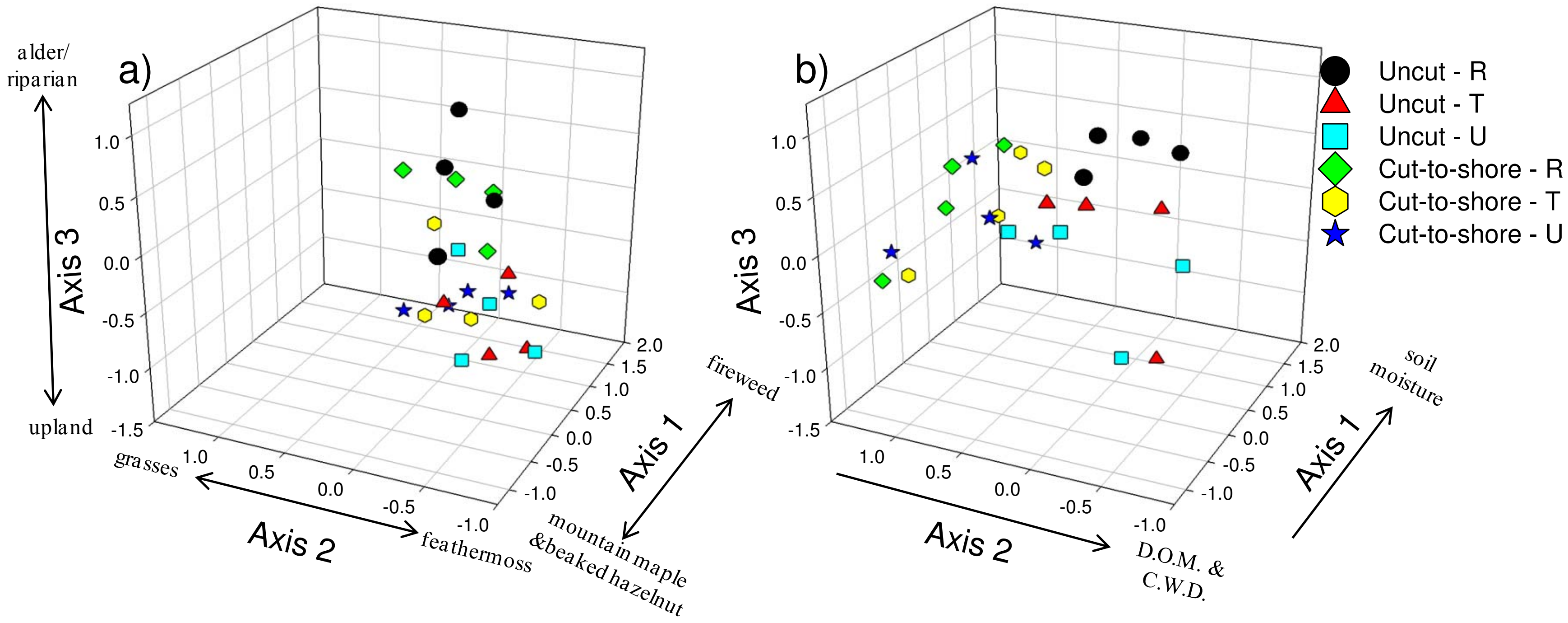


Figure 5.5 NMS ordination of average site data from a) non-scarified, and b) scarified watersheds in species space. Axes 1, 2, and 3 account for 23%, 32%, and 29% of the understory variability, respectively. Species and environmental associations with ordination axes are calculated from Kendall's rank correlation (tau) and Pearson's correlation, respectively. Species space in both ordinations is identical and axes gradients apply to both figures.

5.5 Discussion

Regardless of disturbance severity, vascular and non-vascular diversity (species richness and evenness) was not related to harvesting. Moreover, the diversity-disturbance relationship did not differ detectably among habitats. My results correspond to another study from the central Boreal Shield, which found similar patterns of diversity, in both riparian and upland habitats, following clearcutting with and without scarification (Biswas and Mallik 2010). Changes in the understory plant communities are rapid immediately following disturbance, followed by a gradual return to a condition similar to pre-disturbance (Halpern 1988). I suspect that nine years after the disturbance event, extirpation events of disturbance sensitive species, such as bryophytes, are likely to be similar to initial colonization events, thus balancing species diversity.

The changes to community membership following harvesting were more complex. Differences in understory species composition were not discernible nine years following harvest, in all habitats, in the non-scarified watershed, suggesting these boreal plant communities are resilient to stand-replacing disturbance events that leave the forest floor and soil relatively intact. As found in other studies (Halpern 1988, Nguyen-Xuan et al. 2000), harvesting following by mechanical site preparation had a profound effect on the understory vegetation community. However, in my study this effect varied with habitat. The riparian and upland plots that were harvested and scarified diverged from the uncut plant communities, but the transitional communities did not. Transitional communities retain species of both riparian and upland communities and thus the constitute flora has lesser site fidelity, and likely tolerates a wider range of environmental conditions. Unlike upland communities, transitional communities contain riparian species that are generally tolerant of stand-replacing disturbance

(Lamb et al. 2003, Dynesius et al. 2009), but are not as directly influenced by flow-facilitated propagules distribution, and subsequent colonization, as streamside communities. Riparian plots in the harvested sites of the scarified watershed retained their position along axis 3 of the ordination, which represented the gradient of riparian to upland species, but they did increase in abundance of grasses as indicated by a positive move along the second axis. Grasses are early colonizing species in riparian forests, which exhibit rapid growth through wind and water dispersed seeds and multiple tillers (Lamb and Mallik 2003). Upland plots in the scarified watershed had the greatest shift in species composition (Fig 5.4). Boreal upland forests are often dominated by bryophyte communities, which are generally intolerant to stand-replacing disturbance (Frego and Carleton 1995, Fenton and Frego 2005). Furthermore, scarification reduced coarse woody debris and depth of organic material, which is positively correlated with the growth of bryophytes (He and Barclay 2000), thus exacerbating the effects of harvesting on upland boreal communities.

In conclusion, I report two key findings from this study. First, effects of forest harvesting on boreal understory species diversity were not detectable nine years following harvesting regardless of level of soil disturbance. Second, understory boreal community composition was not strongly affected by harvesting when forest floor and soil disturbance in minimal. Scarification profoundly altered the substrate by breaking up coarse woody debris and decreasing the depth of organic matter, which destroyed forest floor feathermosses and created a habitat suitable for early colonizing species (i.e., grasses).

CHAPTER 6 CONCLUSION

Over the past two decades, there has been a substantial increase in our understanding of the value of riparian areas as unique components across the landscape (Richardson et al. 2005). While it is clear that the stream is strongly linked with the adjacent riparian areas, how this linkage affects the communities' ability to cope with logging disturbance remains elusive. Moreover, what is known about riparian vegetation dynamics is largely a result of studies of medium to large stream systems. Managing ecological values provided by small stream riparian ecosystems continue to be a focus of debate. Current management prescriptions (i.e., static width buffers) have no natural analogue and appear to have little scientific basis. Although it is not my intent, nor possible given the specific objectives of this thesis, to reconcile how small stream riparian systems are managed, the data presented within this dissertation contribute to filling the gap of knowledge of understory vegetation dynamics within small stream systems.

6.1 Effects of harvesting across the riparian ecotone

The main findings of this dissertation support my prediction that disturbance-response relationships vary among habitat type. Specifically, in small stream systems, overstory harvesting exerts stronger controls on understory vegetation with increasing distance from the stream channel. Direct evidence of this was presented in chapter three, as compositional stability of understory vegetation after harvesting decreased from stream to upland. Moreover, shifts in the understory plant diversity, abundance, and species turnover were greater in the upland than in streamside communities. This finding is a direct reflection of the different mechanisms structuring understory flora along a riparian to upland gradient. Riparian flora bordering small stream ecosystems are driven by hydrological processes and frequent flooding regimes, whereas upland flora is driven primarily by the canopy and its strong controls on resource availability. Along the gradient from the stream channel into the upland in the boreal forest, understory species shift from a diverse community of riparian obligates (hydrophilous species), ruderals and generalist understory species to a community dominated by shade-tolerant species adapted to survive in resource-stressed environments at the trade-off of being less competitive in productive habitats. In my boreal study areas, this gradient also included a shift in dominance from vascular species in the streamside communities to non-vascular species in the upland. As indicated in other boreal studies (e.g., Fenton et al. 2003, Hart and Chen 2008), vascular species are more resilient to overstory harvesting than non-vascular species as I found a strong negative relationship between compositional stability following harvesting and pre-harvest non-vascular cover. Moreover, changes in non-vascular species abundance and turnover were greater than those in vascular species following harvesting. Therefore assumptions on effects of overstory harvesting on understory communities derived from upland forests likely do not extrapolate to riparian systems.

6.2 Effect of scarification

Streamside communities did not have detectable changes in community diversity, abundance or composition following overstory harvesting without mechanical site preparation. However, boreal understory communities, in both riparian and upland habitats, were profoundly affected by harvesting when forest floor and soil disturbance is severe. Scarification altered the substrate by breaking up coarse woody debris and decreasing the depth of organic matter, which destroyed forest floor flora, such as feathermosses, and created a habitat suitable for early colonizing species (i.e., grasses).

6.3 Management implications

This study provides evidence of higher resilience of streamside than upland communities in small stream boreal forests; however there are three caveats for management applications stemming directly from these results. First, this study illustrates early seral responses (less than 10 years) and therefore it is possible that that there continues to be changes in riparian communities as directional shifts in species composition and diversity have been shown to last for more than a decade (Thomas et al. 1999, Halpern et al. 2005, Belote et al. 2012). Longer term investigation into riparian dynamics following disturbance harvesting is recommended. Second, in the main Boreal Plain study and one watershed (i.e., Dog River) in the Boreal Shield study, ground disturbance was minimal to not confound effects of overstory removal. Specifically, harvesting was done during the winter months, when the ground was frozen, to minimize soil compaction, and mechanical site preparation (e.g., scarification) was restricted to be outside of 30 m from the stream channel. Extirpation and colonization processes may be exaggerated when ground disturbance is more severe. Third, vegetation responses may not parallel responses in other ecosystem processes such as nutrient leaching, soil erosion, changes to water quality and quantity, or other negative effects from harvesting. Future studies focused on changes in riparian vegetation should be linked with our evolving knowledge of watershed processes following disturbance, such as patterns in surface and sub-surface hydrology (e.g., Parratt 2012).

Finally, although streamside communities were similar among harvesting treatments, the understory communities diverged among harvesting treatments with increasing distance from the stream channel. In other words, communities harboured different species following contrasting levels of harvesting treatments. If increasing diversity across the landscape is a goal of forest managers, than using a variety of riparian management prescriptions to increase habitat heterogeneity, thus meeting the resource and competitive requirements of more species, is recommended.

Literature Cited

Alaback, P. B. 1982. Dynamics of understory biomass in sitka spruce western hemlock forests of southeast Alaska. Ecology 63:1932-1948.

Alaback, P. B. 1986. Biomass regression equations for understory plants in coastal Alaska - effects of species and sampling design on estimates. Northwest Science 60:90-103.

Åström, M., M. Dynesius, K. Hylander, and C. Nilsson. 2007. Slope aspect modifies community responses to clear-cutting in Boreal forests. Ecology 88:749-788.

Bakker, C., J. M. Blair, and A. K. Knapp. 2003. Does resource availability, resource heterogeneity or species turnover mediate changes in plant species richness in grazed grasslands? Oecologia 137:385-391.

Bartels, S. F. and H. Y. H. Chen. 2010. Is understory plant species diversity driven by resource quantity or resource heterogeneity? Ecology 91:1931-1938.

Belote, T. R., R. H. Jones, and R. Wieboldt. 2012. Compositional stability and diversity of vascular plants following logging disturbance in Appalachian forests. Ecological Applications 22:502-516.

Bergeron, Y. and B. Harvey. 1997. Basing silviculture on natural ecosystem dynamics: An approach applied to the southern boreal mixedwood forest of Quebec. Forest Ecology and Management 92:235-242.

Biswas, S. R. and A. U. Mallik. 2010. Disturbance effects on species diversity and functional diversity in riparian and upland plant communities. Ecology 91:28-35.

Bock, M. D. and K. C. J. Van Rees. 2002. Forest harvesting impacts on soil properties and vegetation communities in the Northwest Territories. Canadian Journal of Forest Research 32:713-724.

Braithwaite, N. T. and A. U. Mallik. 2012. Edge effects of wildfire and riparian buffers along boreal forest streams. Journal of Applied Ecology 49:192-201.

Bray, J. R. and J. T. Curtis. 1957. An ordination of the upland forest communities in southern Wisconsin. Ecological Monographs 27:325-349.

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

Brown, G. W. and J. T. Krygier. 1970. Effects of clearcutting on stream temperature. Water Resource Science 6:1133-1139.

Brown, R. L. and R. K. Peet. 2003. Diversity and invasibility of southern Appalachian plant communities. Ecology 84:32-39.

Brumelis, G. and T. J. Carleton. 1989. The vegetation of post-logged black spruce lowlands in central Canada: Understory vegetation. Journal of Applied Ecology 26:321-339.

Buttle, J. M. 2002. Rethinking the donut: the case for hydrologically relevant buffer zones. Hydrological Processes 16:3093-3096.

Caldwell, M. M. 1987. Competition between root systems in natural communities. Pages 167-185 in P. J. Gregory, J. V. Lake, and D. A. Rose, editors. Root Development and Function. Cambridge University Press, Cambridge, UK.

Carleton, T. J. 1979. Floristic variation and zonation in the boreal forest south of James Bay: a cluster seeking approach. Vegetatio 39:147-160.

Chapin, F. S. 1993. Functional role of growth forms in ecosystems and global processes. Pages 287-312 in J. R. Ehleringer and C. B. Field, editors. Scaling physiological processes: leaf to globe. Academic Press, San Diego, CA.

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

Chiarucci, A., J. B. Wilson, B. J. Anderson, and V. De Dominicis. 1999. Cover versus biomass as an estimate of species abundance: does it make a difference to the conclusions? Journal of Vegetation Science 10:35-42.

Clarke, R. K. 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18:117-143.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs - high diversity of trees and corals is maintained only in a non-equilibrium state. Science 199:1302-1310.

Connell, J. H. and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. American Naturalist 111:1119-1144.

Darveau, M., P. Labbe, P. Beauchesne, L. Belanger, and J. Huot. 2001. The use of riparian forest strips by small mammals in a boreal balsam fir forest. Forest Ecology and Management 143:95-104.

De Caceres, M. and P. Legendre. 2009. Associations between species and groups of sites: indices and statistical inference. Ecology 90:3566-3574.

De Caceres, M., P. Legendre, and M. Moretti. 2010. Improving indicator species analysis by combining groups of sites. Oikos 119:1674-1684.

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

Decocq, G. 2002. Patterns of plant species and community diversity at different organization levels in a forested riparian landscape. Journal of Vegetation Science 13:91-106.

Dignan, P. and L. Bren. 2003. A study of the effect of logging on the understorey light environment in riparian buffer strips in a south-east Australian forest. Forest Ecology and Management 172:161-172.

Dong, J., J. Chen, K. D. Brosofske, and R. J. Naiman. 1998. Modelling air temperature gradients across managed small streams in western Washington. Journal of Environmental Management 53:309-321.

Dynesius, M. and K. Hylander. 2007. Resilience of bryophyte communities to clear-cutting of boreal stream-side forests. Biological Conservation 135:423-434.

Dynesius, M., K. Hylander, and C. Nilsson. 2009. High resilience of bryophyte assemblages in streamside compared to upland forests. Ecology 90:1042-1054.

Elton, C. S. 1958. The Ecology of Invasions by Plants and Animals. Methuen, London, UK.

Environment Canada. 2011. Canadian Climate Normals 1981-2010. Accessed on June 25, 2011.

Fenton, N. J. and K. A. Frego. 2005. Bryophyte (moss and liverwort) conservation under remnant canopy in managed forests. Biological Conservation 122:417-430.

Fenton, N. J., K. A. Frego, and M. R. Sims. 2003. Changes in forest floor bryophyte (moss and liverwort) communities 4 years after forest harvest. Canadian Journal of Botany-Revue Canadienne De Botanique 81:714-731.

Fenton, N. J., M. Simard, and Y. Bergeron. 2009. Emulating natural disturbances: the role of silviculture in creating even-aged and complex structures in the black spruce boreal forest of eastern North America. Journal of Forest Research 14:258-267.

Foster, B. L., V. H. Smith, T. L. Dickson, and T. Hildebrand. 2002. Invasibility and compositional stability in a grassland community: relationships to diversity and extrinsic factors. Oikos 99:300-307.

Frank, D. A. and S. J. McNaughton. 1991. Stability increases with diversity in plant communities: empirical evidence from the 1988 Yellowstone drought. Oikos 62:360-362.

Frego, K. A. 2007. Bryophytes as potential indicators of forest integrity. Forest Ecology and Management 242:65-75.

Frego, K. A. and T. J. Carleton. 1995. Microsite conditions and spatial pattern in a boreal bryophyte community. Canadian Journal of Botany 73:544-551.

Fyles, J. W. 1989. Seed bank populations in upland coniferous forests in central Alberta. Canadian Journal of Botany 67:274-278.

Gholz, H. L., R. F. Fisher, and W. L. Pritchett. 1985a. Nutrient dynamics in slash pine plantation ecosystems. Ecology 66:647-659.

Gholz, H. L., G. M. Hawk, A. Campbell, K. Cromack, and A. T. Brown. 1985b. Early vegetation recovery and element cycles on a clear-cut watershed in western Oregon. Canadian Journal of Forest Research 15:400-409.

Gholz, H. L., G. M. Hawk, A. Campbell, K. Cromack, and A. T. Brown. 1985c. Early vegetation recovery and element cycles on a clear-cut watershed in western Oregon. Canadian Journal of Forest Research 15:400-409.

Giese, L. A. B., W. M. Aust, R. K. Kolka, and C. C. Trettin. 2003. Biomass and carbon pools of disturbed riparian forests. Forest Ecology and Management 180:493-508.

Gilliam, F. S. 2007. The ecological significance of the herbaceous layer in temperate forest ecosystems. Bioscience 57:845-858.

Gilliam, F. S. and M. R. Roberts. 2003. The dynamic nature of the herbaceous layer.in F. S. Gilliam and M. R. Roberts, editors. The herbaceous layer in forests of eastern North America. Oxford University Press, New York, New York, USA.

Goebel, P. C., B. J. Palik, and K. S. Pregitzer. 2003. Plant diversity contributions of riparian areas in watersheds of the northern lake states, USA. Ecological Applications 13:1596-1609.

Goldberg, D. E. and A. M. Barton. 1992. Patterns and consequences of interspecific competition in natural communities - a review of field experiments with plants. American Naturalist 139:771-801.

Gregory, S. V., R. Beschta, F. Swanson, J. R. Sedell, G. Reeves, and F. Everest. 1990. Abundance of conifers in Oregon's riparian forests. College of Forestry, Oregon State University, Corvalis, Oregon, USA.

Grime, J. P. 2001. Plant Strategies, Vegetation Processes, and Ecosystem Properties. 2nd Edition edition. John Wiley & Sons, LTD, Chichester.

Gunnarsson, B., K. Nitterus, and P. Wirdenas. 2004. Effects of logging residue removal on ground-active beetles in temperate forests. Forest Ecology and Management 201:229-239.

Gurevitch, J., L. L. Morrow, A. Wallace, and J. S. Walsh. 1992. A meta-analysis of competition in field experiments. American Naturalist 140:539-572.

Haddad, N. M., M. Holyoak, T. M. Mata, K. F. Davies, B. A. Melbourne, and K. Preston. 2008. Species' traits predict the effects of disturbance and productivity on diversity. Ecology Letters 11:348-356.

Haeussler, S., L. Bedford, A. Leduc, Y. Bergeron, and J. M. Kranabetter. 2002. Silvicultural disturbance severity and plant communities of the southern Canadian boreal forest. Silva Fennica 36:307-327.

Halpern, C. B. 1988. Early successional pathways and the resistance and resilience of forest communities. Ecology 69:1703-1715.

Halpern, C. B., D. McKenzie, S. A. Evans, and D. A. Maguire. 2005. Initial responses of forest understories to varying levels and patterns of green-tree retention. Ecological Applications 15:175-195.

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

Hamilton, E. H. and S. Haeussler. 2008. Modeling stability and resilience after slashburning across a sub-boreal to subalpine forest gradient in British Columbia. Canadian Journal of Forest Research 38:304-316.

Hart, S. A. and H. Y. H. Chen. 2006. Understory vegetation dynamics of North American boreal forests. Critical Reviews in Plant Sciences 25:381-397.

Hart, S. A. and H. Y. H. Chen. 2008. Fire, logging, and overstory affect understory abundance, diversity, and composition in boreal forest. Ecological Monographs 78:123-140.

He, F. L. and H. J. Barclay. 2000. Long-term response of understory plant species to thinning and fertilization in a Douglas-fir plantation on southern Vancouver Island, British

Columbia. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 30:566-572.

Hefting, M. M., J. C. Clement, P. Bienkowski, D. Dowrick, C. Guenat, A. Butturini, S. Topa, G. Pinay, and J. T. A. Verhoeven. 2005. The role of vegetation and litter in the nitrogen dynamics of riparian buffer zones in Europe. Ecological Engineering 24:465-482.

Hughes, J. W. and T. J. Fahey. 1991. Colonization dynamics of herbs and shrubs in a disturbed northern hardwood forest. The Journal of Ecology 79:605-616.

Huynh, H. and L. S. Feldt. 1976. Estimation of the box correction for the degrees of freedom from sample data in the randomized block and split plot designs. Journal of Educational Statistics 1:69-82.

Hylander, K. 2005. Aspect modifies the magnitude of edge effects on bryophyte growth in boreal forests. Journal of Applied Ecology 42:518-525.

Ilisson, T. and H. Y. H. Chen. 2009. The direct regeneration hypothesis in northern forests. Journal of Vegetation Science 20:735-744.

Isbell, F., V. Calcagno, A. Hector, J. Connolly, W. S. Harpole, P. B. Reich, M. Scherer-Lorenzen, B. Schmid, D. Tilman, J. van Ruijven, A. Weigelt, B. J. Wilsey, E. S. Zavaleta, and M. Loreau. 2011. High plant diversity is needed to maintain ecosystem services. Nature 477:199-U196.

Ives, A. R. and S. R. Carpenter. 2007. Stability and diversity of ecosystems. Science 317:58-62.

Johnson, C. J., N. D. Alexander, R. D. Wheate, and K. L. Parker. 2003. Characterizing woodland caribou habitat in sub-boreal and boreal forests. Forest Ecology and Management 180:241-248.

Johnson, D. W. and P. S. Curtis. 2001. Effects of forest management on soil C and N storage: meta analysis. Forest Ecology and Management 140:227-238.

Johnson, E. A. 1992. Fire and vegetation dynamics - studies from the North American boreal forest. Cambridge University Press, Cambridge, UK.

Jonasson, S. 1988. Evaluation of the point intercept method for the estimation of plant biomass. Oikos 52:101-106.

Kern, C. C., B. J. Palik, and T. F. Strong. 2006. Ground-layer plant community responses to even-age and uneven-age silvicultural treatments in Wisconsin northern hardwood forests. Forest Ecology and Management 230:162-170.

King, A. W. and S. L. Pimm. 1983. Complexity, diversity, and stability - a reconciliation of theoretical and empirical results. American Naturalist 122:229-239.

Kiniry, J. R., J. D. Macdonald, A. R. Kemanian, B. Watson, G. Putz, and E. E. Prepas. 2008. Plant growth simulation for landscape-scale hydrological modelling. Hydrological Sciences Journal 53:1030-1042.

Knops, J. M. H., T. H. Nash, and W. H. Schlesinger. 1996. The influence of epiphytic lichens on the nutrient cycling of an oak woodland. Ecological Monographs 66:159-179.

Korol, J. B. 1996. Riparian forest communities in the southern boreal region of central Saskatchewan. Prince Albert Model Forest Association Inc.

Kuusipalo, J. 1983. On the distribution of blueberry biomass in different forest stands. Silva Fennica 17:245-257.

Lamb, E. G. and A. U. Mallik. 2003. Plant species traits across a riparian-zone/forest ecotone. Journal of Vegetation Science 14:853-858.

Lamb, E. G., A. U. Mallik, and R. W. Mackereth. 2003. The early impact of adjacent clearcutting and forest fire on riparian zone vegetation in northwestern Ontario. Forest Ecology and Management 177:529-538.

Lavorel, S. and E. Garnier. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Functional Ecology 16:545-556.

Lawton, J. H., S. Naeem, L. J. Thompson, A. Hector, and M. J. Crawley. 1998. Biodiversity and ecosystem function: getting the Ecotron experiment in its correct context. Functional Ecology 12:848-852.

Lee, K. H., T. M. Isenhart, and R. C. Schultz. 2003. Sediment and nutrient removal in an established multi-species riparian buffer. Journal of Soil and Water Conservation 58:1-8.

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

Luke, S. H., N. J. Luckai, J. M. Burke, and E. E. Prepas. 2007. Riparian areas in the Canadian boreal forest and linkages with water quality in stream. Environmental Reviews 15:79-97.

Lyon, J. and C. L. Sagers. 1998. Structure of herbaceous plant assemblages in a forested riparian landscape. Plant Ecology 138:1-16.

Macarthur, R. 1955. Fluctuations of animal populations, and a measure of community stability. Ecology 36:533-536.

Macdonald, E., C. J. Burgess, G. J. Scrimgeour, S. Boutin, S. Reedyk, and B. Kotak. 2004. Should riparian buffers be part of forest management based on emulation of natural disturbance? Forest Ecology and Management 187:185-196.

MacLean, D. A. and R. W. Wein. 1977. Changes in understory vegetation with increasing stand age in New Brunswick forests: species composition, cover, biomass and nutrients. Canadian Journal of Botany 55:2818-2831.

Manders, P. T. 1990. Soil seed banks and postfire seed deposition across a forest-fynbos ecostone in the Cape province. Journal of Vegetation Science 1:491-498.

May, R. M. 1974. Stability and Complexity in Model Ecosystems. Princeton Unversity Press, Princeton, NJ.

McCann, K. S. 2000. The diversity-stability debate. Nature 405:228-233.

McCune, B. and J. B. Grace. 2002. Analysis of Ecological Communities. MjM Software Design, Gleneden Beach, Oregon, USA.

McCune, B. and M. J. Mefford. 2005. PC-ORD Version 5.0. MjM Software Design, Gleneden Beach, Oregon, USA.

McNaughton, S. J. 1977. Diversity and stability of ecological communities - comment on role of empiricism in ecology. American Naturalist 111:515-525.

Messier, C., S. Parent, and Y. Bergeron. 1998. Effects of overstory and understory vegetation on the understory light environment in mixed boreal forests. Journal of Vegetation Science 9:511-520.

Mielke, P. W. and K. J. Berry. 2001. Permutation methods: a distance function approach. Springer, New York, NY.

Mueller-Dombois, D. and H. Ellenberg. 1974. Aims and Methods of Vegetation Ecology. Wiley and Sons, New York, New York, USA.

Muukkonen, P., R. Makipaa, R. Laiho, K. Minkkinen, H. Vasander, and L. Finer. 2006. Relationship between biomass and percentage cover in understorey vegetation of boreal coniferous forests. Silva Fennica 40:231-245.

Naeem, S., L. J. Thompson, S. P. Lawler, J. H. Lawton, and R. M. Woodfin. 1994. Declining biodiversity can alter the performance of ecosystems. Nature 368:734-737.

Naiman, R. J. and H. Décamps. 1997. The ecology of interfaces: riparian zones. Annual Review of Ecology, Evolution and Systematics 28:621-658.

Naiman, R. J., H. Decamps, and M. E. McClain. 2005. Riparia: ecology, conservation and management of streamside communities. Elsevier Academic Press, Amsterday.

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

Naimen, R. J. and H. Decamps. 1997. The ecology of interfaces: riparian zones. Annual Review of Ecology, Evolution and Systematics 28:621-658.

Nelson, C. R. and C. B. Halpern. 2005. Edge-related responses of understory plants to aggregated retention harvest in the pacific northwest. Ecological Applications 15:196-209.

Nguyen-Xuan, T., Y. Bergeron, D. Simard, J. W. Fyles, and D. Pare. 2000. The importance of forest floor disturbance in the early regeneration patterns of the boreal forest of western and central Quebec: a wildfire versus logging comparison. Canadian Journal of Forest Research 30:1353-1364.

Nieppola, J. J. and T. J. Carleton. 1991. Relations between understorey vegetation, site productivity, and environmental factors in Pinus sylvestris L. stands in southern Finland. Vegetatio 73:57-72.

Nierenberg, T. R. and D. E. Hibbs. 2000. A characterization of unmanaged riparian areas in the central Coast Range of western Oregon. Forest Ecology and Management 129:195-206.

Nilsson, M. C. and D. A. Wardle. 2005. Understory vegetation as a forest ecosystem driver: evidence from the northern Swedish boreal forest. Frontiers in Ecology and the Environment 3:421-428.

Noble, I. R. and R. O. Slatyer. 1980. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. Vegetatio 43:5-21.

Norris, V. 1993. The use of buffer zones to protect water quality: a review. Water Resource Management 7:257-272.

O'Neil, R. V. 1976. Ecosystem persistence and heterotrophic regulation. Ecology 57:1244-1253.

Odum, H. T. and R. C. Pinkerton. 1955. Time's speed regulator: the optimum efficiency for maximum power output in physical and biological systems. American Scientist 43:331-343.

Økland, R. H. 1995. Persistence of vascular plant in a Norwegian boreal coniferous forest. Ecography 18:3-14.

Økland, R. H. and O. Eilerston. 1996. Dynamics of understory vegetation in an old-growth boreal coniferous forest, 1988-1993. Journal of Vegetation Science 7:747-762.

Oksanen, J., G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. Simpson, P. Solymus, M. H. H. Stevens, and H. Wagner. 2011. vegan: Community Ecology Package. R package version 2.0-2.

Oliver, C. D. and B. C. Larson. 1996. Forest Stand Dynamics Update Edition. John Wiley & Sons, New York, NY.

Pabst, R. J. and T. A. Spies. 1999. Structure and composition of unmanaged riparian forests in the coastal mountains of Oregon, USA. Canadian Journal of Forest Research 29:1557-1573.

Palik, B. J., K. Cease, and L. Egeland. 2003. Aspen regeneration in riparian management zones in northern Minnesota: Effects of residual overstory and harvest method. Northern Journal of Applied Forestry 20:79-84.

Palik, B. J., R. J. Mitchell, and J. K. Hiers. 2002. Modeling silviculture after natural disturbance to sustain biodiversity in the longleaf pine (Pinus palustris) ecosystem: balancing complexity and implementation. Forest Ecology and Management 155:347-356.

Paquette, A. and C. Messier. 2010. The role of plantations in managing the world's forests in the Anthropocene. Frontiers in Ecology and the Environment 8:27-34.

Parratt, T. 2012. Characteristics of connectivity between harvested landscapes and fixed-width riparian buffers. M.Sc.F. Thesis, Lakehead University.

Payer, D. C. and D. J. Harrison. 2003. Influence of forest structure on habitat use by American marten in an industrial forest. Forest Ecology and Management 179:145-156.

Petit, N. E. and R. J. Naimen. 2007. Fire in the riparian zone: characteristics and ecological consequences. Ecosystems 10:673-687.

Pielou, E. C. 1969. Ecological diversity and it's measurement: An introduction to mathematical ecology. John Wiley & Sons, Toronto.

Pimm, S. L. 1984. The complexity and stability of ecosystems. Nature 307:321-326.

Planty-Tabacchi, A. M., E. Tabacchi, R. J. Naiman, C. Deferrari, and H. Decamps. 1996. Invasibility of species rich communities in riparian zones. Conservation Biology 10:598-607.

Porté, A. J., J. C. Samalens, R. Dulhoste, R. T. Du Cros, A. Bosc, and C. Meredieu. 2009. Using cover measurements to estimate aboveground understorey biomass in Maritime pine stands. Annals of Forest Science 66: 307.

Pysek, P. and K. Prach. 1993. Plant invasions and the role of riparian habitats - a comparison of 4 species allien to central europe. Journal of Biogeography 20:413-420.

Qi, M. Q. and J. B. Scarratt. 1998. Effect of harvesting method on seed bank dynamics in a boreal mixedwood forest in northwestern Ontario. Canadian Journal of Botany 76:872-883.

Qian, H., K. Klinka, and G. J. Kayashara. 1998. Longitudinal patterns of plant diversity in the North American boreal forest. Plant Ecology 138:161-178.

Reeves, G. H., P. A. Bisson, B. E. Rieman, and L. E. Benda. 2006. Postfire logging in riparian areas. Conservation Biology 20:994-1004.

Reich, P. B., P. Bakken, D. Carlson, L. E. Frelich, S. K. Friedman, and D. F. Grigal. 2001. Influence of logging, fire, and forest type on biodiversity and productivity in southern boreal forests. Ecology 82:2731-2748.

Richardson, J. S., R. J. Naiman, F. J. Swanson, and D. E. Hibbs. 2005. Riparian communities associated with Pacific Northwest headwater streams: Assemblages, processes, and uniqueness. Journal of the American Water Resources Association 41:935-947.

Roberts, M. R. 2007. A conceptual model to characterize disturbance severity in forest harvests. Forest Ecology and Management 242:58-64.

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

Roberts, M. R. and F. S. Gilliam. 2003. Interactions between the herbaceous layer and overstory canopy of eastern forests: A mechanism for linkages. Pages 198-223 in F. S. Gilliam and M. R. Roberts, editors. The Herbaceous layer in forests of eastern North America. Oxford University Press, New York.

Roberts, M. R. and L. Zhu. 2002. Early response of the herbaceous layer to harvesting in a mixed coniferous-decidous forest in New Brunswick, Canada. Forest Ecology and Management 155:17-31.

Rottgermann, M., T. Steinlein, W. Beyschlag, and H. Dietz. 2000. Linear relationships between aboveground biomass and plant cover in low open herbaceous vegetation. Journal of Vegetation Science 11:145-148.

Rowe, J. S. 1983. Concepts of fire effects on plant individual and species. Pages 134-154 in R. W. Wein and D. A. MacLean, editors. The role of fire in northern circumpolar ecosystems. John Wiley & Sons Ltd., New York, New York.

Royo, A. A. and W. P. Carson. 2006. On the formation of dense understory layers in forests worldwide: consequences and implications for forest dynamics, biodiversity, and succession. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 36:1345-1362.

Rydgren, K., N. Cronberg, and R. H. Okland. 2006. Factors influencing reproductive success in the clonal moss, Hylocomium splendens. Oecologia 147:445-454.

Saetre, P., L. S. Saetre, P. O. Brandtberg, H. Lundkvist, and J. Bengtsson. 1997. Ground vegetation composition and heterogeneity in pure Norway spruce and mixed Norway spruce - birch stands. Canadian Journal of Forest Research 27:2034-2042.

Scheller, R. M. and D. J. Mladenoff. 2002. Understory species patterns and diversity in old-growth and managed northern hardwood forests. Ecological Applications 12:1329-1343.

Schimmel, J. and A. Granstrom. 1996. Fire severity and vegetation response in the boreal Swedish forest. Ecology 77:1436-1450.

Schneider, R. L. and R. R. Sharitz. 1988. Hydrochory and regeneration in a bald cypress water tupelo swamp forest. Ecology 69:1055-1063.

Senici, D., H. Y. H. Chen, Y. Bergeron, and D. Cyr. 2010. Spatiotemporal variations of fire frequency in central boreal forest. Ecosystems 13:1227-1238.

Seymour, R. S., A. S. White, and P. G. deMaynadier. 2002. Natural disturbance regimes in northeastern North America - evaluating silvicultural systems using natural scales and frequencies. Forest Ecology and Management 155:357-367.

Shea, K., S. H. Roxburgh, and E. S. J. Rauschert. 2004. Moving from pattern to process: coexistence mechanisms under intermediate disturbance regimes. Ecology Letters 7:491-508.

Sibley, P. K., D. P. Kreutzweiser, B. J. Naylor, J. S. Richardson, and A. M. Gordon. 2012. Emulation of natural disturbance (END) for riparian forest management: synthesis and recommendations. Freshwater Science 31:258-264.

Slocum, M. G. and I. A. Mendelssohn. 2008. Use of experimental disturbances to assess resilience along a known stress gradient. Ecological Indicators 8:181-190.

Soil Classification Working Group 1998. The Canadian System of Soil Classification. NRC Research Press, Ottawa.

Sovik, A. K. and N. Syversen. 2008. Retention of particles and nutrients in the root zone of a vegetative buffer zone - effect of vegetation and season. Boreal Environment Research 13:223-230.

Stewart, K. J. and A. U. Mallik. 2006. Bryophyte response to microclimatic edge effects across riparian buffers. Ecological Applications 16:1474-1486.

Swanson, F. 1994. Natural disturbance effects on riparian areas. Pages 11-14 Riparian Resources, Proceedings of the Symposium - a Symposium on the Disturbances, Management, Economics, and Conflicts Associated with Riparian Ecosystems.

Tabachnick, B. G. and L. S. Fidell. 1989. Using multivariate statistics. Second edition. edition. Harper and Row, New York, New York, USA.

Thebaud, C. and M. Debussche. 1991. Rapid invasion of Fraxinus ornus L. along the Herault River System in southern France - the importance of seed dispersal by water. Journal of Biogeography 18:7-12.

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

Tilman, D. 1985. The resource-ratio hypothesis of plant succession. American Naturalist 125:827-852.

Tilman, D. 1996. Biodiversity: Population versus ecosystem stability. Ecology 77:350-363.

Tilman, D. and J. A. Downing. 1994. Biodiversity and diversity in grasslands. Nature 367:363-365.

Tilman, D., P. B. Reich, and J. M. H. Knops. 2006. Biodiversity and ecosystem stability in a decade-long grassland experiment. Nature 441:629-632.

Vanha-Majamaa, I. and J. Jalonen. 2001. Green tree retention in Fennoscandian forestry. Scandinavian Journal of Forest Research 16:79-90.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. River continum concept. Canadian Journal of Fisheries and Aquatic Sciences 37:130-137.

Walker, B. H. 1992. Biodiversity and ecological redundancy. Conservation Biology 6:18-23.

Wang, J., Y. Wang, and S. Yu. 2010. Relationships between diversity and compositional stability in experimental grassland communities exposed to drought stress. Community Ecology 11:105-112.

Wardle, D. A., K. I. Bonner, and G. M. Barker. 2000. Stability of ecosystem properties in response to above-ground functional group richness and composition. Oikos 89:11-23.

Weber, M. G. and K. Vancleve. 1981. Nitrogen dynamics in the forest floor of interior Alaska black spruce ecosystems. Canadian Journal of Forest Research 11:743-751.

Whitney, G. G. and D. R. Foster. 1988. Overstorey composition and age as determinants of the understorey flora of woods of central New England. Journal of Ecology 76:867-876.

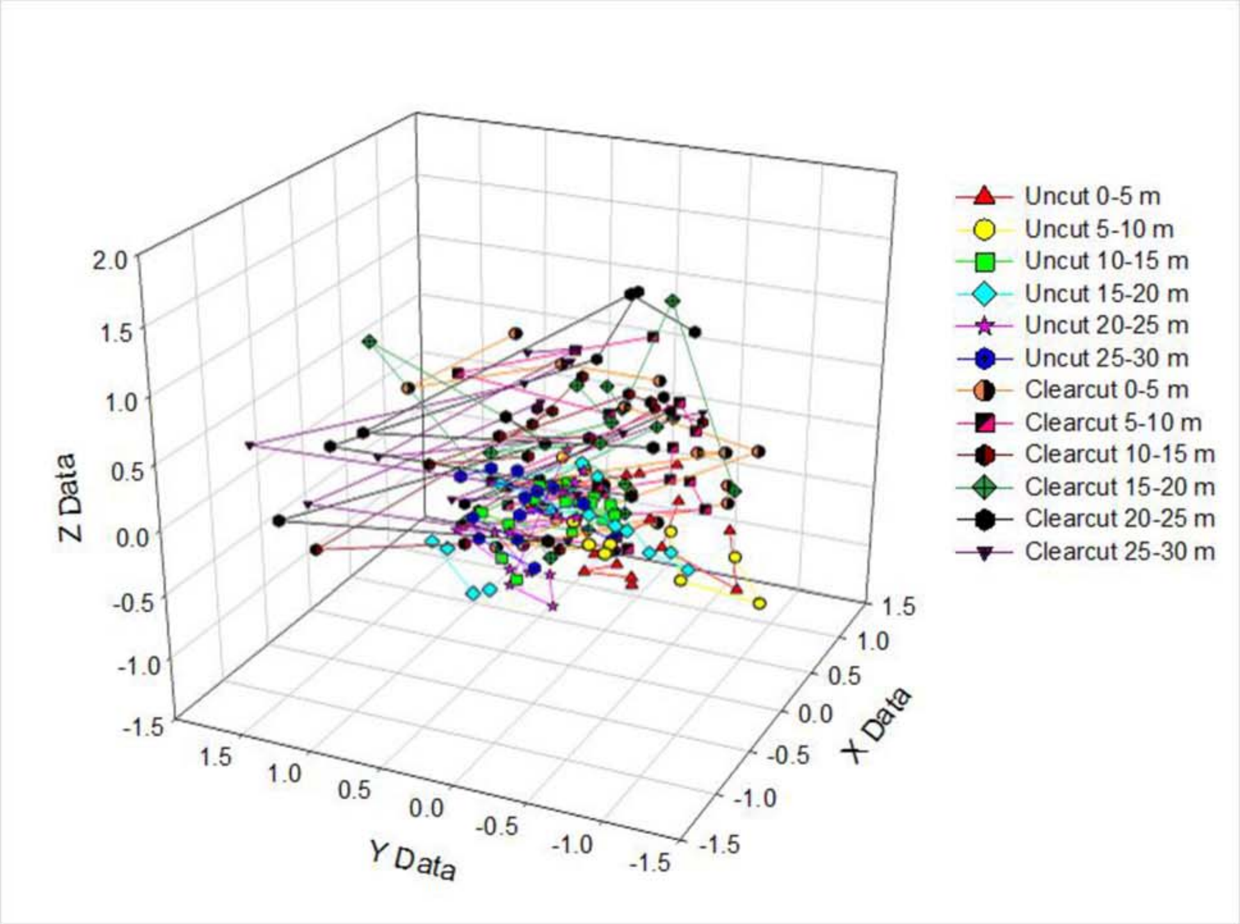
Yachi, S. and M. Loreau. 1999. Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. Proceedings of the National Academy of Sciences, USA 96:1463-1468.

Zar, J. H. 1996. Biostatistical Analysis 2nd Ed. Prentice-Hall, Inc, Upper Saddle River, NJ.

Zavitkovski, J. 1976. Ground vegetation biomass, production, and efficiency of energy utilization in some northern Wisconsin forest ecosystems. Ecology 57:694-706.

Appendices

Appendix A. Non-metric multidimensional scaling ordination of ground-layer species across riparian ecotones on Canadian Boreal Plain watersheds over time. Axes 1, 2 and 3 represent 78% of the ground-layer flora variability. Within the ordination space, successional trajectories were formed by sequentially connecting points representing the early successional pathway of the same community over time. Pre-disturbance condition is represented by the initial point for each trajectory. The second, third and fourth subsequent points corresponds with Year 1, 5 and 7 post-harvest, respectively.



Appendix B. Soil moisture content, coarse woody debris and depth of organic matter in relation to habitat and harvesting in Boreal Shield watersheds.

Source	d.f.	F	P	η^2
Non-scarified				
Soil moisture content ($r^2 = 0.62$)				
Habitat (H_i)	2	7.10	0.005	0.44
Disturbance (D_j)	1	15.03	0.001	0.46
Habitat x disturbance (HD_{ij})	2	0.13	0.88	0.01
Error ($\varepsilon_{(ij)k}$)	18			
Coarse woody debris[†] ($r^2 = 0.13$)				
Habitat (H_i)	2	0.09	0.91	0.01
Disturbance (D_j)	1	2.52	0.13	0.12
Habitat x disturbance (HD_{ij})	2	0.03	0.97	0.01
Error ($\varepsilon_{(ij)k}$)	18			
Depth of organic matter ($r^2 = 0.21$)				
Habitat (H_i)	2	0.86	0.44	0.09
Disturbance (D_j)	1	2.99	0.10	0.14
Habitat x disturbance (HD_{ij})	2	0.02	0.98	<0.01
Error ($\varepsilon_{(ij)k}$)	18			
Scarified				
Soil moisture content ($r^2 = 0.39$)				
Habitat (H_i)	2	5.00	0.02	0.36
Disturbance (D_j)	1	1.32	0.27	0.07
Habitat x disturbance (HD_{ij})	2	0.18	0.84	0.02
Error ($\varepsilon_{(ij)k}$)	18			
Coarse woody debris[†] ($r^2 = 0.32$)				
Habitat (H_i)	2	1.05	0.37	0.10
Disturbance (D_j)	1	6.38	0.02	0.26
Habitat x disturbance (HD_{ij})	2	0.02	0.98	<0.01
Error ($\varepsilon_{(ij)k}$)	18			
Depth of organic matter ($r^2 = 0.66$)				
Habitat (H_i)	2	0.07	0.94	0.01
Disturbance (D_j)	1	34.19	<0.001	0.66
Habitat x disturbance (HD_{ij})	2	0.02	0.98	0.01
Error ($\varepsilon_{(ij)k}$)	18			

[†] Variable was ln-transformed.

Appendix C. Photographs comparing vegetation among treatments and habitats from the Boreal Plain study area.

Riparian habitat in uncut treatment (left) and harvest-to-shore treatment (right) in Central Alberta, Canada.

Vegetation change-over-time following harvesting in an upland permanent plot dominated by feathermosses and ericaceous shrubs before disturbance in Central, Alberta.

Vegetation change-over-time following harvesting in an upland permanent plot dominated by herbaceous species before disturbance in Central, Alberta.