**University of Alberta**

# The effects of variable retention harvesting on understory vegetation in the mixedwood boreal forest in northwestern Alberta

by

Ashley Craig

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## Abstract

I studied the effects of six levels of dispersed green tree retention harvesting (2%, 10%, 20%, 50%, and 75%, and unharvested control) on understory plant communities in the 8th growing season post-harvest in the mixedwood boreal forest in northwestern Alberta. Sample plots were located in the partially harvested (retention) strips as well as in corridors used by the harvesting equipment. As the amount of retention decreased, the difference, as compared to unharvested control, increased. In lower retention levels the cover of understory vegetation, especially graminoids, was higher but species richness was unaffected. Lower retention lead to increased abundance of early successional, shade-intolerant species. The results suggest a possible threshold in response between the 10% and 20% retention. In terms of understory cover and composition machine corridors resembled clearcuts within partially harvested forests.

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# Chapter 1: Introduction

Faced with an increased social pressure to implement sustainable forest practices that incorporate not only the economic value of forest resources, but also social and ecological values, the forest industry has begun to adapt its management practices. Instead of traditional clearcutting, practices such as green tree retention, which leave a biological legacy of live trees within a harvested landscape, are being implemented (Franklin et al., 1997). These techniques are hypothesized to lead to fewer changes from pre-harvest forest communities and faster returns to pre-harvest forest conditions than traditional harvesting methods.

One important element of the forest ecosystem that faces changes in diversity and composition after harvesting is the understory vegetation community. The understory vegetation community is an integral part of many forest processes, including nutrient cycling (Yarie, 1980), productivity, and decomposition (Dearden & Wardle, 2008). The objectives of this study were to determine the effects of various levels of green tree retention harvesting on the understory community in the mixedwood boreal forest including describing these effects in areas that are affected by harvesting equipment. Forests with less retention and greater disturbance were hypothesized to experience a greater degree of change from unharvested forests than areas with more retention.

## Biodiversity and Forest Management

Biological diversity, or biodiversity, has been defined in many ways and on many scales. Biodiversity can most simply be defined as the variety of life in a given area. This definition includes diversity at all scales: from genetic diversity all the way to ecosystem diversity. Species are the most easily recognized and defined elements of biodiversity; monitoring and conserving species diversity is the most feasible way of monitoring and conserving biodiversity as a whole (Hunter, 1990).

Tilman (1999) suggests that biodiversity should be considered one of the major controllers (in addition to species composition, disturbance, nutrient supply, and climate) of population and ecosystem dynamics and structure. There is, however, ongoing debate concerning the effects of diversity on ecosystem stability, productivity, and susceptibility to invasion. Elton (1958) first hypothesized that ecosystems with greater biodiversity should have greater stability and that more diverse communities should be less susceptible to invasion by exotic species than less diverse communities. Diversity is hypothesized to increase primary productivity by increasing the chances that more productive species will be present within a given area and by providing greater coverage of habitats, ensuring that all resources are maximized (Tilman, 1999). Not only do these effects lead to greater utilization of limiting resources, they also decrease the availability of limiting resources for invasive species, thereby decreasing the susceptibility of an ecosystem to invasion. In 1973, however, May claimed that increased diversity lead to lower local stability. It has also been suggested that more diverse communities may appear to be more stable due to the effects of statistical averaging, in that the sum of the variation of several species may be lower than the average variance (Doak, 1998). Biodiversity has been demonstrated to confer resistance (an ecosystem's ability to withstand perturbation) and resilience (an ecosystem's ability to recover from perturbation), two forms of stability, to ecosystems (for example, Frank & McNaughton, 1991). Others, however, have found that diversity does not necessarily promote stability (for example, Pfisterer & Schmid, 2002).

Many ecosystem processes, such as plant productivity, nutrient cycling, and decomposition are dependent upon not only the diversity of life within a system, but also upon the composition (which species are present and their relative abundances) of the organisms within the community (Hobbie, 1996; Tilman et al., 1997). Because different species fulfill different functional roles within an ecosystem, the presence and absence of individual species can have significant effects on physical environments and on ecosystem processes. For example, ecosystem engineers are species that affect the availability of resources for other organisms (Jones et al., 1994). Ecosystem engineers create, modify, and/or maintain habitat for other organisms. Some examples include beavers who build dams and thus flood landscapes, trees that drop branches into streams and divert stream flow, and plants that create litter and alter forest floor conditions (as reviewed in Jones et al., 1994). Individual species can also affect ecosystems by modifying ecosystem process. For example, *Myrica faya* is an invasive tree species in the Hawaiian islands which alters primary succession by increasing the availability of nitrogen in the ecosystem (Vitousek & Walker, 1989). The importance of the composition of organisms within an ecosystem suggests that any factor that alters composition and the presence, absence, or abundance of individual species within a community, whether it is natural or anthropogenic, has the potential to affect ecosystem processes.

## Measures of Biodiversity

There is no single measure of biodiversity that can be applied univaersally (Whittaker, 1972), and no one measure is always appropriate (Purvis & Hector, 2000). Instead, different elements of biodiversity can be measured in different ways (Purvis & Hector, 2000). The most common way of measuring diversity is to measure richness, or counts of species within a given area. To elaborate on richness, it is often important to know how much or how many of each species exist in a studied area. A common measure of abundance for plants is the measurement of cover. Cover measures the percentage of a surface that is covered by a vertical projection of the perimeter of an organism (McCune & Grace, 2002). There are several diversity indices that can be used to quantify the biodiversity of an ecosystem. For example, species evenness is an index that measures how well abundance or biomass is distributed among species within a community while Simpson's index measures the probability that if two individuals are chosen randomly, they will be different species. A variety of other indices continue to refine the measurement of biodiversity.

Whittaker (1972) provided three measures of diversity: alpha, beta, and gamma diversity. Alpha diversity is the species richness per sample unit. Beta diversity is the amount of compositional change between sample units. Gamma diversity is the landscape-level diversity, estimated as the total richness across sample units (McCune & Grace, 2002).

## Maintaining Biodiversity

Maintaining the natural species richness and diversity of ecosystems has many benefits. In addition to the intrinsic value of biodiversity, or the inherent right of all living species to continue to exist (Leopold, 1949), maintaining the variety of life has many benefits to humankind. Humans use other living species to supply the majority of the necessities of life. In addition to the known uses of other species, there is a near infinite potential for known and unknown species to provide direct benefits to humans in the future. Biologically diverse ecosystems also provide a variety of indirect benefits to humans in the form of ecosystem services, such as the decomposition of waste, purification of air and water, and nutrient cycling; processes which ultimately depend upon the natural diversity of ecosystems (Tilman, 1999). These ecosystem services not only provide necessary functions, but would cost astronomical amounts if humans had to pay for them (Costanza et al., 1997).

## The Role of Disturbance in Ecosystems

The diversity and composition of organisms within ecosystems is controlled in large part by the disturbance regime in the area (Oliver, 1981; Belsky, 1992). Sousa (1984) defines a disturbance as "a discrete, punctuated killing, displacement, or damaging of one or more individuals (or colonies) that directly or indirectly creates an opportunity for new individuals (or colonies) to become established." Natural disturbances can be biological, such as disease and insect outbreaks, or physical, such as fires, floods, droughts, large waves, and ice storms.

The effects of anthropogenic disturbances on some ecosystems are causing growing concern. Human activities such as conversion of natural areas to agricultural, urban, and suburban land, fragmentation of landscapes by roads and other anthropogenic structures, over-exploitation of resources, and pollution are all disturbances that act on natural systems in addition to the natural disturbances they already experience. In some cases anthropogenic disturbances can replace natural disturbances, such as wildfires that are limited by timber harvesting or associated activities like fire suppression.

## Managing Forest Resources

Forests are an example of an ecosystem that provides important resources to humans, but which increasingly face loss of biodiversity due to human exploitation. According to the Food and Agriculture Organization of the United Nations (FAO, 2006) wood is the main energy source for more than 2 billion people and 60% of the wood removed from the world's forests is used for energy. In the years from 1990-2000, an average of 8.9 million hectares of forest were lost annually, mainly due to conversion of land to agriculture. From 2000 to 2005 that figure decreased slightly to 7.3 million hectares per year (FAO, 2006).

Because humans are dependent upon forests for a diversity of products, total preservation of all forest resources is not possible. On the other hand, unrestricted exploitation of forest resources is not a sustainable option. Conservation is a middle ground between these extremes and attempts to create a balance between our immediate and future dependence on natural resources (Salwasser, 1990).

## Ecosystem Management

In order to ensure a continued flow of resources while maintaining the biodiversity of forests, a new approach to forest management has evolved. Ecosystem management is a system that "integrates scientific knowledge of ecological relationships within a complex sociopolitical and values framework toward the general goal of protecting native ecosystem integrity over the long term" (Grumbine, 1994). Grumbine (1994) provides five goals of ecosystem management. First, ecosystem management should maintain viable populations of all species represented in an ecosystem. Second, all native ecosystem types should be represented across their natural range of variability. Third, ecosystem management should maintain evolutionary and ecological processes. Fourth, ecosystem management should be done on a time frame long enough to maintain the evolutionary potential of species and ecosystems. Finally, these goals should be accomplished while accommodating human use and occupancy.

Traditional forest harvest methods were created with the objective of regeneration and subsequent regrowth of commercially important tree species. In recent decades, however, forest management has become more complex and taken a more holistic view of the forest; incorporating not only economic, but also social and ecological values. These ecological values include the maintenance of ecosystem processes, such as nutrient cycling and decomposition, and the recognition of the importance of structural elements of the forest, such as woody debris, canopy layers and gaps, and a variety in the size and condition of trees (Franklin et al., 1997). By leaving some elements of the original forest behind after harvesting, forest managers can leave a biological legacy. A biological legacy of snags, logs, soils, etc. can help with the reestablishment of ecosystems after harvesting and result in forests with higher levels of structural, functional, and compositional diversity than would be found after traditional clearcut harvesting. This kind of legacy is what would occur in an ecosystem after a natural disturbance such as a wildfire or storm as opposed to management practices such as clearcutting. (Franklin et al., 1997) The natural retention of some remnants of an original ecosystem after a disturbance spurred a new view of ecosystem management: the natural disturbance paradigm.

## The Natural Disturbance Paradigm

In North American boreal forests wildfire is the major natural disturbance. Although there is a superficial similarity between the disturbances created by wildfire and clearcutting, the effects of each are distinct in terms of resulting physical and chemical properties and species composition (Hansen et al., 1991; Hart & Chen, 2006). Harvesting leaves a greater proportion of the mature understory plant community intact, thereby beginning succession at a later stage compared to burned areas (Rees & Juday, 2002). The ecological communities that result after each of these types of disturbances can thus be significantly different for many decades. To minimize the effects of harvesting on the forest community, forest managers searched for alternatives to conventional harvesting systems.

A potential solution for integrating ecosystem management with a sustainable timber yield is to emulate the natural, heterogeneous processes that drive forest ecosystems in a more realistic way. This natural disturbance paradigm is based on the hypothesis that sustainable and biologically intact forest ecosystems can be re-created if forest management can mimic the structural and compositional changes induced by disturbances that are naturally occurring in the boreal forest (Angelstam, 1998). By mimicking natural disturbances to which species are adapted, forests may be better able to recover after harvesting. Although it is impossible for harvesting to perfectly mimic natural disturbances, this technique may have the potential to be more sustainable in the long term.

## Variable Retention Harvesting

One way to emulate the dynamics of natural forest disturbances is to use variable retention harvesting. Variable retention harvesting leaves structural elements within a harvested area. By retaining specific structural elements within a harvested stand, specific management goals, such as the maintenance and/or rapid restoration of the structural complexity associated with pre-harvest and mature forests can be achieved. Variable retention harvest systems are flexible in terms of potential outcomes because they can include a continuum of retention levels and present options for which structural elements are maintained, thus allowing different goals to be achieved (Franklin et al., 1997).

There are three major purposes of variable retention harvest systems (Franklin et al., 1997). First, retention provides refugia for species that might otherwise be lost after harvest. Franklin et al. (1997) hypothesized that this lifeboat effect works in three ways. First, remaining structural elements can provide habitat for a variety of species. Second, structural elements can improve microclimatic conditions compared to those found following clearcutting. Finally, remaining structural elements can provide substrates and energetic substances for heterotrophic organisms.

The second purpose of variable retention harvest systems is to enrich the re-established forest with structural elements (Franklin et al., 1997). Structural elements such as trees, snags, and logs increase structural diversity, thereby increasing habitat carrying capacity. This has been found to be true for a diversity of organisms. For example, the species richness of voles (*Clethrionomys glareolus*, *Clethrionomys rufocanus*, and *Microtus agrestis*) is positively related to structural complexity (Ecke et al., 2002). The American marten (*Martes americana*) has been found to preferentially use forest areas with a greater volume of snags (Payer & Harrison, 2003) and for winter habitat white tailed deer prefer forests with structural similarity to old-growth forests (Pauley et al., 1993).

The third purpose of variable retention harvesting is to enhance connectivity within a managed landscape to facilitate dispersal of organisms

(Franklin et al., 1997). By improving the conditions around retained elements and reducing the distance colonizers need to travel, variable retention harvesting can improve the repopulation of harvested areas when compared to clearcutting.

There are two main patterns of variable retention: dispersed and aggregated retention (Franklin et al., 1997). Aggregated retention leaves small unharvested patches within a harvested area that are representative of the original stand conditions. Aggregated retention provides patches of undisturbed soil, understory vegetation, and trees that are representative of the initial stand in terms of composition and size distribution of the trees (Franklin et al., 1997). Dispersed retention leaves the structures that are selected for retention distributed across a harvested landscape and often focuses on the retention of large trees.

With any type of variable retention harvesting there are several main questions that need to be answered. What should be retained? How much should be retained? What spatial pattern of retention should be used? (Franklin et al., 1997) This study examines the effects of various levels of dispersed green tree retention harvesting on one element of the forest: the understory vegetation community.

## The Understory Vegetation Community

Understory vegetation is an important driver of many forest processes, including nutrient cycling (Yarie, 1980), decomposition (Dearden & Wardle, 2008), light transmittance (Messier at al., 1998), productivity (Nilsson & Wardle, 2005; Kolari et al. 2006), and wildlife diversity. By competing with woody plants at the time of regeneration (Landhausser & Lieffers, 1998; George & Bazzazz,

1999) and throughout succession (Lorimer et al., 1994; Saunders & Puettmann, 1999), understory vegetation can affect forest dynamics in both the short and long term and can thus shape how a forest will develop and what it will produce in the future. Understory vegetation also provides the food source, structural habitat, and cover for a diversity of biota. For example, small mammal (Friend & Taylor, 1985; Litvaitis et al., 1985), bird (Anderson & Shugart, 1974), and rodent (Kaufman & Fleharty, 1974) habitat selection and elk foraging behaviour (Canon et al., 1987) are dependent upon both structural and compositional elements of the understory community.

Many of the processes that occur in the understory are influenced by the forest canopy. Variations in forest canopy composition and density can affect ecosystem processes involving the understory such as nutrient cycling (Légaré et al., 2002), light transmittance (Messier et al., 1998), and throughfall precipitation (Anderson, 1969). In turn, as changes occur in the canopy, through the formation of gaps, the understory can develop in such a way that it arrests, delays, or alters forest succession (Royo & Carson, 2006). For example, when gaps form in forests with ericaceous vegetation and there is a lack of high severity fire, the ericaceous understory can regenerate vegetatively and inhibit conifer regeneration by producing phenolic compounds that inhibit seed germination and seedling growth of conifers (Mallik, 2006).

## The Understory Vegetation Community in the Boreal Forest

Most understory plant species in the boreal forest are widespread throughout forest types (Carleton & Maycock, 1981). The composition and abundance of understory vegetation, however, can be significantly different under different canopy types, even across similar edaphic conditions (Saetre, 1997; Légaré et al., 2001; Légaré et al., 2002). One reason for this is the differences in light availability under different canopy types. Deciduous canopies allow more light to reach the understory than coniferous or mixed deciduous and coniferous canopies, especially during the leaf-off period in the spring and autumn (Lieffers & Stadt, 1994; Constabel & Lieffers, 1996; Messier et al., 1998). In addition to differences in light conditions, coniferous and deciduous trees create differences in litter chemistry (Brais et al., 1995; Ste-Marie & Paré, 1999; Hart & Chen, 2008). Mixed-species stands can potentially support a greater diversity of understory vegetation by creating heterogeneous conditions that support the establishment of a variety of species (Saetre et al., 1997; Pitkänen, 2000; Hart & Chen, 2008).

## The Role of Disturbance in the Understory Community

Boreal plant communities are disturbance dependant. Understory diversity in the Canadian boreal forest tends to be the highest in the central boreal and higher in the western boreal than in the eastern boreal (Hart & Chen, 2006). The central boreal has an intermediate fire return interval, which leads to forests of intermediate age that are able to maintain both early and late successional species.

The western boreal has shorter fire return intervals, which prevents forests from reaching late successional stages and limits the number of late successional species. The eastern boreal has the longest fire return interval, resulting in more old stands which have lower diversity. When a diversity of stand ages co-exist there is a potential for higher richness and diversity on a landscape (De Grandpré et al., 1993; Chipman & Johnson, 2002). This pattern supports the intermediate disturbance hypothesis, which suggests that the highest number of species will be achieved at intermediate levels (in terms of both size and frequency) of disturbances (Connell, 1978). If disturbances are too large or too small or too frequent or infrequent, lower richness will result.

While the intermediate disturbance hypothesis applies only to richness, disturbances can also affect the composition of the understory community. The severity of a disturbance can influence the magnitude of change from pre- to post-disturbance understory composition. More severe disturbances can lead to greater changes in the understory community from the pre-harvest community (Roberts, 2004).

## Clearcut Harvesting and Understory Vegetation

Clearcut harvesting is an anthropogenic disturbance and the most severe form of harvesting. Clearcutting affects the initial response and regeneration of the understory in a variety of ways. The richness of understory species has been found to initially increase after clearcutting, by up to 35% (Haeussler et al., 2002). However, much of this increase may be due to an increase in pioneering and ruderal species (Haeussler et al., 2002) and species that are not found in mature, unharvested forests (Pykälä, 2004). The composition of the understory can thus be drastically different after clearcutting than in unharvested forests (Pykälä, 2004).

Some of the effects of clearcut harvesting on understory vegetation can be at least partially attributed to changes in microclimate associated with clearcutting, such as increased air and soil temperatures, increased wind velocity, and changes in soil and air moisture compared to what would be found in an unharvested forest (Chen et al., 1993). The effects of clearcutting on the understory can persist for many years after harvesting (Ruben et al., 1999) and in fact, Duffy and Meier (1992) found that the cover and richness of herbaceous understory plants in Appalachian forests may not fully recover within planned logging cycles of 40-150 years.

### The Effects of Variable Retention Harvesting on the Understory Vegetation Community

To mitigate the disturbance effects of clearcutting and to be more aligned with the natural disturbance paradigm, the forest industry has begun to implement variable retention or partial harvesting.

Removal of canopy trees increases light and water availability to the understory and this increase in resource availability can be expected to increase richness in the understory (White, 2004). However, studies of partial harvesting have found mixed effects on the richness of understory vegetation. In a number of studies richness has indeed been found to increase after partial harvesting (North et al., 1996; Thomas et al., 1999; Battles et al., 2001; Haeussler et al., 2002;

Götmark et al., 2005), with the greatest increases in richness being associated with the lowest levels of retention (Haeussler, et al., 2002). Increases in richness are often associated with invasions by shade intolerant and ruderal species that establish quickly after harvesting (Haeussler, et al., 2002, Shields & Webster, 2007).

Alternatively, several studies have found no changes in richness after partial harvesting in a variety of forest types (Reader & Bricker, 1992; Fredericksen et al., 1999; Nagaike et al., 1999; Zenner et al., 2006). Such studies suggest partial harvesting could be a harvesting technique used to conserve biodiversity of understory species while successfully avoiding the invasion of exotic and ruderal species following harvesting.

The response of species richness and abundance to harvesting is dependent upon the level of retention. For example, Vanha-Majamaa & Jalonen (2001) found that at 7% retention the cover and richness of vascular species was significantly reduced, while at 70% retention the abundance of vascular species that were dominant before harvesting was reduced but total richness remained at pre-harvest levels. Similarly, Halpern et al. (2005) found that vegetation response variables, including abundance, were affected to a greater degree in areas with less retention (15% retention vs. 40% retention). Zenner et al. (2006) studied a range of harvesting intensities from 12.8% to 83.6% retention and found that species richness and total cover of understory vegetation increased proportionally in response to the intensity of harvesting. Overall, higher levels of retention result in only minor responses of plants to harvesting and only clearcuts were consistently different from unharvested controls (Zenner et al., 2006). Some individual species showed changes in abundance only when retention levels dropped to below 20% retention (Bergstedt & Milberg, 2001).

While richness may or may not be affected by partial harvesting, the composition of understory communities can be significantly different among harvesting treatments and retention levels. For example, Shields & Webster (2007) studied a range of retention levels in a group selection harvest system. Group-selection harvesting is a technique that removes trees in groups of varying sizes with the aim of regenerating species with a range of shade tolerances, thereby increasing tree diversity (Shields & Webster, 2007). Shields and Webster (2007) found that understory composition changed as retention decreased in a group-selection harvest system. Species composition in partially harvested areas has been found to be more similar to clearcuts than to intact forests (North et al., 1996). Vanha-Majamaa & Jalonen (2001) found that 7% retention resulted in composition that was not significantly different from clearcuts. Even at retention levels of up to 20% the understory composition may still be comparable to that found in clearcuts (Macdonald & Fenniak, 2007). Higher levels of retention (around 70% retention), however, can result in partially harvested areas that are not significantly different in understory composition from unharvested controls, at least in the first two years after harvest (Macdonald & Fenniak, 2007).

Changes in composition after partial harvesting may be due in part to differing responses among functional groups. Early-seral and exotic species are often more common in more intensely harvested sites (Battles et al., 2001). Non-vascular species are more sensitive to disturbance than vascular species (Haeussler et al., 2002) and woody species are more sensitive than herbaceous species (Reader, 1987). North et al. (1996) found that shade tolerant species were more abundant in partially harvested forests than in clearcuts, suggesting that the shade provided by the residual trees or the reduced disturbance affects the composition of the understory vegetation.

Another factor influencing the response of understory vegetation in partially harvested landscapes is the time since harvest. Immediately after harvest the effects of the disturbance caused by harvesting itself may be influencing the understory response. As time since harvesting increases, the effects of the disturbance may subside and the effects of the harvesting treatment and retention level should begin to be discernable from responses to disturbances (Halpern et al., 2005). Additionally, some species have been found to show a lag of up to several years after harvesting before they respond to a harvesting treatment (Bergstedt & Milberg, 2001). The redevelopment of the canopy will also have an important ongoing effect on the understory vegetation community.

## Machine Corridors

Partial harvesting treatments typically have a portion of the total harvest area that is particularly influenced by machine traffic. Harvesting equipment such as feller bunchers and skidders travel along corridors that are approximately 5 m wide. The harvesting equipment reaches into retention areas to remove trees, and thus direct disturbance effects are restricted to these narrow corridors (Fig. 1-1).

Few studies have examined the response of vegetation communities within these corridors; however it is known that machine corridors are exposed to a greater intensity of disturbance than the retention strips (areas from which trees are removed but which are not exposed to machine traffic). In these machine corridors forest floor disturbance has been found to be more important in controlling vegetation establishment than is partial canopy retention (Frey et al., 2003). Haeussler et al. (2002) showed that low intensity soil disturbances lead to plant communities dominated by residual and resprouting understory vegetation, while higher intensity soil disturbances lead to communities dominated by pioneering and ruderal species and a greater chance of invasion by non-native species. This effect was described specifically in machine corridors by Harvey & Brais (2002) who found machine corridors to be characterized by a greater abundance of pioneering species, including sedges, grasses, and raspberry (*Rubus idaeus* L.) than adjacent retention areas. Also, favourable conditions in machine corridors allowed grasses and sedges to achieve a greater mean height in the corridors and at the outer edge of retention strips than in the center of the retention strip (Harvey & Brais, 2002). It is also possible that harvesting equipment could introduce propagules of weedy and invasive species.

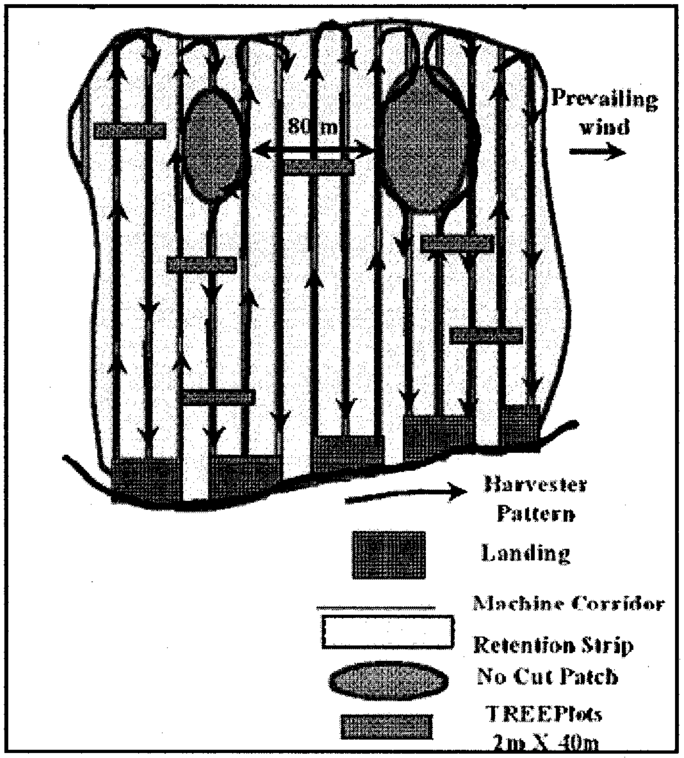

Fig. 1-1. Diagram of the harvesting pattern at the EMEND landbase in northwestern Alberta, including machine corridors and retention strips. This figure represents one 10 ha compartment. Harvesting equipment traveled along 5 m wide corridors and reached into 15 m wide retention strips to remove trees. Diagram: D. Sidders. EMEND website.

Areas with more intense machine traffic have lower rates of aspen (*Populus tremuloides* Michx.) suckering and the suckers that are present are smaller and have reduced leaf area than those in retention areas (Fraser et al., 2004). Ectomycorrhizae associated with white spruce have lower diversity and richness in machine corridors; a response that was comparable to that seen in clearcuts (Lazaruk et al., 2005). Also, the abundance or soil dwelling oribatid mites was found to be lower in machine corridors (Lindo & Visser, 2004).

## EMEND

The data for this study were gathered in the mixedwood boreal forest at the Ecosystem Management Emulating Natural Disturbance (EMEND) study site. EMEND is a large-scale variable retention harvest experiment that was begun in 1998 and which was designed to test the effects of residual forest structure on ecosystem integrity and forest regeneration (Spence et al., 1999). The project is a collaboration between researchers, government, and industry partners.

The EMEND project was designed to test the effects of a range of retention levels in both dispersed and aggregated patterns in different forest types. This study tested the effects of variable retention harvesting in only dispersed retention in mixedwood forests. Retention was calculated based on the number of trees present before harvesting (Appendix A). Each cover and treatment combination was replicated in three 10 ha compartments (Appendix C). Harvesting treatments were applied in the winter of 1998/1999. (http://www.emend.rr.ualberta.ca/)

EMEND is located approximately 90 kilometers northwest of Peace River in the Lower Boreal-Cordilleran ecoregion of Alberta, Canada (Strong & Leggat, 1992). The approximate centre of the site is located at 56° 46' 13" N - 118° 22' 28" W. The dominant tree species are white spruce, aspen (*Populus tremuloides*), and poplar (*Populus balsamifera* L.). The mean summer temperature in the region is 12.8° C and the mean winter temperature is -7.8° C. Mean annual precipitation in the region is 397 mm with two thirds of this amount falling as rain (Strong & Leggat, 1992). The soils at EMEND are fine-textured, formed predominantly on glacio-lacustrine deposits. A detailed analysis and description of EMEND soils can be found in Kishchuk (2004).

There are two goals of the EMEND project. The first is to determine which forest harvesting practices maintain forest integrity compared to forest landscapes that originated through natural disturbances. The second goal is to evaluate these harvest practices in terms of sustainability and social and economic viability. To achieve these goals, experiment-wide data are collected and projects are carried out by graduate students and researchers. The EMEND project is anticipated to run for approximately 80-100 years, or one stand rotation. (http://www.emend.rr.ualberta.ca/)

## Objectives

Within the objectives and scope of the EMEND project, this study had two objectives. The first was to determine the effects of various levels of dispersed green tree retention harvesting on the diversity and composition of the vascular understory plant community in the eighth growing season after harvesting. A study conducted in the first and second years after harvesting indicated that low and high levels of retention resulted in understories that resembled clearcuts and unharvested forests, respectively (Macdonald & Fenniak, 2007). This finding suggests that there is a threshold level of retention that results in significant changes in the understory. In the research presented here I followed up on the study of Macdonald and Fenniak (2007) and examined whether there was a specific level of green tree retention that lead to a significant change in species diversity, richness, abundance, and composition eight growing seasons after harvesting. Some species may respond dramatically to high levels of retention, while others may not be affected until very little retention is left. The responses of various species should interact to create community responses that are reflective of the overall effect of different levels of retention.

Figure 1-2 illustrates some of the potential responses of the understory community to partial harvesting both immediately following harvesting (Fig. 1-2a) and after time has elapsed since harvesting (Fig. 1-2b). Several responses are possible. The understory may respond immediately to any canopy removal and reach a plateau of maximum response at lower retention levels (Fig. 1-2a c). Alternatively, the understory may not respond to harvesting with relatively high levels of retention until a threshold of retention is reached, when a significant response would be seen (Fig. 1-2a a). This scenario is supported by previous studies (Vanha-Majamaa & Jalonen, 2001; Macdonald & Fenniak, 2007). A third scenario suggests a linear response to the amount of retention (Fig. 1-2a b).

As time elapses since harvesting and the response to retention level becomes more distinct from the response to initial disturbances, the response of the understory may shift (Fig. 1-2b). The understory may respond linearly to increasing retention (Fig. 1-2b a). Alternatively, forests with high levels of retention may show little response while those with low levels of retention show more noticeable effects such that a threshold exists at intermediate retention levels (Fig. 1-2b c). Finally, areas with high levels of retention may be similar to unharvested forests and areas with low levels of retention may be similar to clearcuts while areas with intermediate levels of retention show an intermediate response (Fig. 1-2b b). For many of these responses it is the retention level at the inflection point of thresholds that should be determined and that is of particular interest for management planning.

Regardless of the identification of specific threshold levels of partial harvesting, this study aimed to describe the differences in the understory community at various levels of retention harvesting. These differences were described in terms of percent cover, species richness, β diversity, and species composition. Cover, richness, and composition are common measures of plant abundance and diversity and β diversity provides information about the compositional heterogeneity of the understory community and whether different retention levels result in differences in the heterogeneity of understory plant communities.

A second objective of this study was to examine the effects of the machine corridors on understory plant communities and determine if a difference exists between the machine corridors and the retention strips in terms of percent cover, species richness, and composition. Due to soil compaction and more intense disturbances caused by the harvesting machinery, the diversity, richness, and species composition of understory vegetation in the machine corridors were hypothesized to be different from that found in the retention strips. This study also aimed to determine if there is an influence of harvesting intensity on the response of the vascular understory plant community in the machine corridors.

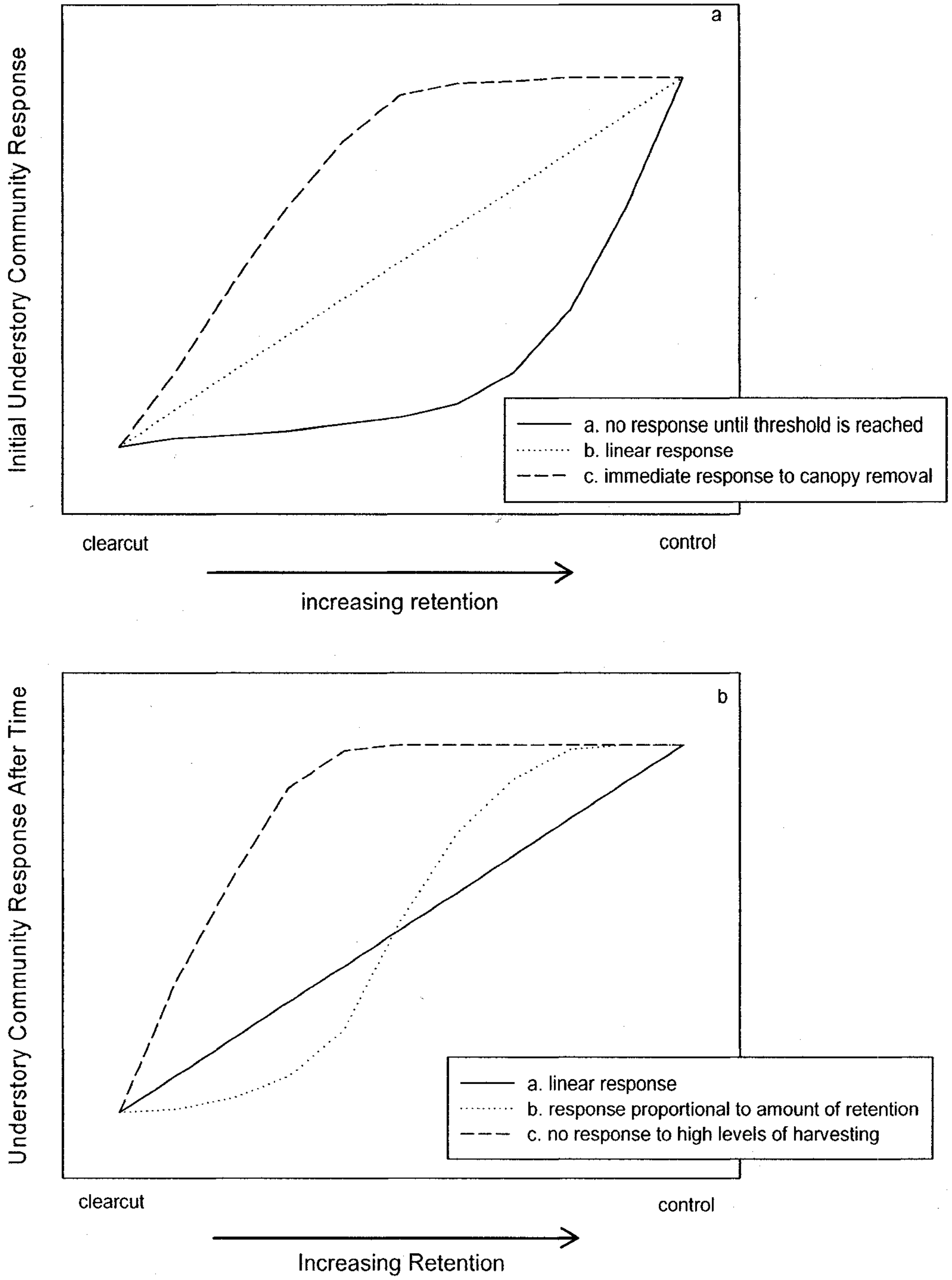

Figure 1-2. Potential responses of the understory vegetation community to varying levels of green tree retention in a) the first years immediately after harvesting and b) after some time has elapsed since harvesting (the eighth season after harvesting).

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# Chapter 2: The effects of partial harvesting on understory vegetation in the mixedwood boreal forests in Northwestern Alberta

## Introduction

Understory vegetation (plants growing beneath a forest's canopy, including shrubs, graminoids, forbs, bryophytes, and tree seedlings) is an important driver of many forest processes, including nutrient cycling (Yarie, 1980), decomposition (Dearden & Wardle, 2008), light transmittance (Messier et al., 1998), productivity (Nilsson & Wardle, 2005; Kolari et al., 2006), and provides the food source, structural habitat, and cover for a diversity of biota. By competing with woody plants at the time of regeneration (Landhäusser & Lieffers, 1998; George & Bazzazz, 1999) and throughout succession (Lorimer et al., 1994; Saunders & Puettmann, 1999), understory vegetation can affect forest dynamics in both the short and long term and can thus shape forest development and productivity in the future.

Most vascular understory species in the boreal forest are widespread throughout forest types (Carleton & Maycock, 1981). One major factor influencing which species are present at a particular site and their relative abundances, or the species composition of a given site, is the composition of the forest canopy (Saetre et al., 1997; Légaré et al., 2001; Légaré et al., 2002). Forest canopy composition has an important influence on conditions in the understory, such as light and nutrient availability. Understory biomass increases as incident solar energy increases (Zavitkovski, 1976) and is continuously affected by changes in light availability as canopy closure changes throughout succession

(Gilliam & Turrill, 1993). More light is transmitted to the understory when the canopy is composed of shade-intolerant species (such as aspen (*Populus tremuloides* Michx)) than under canopies composed of shade-tolerant species (such as white spruce (*Picea glauca* Moench (Voss)) (Messier et al 1998). Coniferous and deciduous trees also create differences in soil and litter chemistry, including pH levels and nutrient availability (Ste-Marie & Paré, 1999; Hart & Chen, 2008). For example, broadleaf forest stands have been shown to have higher nitrogen (Jerabkova et al., 2006) and calcium availability (Brais et al., 1995) while mixed coniferous and broadleaf forests have higher rates of net nitrogen mineralization than coniferous dominated forests (Jerabkova et al., 2006). By creating heterogeneous conditions that support the establishment of a variety of understory species, mixed-species stands are hypothesized to support a greater diversity of understory vegetation (Saetre et al., 1997; Pitkänen, 2000; Hart & Chen, 2008).

Natural disturbances are fundamental to the development of most forest ecosystems (Attiwill, 1994). In the past forest management relied on this principle to justify large-scale forest harvesting operations such as clearcutting in areas dominated by large-scale natural disturbances such as fire. Theoretically, because natural disturbances influence canopy cover and composition, anthropogenic disturbances that alter the canopy could be equivalent to natural disturbances. However, there is mounting evidence that clearcut harvesting and fire are not comparable disturbances (Niemelä, 1999). In an attempt to maintain natural ecosystem processes, and with growing interest in maintaining a diversity of ecological values in managed forests, the forest industry has begun to implement forest management strategies that attempt to better emulate natural disturbances (Franklin et al., 1997). These management strategies could have benefits for ecosystem processes, biodiversity of flora and fauna, and other ecosystem values, including social and recreational values (Franklin et al., 1997). Partial harvesting systems are being increasingly explored for use as part of ecosystem management operations. Green tree retention harvesting, a partial harvesting system, is a technique that attempts to mimic natural disturbances by leaving some live trees in a harvested area. Given the importance of the canopy to the understory, the intensity of harvesting and any subsequent effects on the canopy composition will be important drivers of the response of the understory community (Halpern, 1988).

Within the understory plant community, changes in composition of plant species are some of the most notable ecological effects associated with partial harvesting. The degree of change in the understory community reflects the level of retention and as the level of retention decreases the composition of the understory in harvested areas more closely resembles that found in clearcut forests (North et al., 1996; Vanha-Majamaa & Jalonen, 2001; Macdonald & Fenniak, 2007). A previous study by Macdonald & Fenniak (2007) in the first and second years post-harvest at the same site as the current study found that leaving 20% of the trees in a partially harvested area resulted in understory composition that was not significantly different from clearcuts while higher levels of retention (approximately 75%) resulted in partially harvested areas that were not significantly different from unharvested controls. There were, however, significant differences in understory composition between areas with low levels of retention (clearcut and 20% retention) and those with high levels of retention (75% retention and control).

Changes in understory composition are often associated with changes in the richness of understory plant species. Increases of ruderal and early seral species have been found to lead to an initial increase in richness after partial harvesting (North et al., 1996; Thomas et al., 1999; Battles et al., 2001; Haeussler et al., 2002; Götmark et al., 2005; Shields & Webster, 2007). However, observed changes in richness after harvesting have not always been consistent and other studies have found no change in richness after partial harvesting (Reader & Bricker, 1992; Fredericksen et al., 1999; Nagaike et al., 1999; Zenner et al., 2006). Macdonald & Fenniak (2007) found that richness decreased in the 1st and 2nd growing seasons after partial harvesting.

Partial harvesting treatments typically result in a portion of the total harvest area that is particularly heavily influenced by machine traffic ("machine corridors"). These machine corridors are necessarily exposed to a greater intensity of disturbance than the portions of partially harvested areas that are not exposed to machine traffic ("retention strips"). Machine corridors have been shown to have differences in understory vegetation composition (Harvey & Brais, 2002), reduced aspen suckering (Fraser et al., 2004), reduced oribatid mite density (Lindo & Visser, 2004) and reduced abundance of ectomycorrhizae associated with white spruce (Lazaruk et al., 2005) when compared to retention strips.

Machine corridors can comprise a substantial portion of the total area in a partially harvested area. A comprehensive assessment of any partial harvesting treatment therefore needs to consider impacts on all parts of the harvested area.

### *Objectives*

The first objective of this study was to examine the effects of various levels of green tree retention harvesting on the diversity and composition of the vascular understory community in the mixedwood boreal forests of the Ecosystem Management Emulating Natural Disturbance (EMEND) experimental site in the eighth growing season after harvesting. Previous studies indicated that in the short term, low (20%) and high (75%) levels of retention resulted in vascular understory composition that resembled clearcuts and unharvested forests, respectively (Macdonald & Fenniak, 2007). These results suggested that there is a threshold level of harvesting somewhere between 20% and 75% retention at which more intense harvesting causes significant changes in the understory as compared to unharvested forests. In this study I examined whether there is a specific threshold level of green tree retention harvesting that affects vascular understory plant species composition, diversity, and richness. Regardless of whether a specific threshold level was identified, I also sought to describe the differences in the understory community at various levels of partial harvesting. Differences in the understory community were described in terms of percent cover, species richness, and species composition.

A second objective of this study was to determine the effects of the machine corridors on vascular understory plant communities in the eighth growing season after harvesting. I tested whether a difference exists between the machine corridors and the retention strips in terms of percent cover, species richness, and composition of the understory community. I hypothesized that the understory community in the machine corridors would be different than retention strips in terms of species composition, diversity, and richness as a result of soil compaction, complete removal of the tree canopy, and more severe disturbance of the understory vegetation caused by the harvesting machinery. I also examined whether the intensity of the harvesting in the surrounding retention strips affected the response of the understory vegetation community in the machine corridors.

## Methods

### *Study Site*

The data for this study were gathered from the mixedwood boreal forest at the EMEND study site. EMEND is a large-scale variable retention harvest experiment that began in 1998 and was designed to test the effects of residual forest structure on ecosystem integrity and forest regeneration. EMEND is located approximately 90 km northwest of the town of Peace River in the Lower Boreal-Cordilleran ecoregion of Alberta, Canada (Strong & Leggat, 1992). The approximate centre of the site is located at 56° 46' 13" N-118° 22' 28" W. The dominant tree species are white spruce, aspen, and poplar (*Populus balsamifera* L.). Mixedwood forests were defined as having between 40% and 60% of both broadleaf trees (primarily aspen) and conifer (primarily white spruce) in the canopy. The mean summer temperature in the region is 12.8° C and the mean winter temperature is -7.8° C. Mean annual precipitation in the region is 397 mm with two thirds of this amount falling as rain (Strong & Leggat, 1992). The soils at EMEND are mostly fine-textured luvisolic soils, formed predominantly on glacio-lacustrine deposits. A detailed analysis and description of EMEND soils can be found in Kishchuk (2004).

In the winter of 1998/1999, the following six harvesting treatments were applied to the forest: clearcut (2% retention), 10% retention, 20% retention, 50% retention, 75% retention (tree removal only in machine corridors), and unharvested control. Each treatment was applied to three 10 ha compartments. Harvesting equipment was maintained in 5 m wide corridors and reached into 15 m wide retention strips to remove trees. Retention was calculated by the number of trees present in the compartment before harvesting, as described in Appendix A. Basal area of aspen, poplar, and spruce trees before and after harvesting are listed in appendix B. Each replicate of six treatments was grouped spatially and temporally into a block; resulting in three blocks containing one replicate of each of the six treatments (see Appendix C for diagram). All compartments in a single block were sampled within a two week period.

### *Understory Vascular Plant Sampling*

Sampling was conducted between June and August of 2006. Twenty sample points were distributed throughout the compartment in such a way as to avoid edges of compartments, sub-treatments within the compartments, and other experiments. Sample points were located at least 10 m apart in each of 18 compartments for a total of 360 plots. A 1x1 m plot was located randomly within the vicinity of the sample point. Within each compartment five plots were located within the machine corridors and 15 were located in the retention strips (Appendix C). This distribution of plots represented the relative proportions of the area in a given cutover that were covered by the machine corridors and retention strips, respectively. Clearcut and control compartments did not have machine corridors or retention strips, thus there was no difference between any of the 20 plots in these two treatments. Species-area curves suggest that this sampling effort was sufficient to capture the total richness (Table 2-1). Within each plot all vascular plants (forbs, graminoids, shrubs, and tree seedlings) were identified to species. Nomenclature followed Moss (1983). The percent cover of each species in every plot was visually estimated. Percent cover was estimated to the nearest 0.5% from 0-1%, to the nearest 1% from 1% to 10%, to the nearest 5% from 10% to 50%, and to the nearest 10% from 50 to 100%. The percent cover was summed over each species within a plot to obtain a total percent cover for each plot. Overlap among species was possible, allowing total percent cover for a plot to exceed 100%. Saplings (defined as tree species having a diameter at breast height (dbh) of less than 5 cm) within a 2 m radius from the centre of the plot were counted and recorded by species. The modal height of each sapling species was measured by visually estimating the most common height of saplings. Within a 5 m radius from the centre of the plot all trees (dbh >5 cm) were identified, counted, and their diameters were measured. Tree density was measured in order to account for discrepancies in tree densities within harvesting treatments in compartments (due to higher or lower tree density before harvesting or trees that had blown down since harvesting, for example) (Fig. 2-1). Originally I intended to inventory stumps from harvested trees, but due to burial under litter and decomposition, this proved impossible.

### *Data Analysis*

Prior to all analyses the presence of spatial autocorrelation among individual plots within and between compartments was investigated to determine whether plots could be considered independent for the purposes of subsequent analyses. The program PASSaGE (Pattern Analysis, Spatial Statistics, and Geographic Exogenesis) (Rosenberg, 2004) was used to calculate Moran's I values for univariate responses such as total percent cover, richness, and sapling density. The vegan library (Therneau & Atkinson, 2007) in the R statistical package (v. 2.5.1 R Development Core Team, 2005) was used to produce Mantel correlograms to examine spatial autocorrelation among plots in terms of their species composition. The Mantel test calculated correlations between two matrices in which one matrix represented spatial distances while the other represented differences in dependent variables (cover of understory plants, for example) between pairs of plots and returns an r statistic.

Mantel correlograms and Moran's I correlograms indicated that most plots were independent but that some spatial autocorrelation existed at the closest distances (generally between plots $\leq$50 m apart). Thus, for all analyses plots were considered to be independent replicates of treatments but an alpha of 0.01 was used to reduce the risk of making a Type I statistical error.

To determine the effects of partial harvesting in machine corridors, retention strips, and the whole harvested area combined, three levels of analyses were undertaken: once for all plots within a compartment (plots in both machine corridors and retention strips) and once for each plot type within a compartment: machine corridors and retention strips. These tests were conducted for all vascular understory species together and for three groups of vegetation types: shrubs, graminoids, and forbs. Prior to all analyses data were checked for normality using Kolmogorov-Smirnov's test and for homoscedasticity using Levene's test in SAS v. 9.1 (SAS Institute Inc., Cary, NC).

To test for differences in percent cover and species richness (total and by plant group) among retention levels, mixed model analyses of variance (ANOVA) were conducted using Proc Mixed in SAS (v. 9.1 Littell et al., 1996). The ANOVA model was as follows:

$$Y_{ijk} = \mu + R_i + B_j + \varepsilon_{ijk}$$

Where Y is equal to individual measurements (percent cover or species richness), $\mu$ is the overall mean, R is the variation due to retention level (i = 1-6 harvesting treatments, fixed), B is variation due to blocks (j = 1-3, random), and $\varepsilon$ is variation among the experimental units (plots). This was done once using all plot types, once with only retention strips and all plots for clearcut and control, and again with only machine corridors and all plots for clearcut and control.

To test for the effect of plot type and the interaction of plot type (machine corridor or retention strip) and retention level only data for the four partial harvest treatments were used (clearcut and control did not have defined machine corridors and retention strips). The ANOVA model was as follows:

$$Y_{ijkl} = \mu + R_i + P_j + R_iP_j + B_k + \varepsilon_{ijkl}$$

Where Y is equal to individual measurements (percent cover or species richness), $\mu$ is the overall mean, R is the variation due to retention level (i = 1-4 harvesting treatments, fixed), P is variation due to plot type (j = machine corridor or retention strip, fixed), $R_iP_j$ is the variation due to the interaction of retention level and plot type, B is variation due to block (k = 1-3, random), and $\varepsilon$ is variation among the experimental units (plots).

Post hoc testing for differences between individual pairs of treatments was done by comparing least square means using the PDIFF function in SAS. To maintain an overall $\alpha$ of 0.01, a Bonferroni correction was used to obtain a significant $\alpha$ for individual contrasts among pairs for all treatments of 0.0006. For contrasts within one plot type (machine corridor or retention strip, excluding clearcut and control), the significant $\alpha$ for each contrast was 0.0007.

To examine the influence of retained tree density on the upper limit of response variables such as percent cover and richness, boundary line analysis was conducted in SAS. This analysis examined how retained tree density influences the upper limit of cover and richness while excluding the effects of the many factors that may be causing lower levels of cover or richness at any given tree density (such as poor soil conditions, lack of nutrients or moisture, etc). Webb

(1972) suggested the use of boundary line analysis to interpret single variable relationships. Webb (1972) claims that scatter below the boundary line can be due to variability that is inherent in biological data, errors in measurement, or overall variation caused by other interacting or controlling factors. By conducting a regression using tree density I could more precisely account for the retained tree density at any individual plot; accounting for prior tree density, variability in treatment application, and trees that blew down since harvesting. To conduct this analysis the data were divided into five categories of tree densities (number of trees within a 5 m radius from the centre of the plot): 0-3 trees, 4-7 trees, 8-11 trees, 12-15 trees, and 16-20 trees. One plot, which had 29 trees, was excluded as an outlier. The top 10% of response variable values in each category of tree density (i.e. highest 10% of values of percent cover or richness within each category) were used in a regression against tree density. Linear regression was the best fit for the responses of cover and richness in all cases except graminoid cover which fit a cubic model.

$\beta$ diversity, or species turnover, among plots within compartments was quantified using Whittaker's measure which is calculated as follows: $\beta_w = \gamma/\alpha - 1$, where $\gamma$ = total number of species found in a compartment and $\alpha$ = mean number of species per plot for that compartment. Testing was repeated for each of the three compartments of each treatment and differences in average $\beta$ diversity among treatments were subsequently tested using ANOVAs with a significant $\alpha$ of 0.05. The ANOVA model was as follows:

$$Y_{ij} = \mu + R_i + \varepsilon_{ij}$$

Where Y is equal to individual measurements of β diversity, μ is the overall mean, R is the variation due to retention level (i = 1-6 harvesting treatments, fixed), and ε is variation among the experimental units (compartments).

To detect differences in understory composition among different retention levels, distance-based redundancy analysis (dbRDA) (Legendre & Anderson, 1999) was used to conduct a multivariate analysis of variance in CANOCO (v. 5.54, ter Braak & Šmilauer, 2002). Data were log transformed to prevent dominant species being emphasized at the expense of rare species (McCune & Grace, 2002). It is important not to minimize the effects of partial harvesting on rare species, as they may be more likely to be negatively affected or potentially lost after harvesting. Using the log transforming the data, PrCoord in CANOCO was used to conduct a principle coordinates analysis. A Bray-Curtis distance measure was used and the resulting matrix was entered into a redundancy analysis as species data. Retention level was entered as a matrix of orthogonal dummy variables. Following on significant treatment effects pairwise contrasts were subsequently conducted using dbRDA to test for differences between individual pairs of harvesting treatments. Significance testing was done using Monte Carlo permutation testing with randomization restricted to within blocks, thus taking into account the spatial and temporal variation represented by the blocks. I chose species associated by at least 25% to at least one ordination axis and further explored their affinities to particular harvesting treatments.

Indicator species analysis (Dufrene & Legendre, 1997) was conducted to examine species affinities for the groups of harvesting intensities created by separations indicated by dbRDAs (using PC-ORD v. 5.0, McCune & Mefford, 1999). For plots in both machine corridors and retention strips three groups were constructed: plots in clearcut and 10% retention, plots in 20%, 50%, and 75% retention, and plots in unharvested controls. For plots in only machine corridors two groups were created; one group consisted of plots in clearcuts, 10%, 20%, 50%, and 75% retention and the second group consisted of plots in unharvested controls. For plots in only retention strips, three groups were created: one group of plots in clearcut and 10% retention, one group of plots in 20%, 50%, and 75% retention, and one group of plots in the unharvested control. Indicator values range from 0 to 100, where 100 is a perfect indicator. Those species with indicator values $\geq 25$ were included in the results.

Sapling count data did not meet the assumption of normality and therefore Proc Mixed could not be used. Instead, to determine how harvesting treatments affected the density of saplings (spruce, aspen, and poplar separately) Proc Glimmix (in SAS v. 9.1, Schabenberger, 2005) was used with a Poisson distribution. Proc Glimmix fits generalized linear mixed models to data that are not normally distributed. One plot which contained 89 spruce saplings was excluded as an outlier.

Because the data were highly skewed, sapling abundance data were plotted using the median values and distribution free confidence intervals.

Spruce sapling height was Box-Cox transformed in SAS to maximize normality and homoscedasticity (Sokal & Rohlf, 1995). The height data of spruce, aspen, and poplar saplings were analyzed using Proc Mixed (SAS v. 9.1) with the following model:

$$Y_{ijk} = \mu + R_i + B_j + \varepsilon_{ijk}$$

Where Y is equal to individual measurements, $\mu$ is the overall mean, R is the variation due to retention level, (i = 1-6 harvesting treatments, fixed), B is variation due to blocks (j = 1-3, random), and $\varepsilon$ is variation among the experimental units (compartments).

To test for the effect of plot type and the interaction of plot type (machine corridor or retention strip) and retention level on sapling height only the data from the four partial harvest treatments were used. The ANOVA model was as follows:

$$Y_{ijkl} = \mu + R_i + P_j + R_iP_j + B_k + \varepsilon_{ijkl}$$

Where Y is equal to individual measurements, $\mu$ is the overall mean, R is the variation due to retention level (i = 1-4 harvesting treatments, fixed), P is variation due to plot type (j = machine corridor or retention strip, fixed), $R_iP_j$ is the variation due to the interaction of retention level and plot type, B is variation due to blocks (k = 1-3, random), and $\varepsilon$ is variation among the experimental units (compartments).

## Results

### *Percent Cover*

Retention level had a significant effect on total percent cover (of all species) of understory vegetation (Table 2-2). Clearcut and 10% retention had significantly greater percent understory cover than the unharvested control (Fig.

2-2a). The other partial harvest treatments were not significantly different from the control, although the unharvested control had the lowest overall average percent cover.

Machine corridors had a significantly greater percent cover (8-20% higher) of understory vegetation than retention strips (Fig. 2-2b). Although the difference in percent cover between the plot types was the least in the 10% retention and the greatest in the 75% retention, there was no significant interaction between plot type (machine corridor vs. retention strip) and retention level (Table 2-2).

In machine corridors (plots in machine corridors, clearcuts, and controls), after correcting for multiple contrasts no significant differences were found (Fig. 2-2b). In retention strips (plots in retention strips, clearcuts, and controls), plots in the 10% retention had significantly greater cover than plots in the 20% retention ($p < 0.0001$) and control ($p = 0.0004$) (Fig. 2-2b).

Results from the boundary line analysis indicate a significant inverse relationship between the upper limit of percent cover in all plots (both machine corridors and retention strips) and tree density ($p = 0.0001$) (Fig. 2-3). When there were no trees the upper limit for total percent cover of understory vegetation was 130%. As tree density increased, the upper limit of percent cover decreased until it reached less than 10% at a density of 20 trees/plot.

When boundary line analysis was conducted for machine corridors and retention strips separately, retention strips showed a significant inverse relationship between the upper limit of percent cover and tree density ($p < 0.0001$,

Fig. 2-4) but plots in machine corridors did not show any significant relationship ($p = 0.1498$, Fig. 2-4).

The effect of retention level and plot type was different for each vegetation group (shrubs, graminoids, and forbs) (Fig. 2-5). The percent cover of shrubs was not significantly affected by retention level, plot type, or an interaction between the two (Table 2-2, Fig. 2-5a).

The percent cover of graminoid species was significantly affected by the amount of retention and the plot type (Table 2-2, Fig. 2-5b). The greatest percent cover of graminoids was in the clearcut plots, followed closely by plots with 10% retention. The percent cover of graminoids generally decreased with the amount of retention and was lowest in the control plots. There was significantly more graminoid cover in the machine corridors than in the retention strips. There was no effect of the interaction of retention level and plot type on the cover of graminoids (Table 2-2).

In machine corridors (plots in machine corridors, clearcuts, and controls) graminoid cover in the 10%, 20%, and 50% retention was significantly greater than in the controls ($p = 0.0005$, 0.0001, and 0.0003 respectively) (Fig. 2-5b). In retention strips (plots in retention strips, clearcuts, and controls) graminoid cover in the 10% retention was significantly greater than in the 20%, 75%, and controls ($p < 0.0001$ for each). Also, cover of graminoids in the retention strips in the 20%, 50%, and 75% retention was significantly less than in the clearcuts ($p < 0.0001$ for each) (Fig. 2-5b).

The cover of forb species was not significantly affected by the amount of retention (Table 2-2, Fig. 2-5c). In general, the percent cover of forbs was greater in the machine corridors than in the retention strips, however this trend was not significant.

Boundary line analysis for each vegetation group (shrubs, graminoids, and forbs) showed that for each group the upper limit of percent cover in all plots (both machine corridors and retention strips) was highest at low tree densities and decreased steadily as tree density increased (Fig. 2-6). For each vegetation group this relationship was maintained in retention strips but not in machine corridors (Fig. 2-7, Table 2-3).

### *Richness*

Richness was highest in the 10% retention and lowest in the clearcut but overall richness was not affected by the amount of retention (Table 2-2) and ranged from an average of 11 to 13 species per plot in each harvesting treatment (Fig. 2-8a). Average total richness per compartment was 39.67 species per compartment in clearcut compartments, 44 species/compartment in 10% retention, 38.67 species/compartment in 20% retention, 40.67 species/compartment in 50% retention, 39.33 species/compartment in 75% retention, and 39.67 species/compartment in controls. Average total richness per compartment (the total number of species in each compartment of a treatment) was not significantly affected by retention level ($p = 0.8723$). Richness was not significantly affected by plot type (machine corridor vs. retention strip) or an interaction of retention level and plot type (Table 2-2, Fig. 2-8b).

Boundary line analysis showed that the species richness in plots in both machine corridors and retention strips had a significant inverse relationship with tree density ($p < 0.0001$) (Fig. 2-9). Plots with no trees had an upper limit of 19 species while plots with a density of 20 trees/plot had an upper limit of richness of approximately seven species. When boundary line analysis was conducted for machine corridors and retention strips separately, retention strips showed a significant inverse relationship between the upper limit of richness and tree density while plots in machine corridors there was no significant relationship between the upper limit of richness and tree density (Fig. 2-10).

Richness varied among vegetation groups (Fig. 2-11, Table 2-2). Shrub richness was relatively low in both the clearcut and control treatments and higher in the four partially harvested treatments but this pattern was not significant (Fig 2-11a). Shrub richness was not significantly affected by retention level, plot type, or an interaction of the two (Table 2-2).

Graminoid richness decreased significantly as retention level increased and was lowest in the 75% retention and control (Table 2-2, Fig. 2-11b). Graminoid richness was significantly higher in machine corridors than in retention strips (Table 2-2, Fig. 2-11b). There was no significant effect of the interaction of plot type and retention level. Graminoid richness overall was low and the maximum number of species per plot was four.

In machine corridors (plots in machine corridors, clearcuts, and controls) graminoid richness was significantly greater in the 10% retention than in the control ($p < 0.0001$, Fig. 2-11b). In retention strips (plots in machine corridors, clearcut, and controls) graminoid richness was significantly greater in the clearcut than in the 20% or 75% retention ($p = 0.0001$ and $< 0.0001$, respectively, Fig. 2-11b).

Forb richness was highest in the 10% retention and lowest in the 20% retention (Fig. 2-11c) but was not significantly affected by retention level, plot type, or an interaction between them (Table 2-2).

Boundary line analysis for each species group indicated that the upper limit of richness was highest in plots with fewer trees and decreased linearly as the number of trees increased (Fig. 2-12). This response was also seen in retention strips but in machine corridors there were no significant relationships between the upper limit of richness and tree density for the three vegetation groups (Fig. 2-13, Table 2-3).

### *Beta Diversity*

At the compartment level (regardless of plot type) beta diversity was not affected by retention level ($p = 0.068$) (Fig. 2-14). Beta diversity in the retention strips was also not affected by retention level ($p = 0.8963$). Beta diversity in the machine corridors, however, was significantly affected by retention level ($p = 0.0096$) and was highest in the 20% retention and significantly lower in the 10% and 75% retention.

### *Composition*

Distance-based redundancy analysis (dbRDA) of all plots (plots in both machine corridors and retention strips) showed separation of plots based on the retention level (Fig. 2-15a, Table 2-4). The clearcut and 10% plots are concentrated in the lower right of the diagram. Plots from compartments with increasing retention levels were located in sequential counterclockwise order from the clearcut and 10% retention. Paired contrasts showed that all harvesting intensities were significantly different from one another except for 10% retention vs. clearcut, and 50% retention vs. 75% retention (Table 2-5). The following species were positively associated with the clearcut and 10% retention (strongest interset correlation in parentheses): *Epilobium angustifolium* (L.) Holub (0.7061, axis 1), *Calamagrostis canadensis* (Michx.) Beauv. (0.5411, axis1), *Rubus idaeus* L. (0.3446, axis 1), *Equisetum sylvaticum* L. (0.0.28, axis 1), and *Aster conspicuus* (Lindl.) Nesom. (0.2961, axis 1). *Mitella nuda* L. (-0.3492, axis 1) was associated with the control while *Cornus canadensis* L. (-0.547, axis 1) was associated with both the 50% and 75% retention (Fig. 2-15b). *Linnaea borealis* L. (0.5067, axis 2) and *Vaccinium vitis-idaea* L. (0.518, axis 2) were associated with the 20% retention.

Distance-based redundancy analysis for plots in only the retention strips again showed separation based on retention level (Fig. 2-16a, Table 2-4). Plots from the clearcut and 10% retention were concentrated to the right of the figure and increase sequentially in a clockwise order. Paired contrasts showed that with the exception of 50% retention vs. 75% retention, the composition of the understory vegetation in all retention levels was significantly different from one another (Table 2-5). Species associated with the clearcut and 10% retention included *Epilobium angustifolium* (0.7079, axis 1), *Calamagrostis canadensis* (0.5342, axis 1), *Rubus idaeus* (0.3127, axis1), *Equisetum sylvaticum* (0.2818, axis 1), and *Aster conspicuus* (0.2563, axis 1) (Fig. 2-16b). Species associated with the control included *Mertensia paniculata* (Ait.) G. Don (0.4897, axis 2), *Mitella nuda* (0.4065, axis 2), and *Aralia nudicaulis* L. (0.363, axis 2). *Cornus canadensis* (-0.5522, axis 1) was associated with 75% retention.

Distance based redundancy analysis for plots in only the machine corridors showed separation of plots based on retention level (Fig. 2-17a, Table 2-4). Plots from the clearcut and 20% retention were concentrated to the lower left of the figure. Plots from compartments increased sequentially (with the exception of 10% and 20% being inverted) in a clockwise direction from the clearcut and 20% retention. Paired contrasts showed that the composition of the understory community in machine corridors in all retention levels was significantly different from the unharvested control. For all retention levels except 75%, composition in the machine corridors was not significantly different from the clearcut. Otherwise there were no significant differences among retention levels in composition in machine corridors (Table 2-5). *Epilobium angustifolium* (-0.7183, axis 1) was associated with the clearcut while *Rubus idaeus* ((0.4209, axis 2), *Calamagrostis canadensis* (-0.4525, axis 1), and *Equisetum sylvaticum* (-0.397, axis 1) were associated with 10% retention. *Galium triflorum* (0.4334, axis 2) Michx. was associated with the 50% and 75% retention. *Cornus canadensis* (0.3872, axis 1) and *Pyrola asarifolia* Michx. (0.3872, axis 1) were associated with the control (Fig. 2-17b).

Indicator species analysis for groups created by dbRDAs showed several good indicators for each group (Table 2-6) and supported the species associations described in the ordinations. In each case (both machine corridors and retention strips, retention strips only, and machine corridors only) *Epilobium angustifolium* and *Calamagrostis candensis* were found to be good indicators of the groups with the least retention. *Cornus canadensis* and *Mitella nuda* were good indicators of groups with more retention. *Linnaea borealis* was found to be an indicator of intermediate levels of harvesting.

### *Saplings*

Spruce sapling density was low overall but was significantly affected by retention level (Fig. 2-18a, Table 2-7). Spruce density was highest in the 20% retention. Spruce density was significantly greater in the machine corridors than in the retention strips and was affected by an interaction of retention level and plot type (Fig. 2-18a, Table 2-7). Spruce sapling density in machine corridors (plots in machine corridors, clearcuts, and controls) was significantly different for every contrast ($p < 0.0001$) except clearcut vs. 50% retention ($p = 0.4540$), 10% retention vs. 20% retention ($p = 0.0076$), and 10% retention vs. 20% retention ($p = 0.0265$). Spruce sapling density in retention strips (plots in retention strips, clearcuts, and controls) was significantly greater in the 20% retention than in the

50%, 75%, or control ($p = 0.0006$, $< 0.0001$, and $< 0.0001$, respectively) (Fig.2-18a).

Aspen sapling density was significantly affected by retention level and was greatest in the clearcut and lowest in the control (Fig.2-18b, Table 2-7). Aspen saplings were significantly more abundant in the retention strips than in the machine corridors (Table 2-7). There was no effect of the interaction of retention level and plot type on aspen sapling density (Table 2-7). Aspen saplings were far more abundant than spruce or poplar saplings (Fig. 2-18). Aspen sapling density in machine corridors (plots in machine corridors, clearcuts, and controls) was significantly different for every contrast ($p < 0.0001$) except 10% vs. 20% retention ($p = 0.2067$) and 50% vs. 75% retention ($p = 0.0551$). In retention strips (plots in retention strips, clearcuts, and controls) aspen sapling density was significantly different in every contrast ($p < 0.0001$) except 10% vs. 20% retention ($p = 0.004$) (Fig. 2-18b).

Poplar sapling density was significantly affected by retention level, plot type, and the interaction of retention level and plot type (Fig. 2-18c, Table 2-7). Poplar sapling density was highest in the 10% retention and was significantly higher in the machine corridors, although this relationship appears to be driven by the response in the 50% retention. Poplar sapling density in machine corridors (plots in machine corridors, clearcuts, and controls) was significantly different ($p < 0.0001$) in every contrast except clearcut and 10% vs. 50% retention ($p = 0.0015$ and $0.1682$, respectively), 20% and 75% retention vs. control ($p = 0.0228$ and $0.0014$, respectively), and 20% vs. 75% retention ($p = 0.4940$). Poplar sapling density in retention strips (plots in retention strips, clearcuts, and controls) was significantly different in every contrast ($p < 0.0001$ for each contrast except clearcut vs. 75% retention: $p = 0.0002$) except 10% vs. 20% retention ($p = 0.0007$), 20% retention vs. control ($p = 0.0443$), and 50% vs. 75% retention ($p = 0.0212$) (Fig. 2-18c).

The heights of both aspen and poplar saplings (in all plots, machine corridors and retention strips) were affected by retention level (Fig. 2-19b and c, Table 2-7). In all plots (machine corridors, retention strips, clearcuts and controls) aspen and polar saplings were tallest in the clearcut while spruce saplings were tallest in the control plots (Fig. 2-19). Aspen sapling height was significantly affected by retention level and aspen saplings were significantly taller in the machine corridors than in the retention strips but were not affected by the interaction of plot type and retention level (Table 2-7). In machine corridors (plots in machine corridors, clearcuts, and controls) aspen height in the 10%, 20% and 50% retention was significantly greater than in controls ($p < 0.0001$, $< 0.0001$, $= 0.0004$, respectively). Aspen sapling height was also significantly lower in the 75% retention than in clearcuts ($p < 0.0001$) (Fig. 2-19b). In retention strips (plots in retention strips, clearcuts, and controls) aspen sapling height in the 10%, 20%, and 50% was significantly greater than in controls ($p < 0.0001$ for each) and those in the 10% and 20% were significantly taller than in the 75% retention ($p < 0.0001$, $= 0.0004$, respectively). Aspen saplings in the 50% and 75% retention were significantly shorter than those in clearcuts ($p = 0.0002$, $< 0.0001$, respectively) (Fig. 2-19b).

Spruce saplings tended to be taller in higher retention compartments but not significantly so (Fig. 2-19a). Spruce sapling height was not affected by plot type or the interaction of plot type and retention level. Poplar saplings were affected by retention level but did not show a clear response pattern and only the 10% and 75% retention were significantly different from one another (Fig. 2-19c). Poplar sapling height was not affected by plot type or the interaction of plot type and retention level (Table 2-7).

## Discussion

Eight years post-harvest the understory vascular plant community in partially harvested areas had increased cover and different composition but similar richness when compared to an unharvested control. The compartments with the least retention were the most different from unharvested controls. There was evidence that a threshold level for several responses exists between 10% and 20% retention. Machine corridors experienced a greater degree of change than retention strips and in some ways appeared to function as clearcuts within the partially harvested areas.

The percent cover of understory vegetation was higher in more heavily harvested areas; in particular the clearcut, 10% retention, and the machine corridors. Total understory cover in machine corridors in all retention levels was similar to that in clearcuts. In the first and second growing seasons after harvesting at the same study site Macdonald & Fenniak (2007) found that cover in retention strips was lower than pre-harvest cover and unharvested controls, which was presumed to be due to disturbances caused by harvesting. Other studies conducted in the first growing seasons after partial harvesting have found that cover in areas with low retention (7% retention by volume) is not significantly different from clearcuts but is significantly different from unharvested controls (Jalonen & Vanha-Majamaa, 2001). The magnitude of understory composition change in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests is greater in areas with less retention than in areas with more retention (Halpern et al., 2005). Thysell & Carey (2001) found that while cover was reduced in Douglas-fir forests in the first year after the removal of 30% of trees, it recovered to levels equivalent to or greater than those found in unharvested controls by the third year after harvest. Alternatively, Duffy & Meier (1992) found that the cover of understory vegetation in Appalachian forests was significantly greater in unharvested forests than in forests that had been clearcut decades earlier. These results also suggest that forest canopy composition is an important factor affecting the response of the understory vegetation community to partial harvesting.

Boundary line analysis confirmed that the upper limit of understory vegetation cover decreased as the number of trees within a 5 m radius increased, independent of an assigned "retention level". Similarly, Zenner (2006) found that in mixed oak forests the percent cover of understory vegetation decreased proportionally to amount of canopy that was retained. The upper limit of cover decreased as tree density increased for total cover (summed cover of each species) and for each vegetation group (shrubs, graminoids, and forbs) but only in retention strips. Generally machine corridors had very few trees within a 5 m radius from the centre of the plot (this radius extends beyond the edge of the machine corridor and into the adjacent retention strips), thus limiting the ability to detect a relationship in these areas.

The observed effects of partial harvesting on total understory cover were largely due to responses of graminoids. The cover of graminoid species mirrored the response of overall cover and was significantly greater in the clearcut and 10% retention than in the control. Graminoid cover was also significantly greater in machine corridors than in retention strips, supporting the findings of Harvey & Brais (2002). Graminoids have previously been found to be ready colonizers of heavily disturbed sites (Peltzer, 2000) and their cover is known to be positively influenced by the amount of sunlight they receive (Naumberg & DeWald, 1999).

Eight years after harvest the retention level is an important driver of understory cover, despite vigorous aspen regeneration. Percent cover of understory vegetation was significantly affected by partial harvesting, especially in areas with more intense harvesting, such as clearcuts, 10% retention, and machine corridors. A potential threshold for the response of percent cover was identified between low levels of retention (clearcut and 10% retention) and higher levels of retention (20%, 50%, 75% retention, and control). The upper limit of understory vegetation cover was influenced by tree density, independently from retention level. These responses were especially prevalent for graminoid species.

Mean richness was not affected by the retention level, which supports several previous studies (Reader & Bricker, 1992; Fredericksen et al., 1999; Nagaike et al., 1999; Zenner et al., 2006). Macdonald & Fenniak (2007) found a trend for decreasing herb richness with between the 75% retention and 20% retention in the first two growing seasons after harvest and no effect of harvesting on shrub richness. Although richness appears to have recovered, there are differences in species composition.

At low tree densities, richness was extremely variable and ranged from six to 22 species per plot. This variation lead to a lack of overall response of richness to tree density. By describing the upper limit of richness, boundary line analysis ignores low species richness, which could be due to any number of factors, and allows interpretation of how tree density (as a proxy for light/canopy cover) influences richness. Boundary line analysis proved to be effective and identified a significant relationship that was not seen in regressions with all plots or in analyses using retention level.

Although there were no significant effects of retention level on overall richness, boundary line analysis of richness vs. tree density showed that the upper limit of richness increased as the density of neighbouring trees increased. As with percent cover, this relationship was true for total richness (summed for each species) and for each vegetation group (shrubs, graminoids, and forbs) in retention strips but not in machine corridors. A decrease in overall richness with increasing tree density has been found in several previous studies (North et al., 1996; Thomas et al., 1999; Battles et al., 2001; Haeussler et al., 2002; Götmark et al., 2005). The largest values of richness have been associated with the most intense harvesting, or the fewest residual trees (Haeussler et al., 2002). The increases in richness that have been seen in other studies were often associated with invasions by shade intolerant and ruderal species that establish quickly after harvesting (Haeussler et al., 2002; Shields & Webster, 2007) and are often associated with changes in composition.

β diversity was significantly affected by retention level only in machine corridors. β diversity in machine corridors was highest in the 75% retention and significantly lower in the 10% and 75% retention but did not appear to follow a pattern related to retention level. Also, the lack of response in retention strips suggests that any amount of retention limits species turnover, perhaps by creating relatively homogenous environmental conditions within retention strips. However, β diversity does not consider species abundance and thus does not fully reflect the response of species to harvesting.

The differences in understory cover and the upper limit of richness cannot be completely understood without considering the associated differences in composition. Although mean richness was not significantly different in each retention level, there were differences in species composition.

Composition of the understory plant community was not significantly different between the 10% retention (all plots: both machine corridor and retention strip) and clearcut. This supports the findings of North et al. (1996) and Vanha-Majamaa & Jalonen (2001) who found that low levels of retention resulted in understory community composition that was not significantly different from that found in clearcuts. This result may indicate that leaving 10% of the trees within a harvested area is essentially the same as a clearcut and is not sufficient to help the understory vegetation community recover more quickly after harvesting than it would in a clearcut. Macdonald and Fenniak (2007) found that in the first two growing seasons after harvest composition in the 20% retention strips was not significantly different from clearcuts. In the eighth growing season after harvesting, however, 20% retention strips are significantly different from clearcuts, suggesting that 20% retention has recovered faster than the clearcut in the intervening years.

Composition in the retention strips of the 75% retention was significantly different from the control. In contrast, in the first and second growing seasons after harvest, Macdonald & Fenniak (2007) found that composition in retention strips in the 75% retention were not significantly different from controls. This discrepancy suggests there was a lag in the response of the understory community at this retention level. Tree removal in the 75% retention was strictly in machine corridors, leaving the understory in the retention strips completely free from the direct disturbance of harvesting. Understory plants in the retention strips were left to respond to changing light and nutrient conditions created by the loss of trees and changing conditions in the machine corridors, a response that may have taken several growing seasons to become fully apparent. Other studies have also found a lag in understory response time at forest edges (Williams-Linera, 1990; Matlack, 1994). Harper and Macdonald (2002) found that older edges experienced a stronger edge influence on understory composition than younger edges and estimated the distance of edge influence (DEI) to be 20-60 m in *Populus* dominated forests. Although this DEI is shorter than that reported for other forest types (for example, Laurance et al. (1998) found a DEI of 85-335 m in tropical forests and Chen et al. (1995) found a DEI of 16-137 m in Douglas-fir forests) it is enough to cover the entire width of the retention strips.

Understory composition in machine corridors was not significantly different from that found in clearcuts except in the 75% retention. All machine corridors are significantly different from controls. These results suggest that machine corridors act as strips of clearcuts within an area of retention. Being surrounded by partially harvested forest was not sufficient to counter the effects of total tree removal within the machine corridors. However, intact forests appear to influence conditions in machine corridors enough that the composition of the understory in the 75% retention strips was significantly different from clearcuts. The residual trees may help the understory community in the machine corridors recover faster than in the clearcuts, especially in the 75% retention.

*Calamagrostis canadensis* and *Epilobium angustifolium* were found to be good indicators of more heavily harvested sites. The abundance of these species in the clearcuts and lower retention areas can be at least partially attributed to decreased canopy cover and increased light in these areas (Lieffers & Stadt, 1994). When *C. canadensis* and *E. angustifolium* occur at high densities they can impede the growth and survival of conifer seedlings (Lieffers & Stadt, 1994), which may affect regeneration of spruce in more heavily harvested areas.

Some species that were indicators of unharvested controls, such as *Mitella nuda* and *Linnaea borealis* have previously been classified as understory obligates, or species that are adapted to conditions in intact forest understories

(Lieffers, 1995), suggesting that understory conditions in harvested forests are not similar to those found in unharvested controls.

Some species were found in only one treatment. For example, *Corallorhiza trifida* Chatelain, a species of orchid, was found only in the control treatment. Battles et al. (2001) found two species of orchids (*Corallorhiza striata* and *Cephalanthera austiniae*) to be unique to unharvested forests when compared to a range of management techniques. *Corallorhiza trifida* is a myco-heterotrphic species (dependent upon a fungal symbiont) (McKendrick et al., 2000). *C. trifida* is known to associate with a narrow group of fungi in the family Thelophoraceae, a family which is otherwise exclusively ectomycorrhizal (McKendrick et al., 2000). Ectomycorrhizae associated with other species have been found to decrease after harvesting (Lazaruk et al., 2005). Other soil dwelling organisms, such as oribatid mites, have also been found to decrease after partial harvesting at EMEND (Lindo & Visser, 2004). Associations with soil organisms that are influenced by harvesting may be another factor influencing the distribution and composition of species after harvesting.

Species that were seen only in the clearcut treatment were graminoid species (*Agrostis scabra* Willd., *Carex aurea* Nutt, *Carex backii* Boott, *Carex sicata* Dewey), likely due to the highly disturbed conditions and these species' abilities to act as pioneer species and readily colonize disturbed areas. The seeds of early successional species such as *Carex* sp., *Epilobium* sp., and *Rubus idaeus* are found in high abundance in the seed bank even in the absence of parent plants (Fyles, 1989; Qi & Scarratt, 1998). By having seeds that are able to persist in the seed bank for extended periods between disturbances, these species are able to take advantage of post-disturbance conditions and colonize readily.

Macdonald & Fenniak (2007) noted that some species were seen pre-harvest but were not found again post-harvest. One of these species, *Moneses uniflora* (L.) Grey, was found in the harvested areas in the current study, indicating that conditions may have become more similar to pre-harvest conditions in the years since harvesting, allowing species associated with the pre-harvest forests to re-establish themselves. Some species were not found preharvest but were seen in the first years postharvest, such as *Corydalis aurea* Willd. *Corydalis aurea* is a seed dispersed species that is common after disturbances and can be classified as an understory avoider due to its tendency to grow best in the open conditions present immediately after disturbance (Lieffers, 1995). The absence of this species may be another indication that understory conditions are returning to pre-harvest conditions. These observations, however, could also be a result of sampling effects or pseudoturnover. Pseudoturnover occurs when comparisons are made between surveys that are completed by different observers (Lynch & Johnson, 1974) and has been found to be a major source of apparent turnover in studies of vascular plants (Nilsson & Nilsson, 1982).

Clearcuts had an average of more than 25 times more aspen saplings than the controls. *Populus tremuloides* is an early successional species that is adapted to frequent disturbances from fire. When trees are lost due to fire or harvesting apical dominance is removed and suckering is initiated. Suckering can be increased in warmer soils (Maini & Horton, 1966; Steneker, 1974), which can be seen after clearcutting (Frey et al., 2003). Aspen sapling density was higher in the clearcut than in any of the partially harvested areas. In a study at EMEND Frey et al. (2003) found that suckering was reduced in partial cuts (50% retention) relative to clearcuts. Aspen sapling density was lower in the machine corridors, which could be partially caused by competition from *Calamagrostis canadensis*, which was more abundant in the machine corridors than in the retention strips (p = 0.0018). This idea is supported by Landhäusser et al. (2007) who found that *C. canadensis* sod inhibits the emergence of aspen suckers above the soil. Aspen saplings that were able to establish themselves in the machine corridor were taller than those growing in retention strips. This result does not support the findings of Landhäusser and Lieffers (1998) who found that the presence of *C. canadensis* negatively affects aspen plant height.

## Conclusions

### *Threshold Levels of Harvesting*

Generally, within the partially harvested forests as the amount of retention decreased, the degree of change from an unharvested control increased. In particular, the degree of change in response variables between the 10% and 20% retention levels indicated a threshold in responses. The total percent cover of all species decreased significantly between 10% and 20% retention. The species richness and percent cover of graminoids experienced a significant decrease between the 10% and 20% retention levels, and again between the 50% and 75%

levels. Composition of understory vegetation at the compartment level (plots in both machine corridors and retention strips) was not significantly different in the clearcut and 10%, but retention above 10% lead to significantly different understory communities, except in the 50% and 75% retention. The above results suggest that significant differences in the response of understory vegetation to partial harvesting occur somewhere between 10% and 20% retention.

### *Machine Corridors*

Many response variables, including total percent cover of all species, percent cover and richness of graminoid species, and sapling density were different in machine corridors vs. retention strips. The composition of the understory vegetation in the machine corridors at every retention level was significantly different from the composition in the retention strips and at every retention level (except 75% retention) composition in the machine corridors was not significantly different from the composition in the clearcuts. These results suggest that machine corridors are essentially strips of clearcuts within harvested landscapes and should be considered independently of retention strips when determining the effects of partial harvesting. Harvesting at EMEND was done in the winter to minimize soil compaction by harvesting equipment, however it is possible that there were some effects of harvesting equipment on the soil. The different responses of machine corridors and retention strips indicate that machine corridors need to be taken into consideration when assessing the effects of partial harvesting on a landscape.

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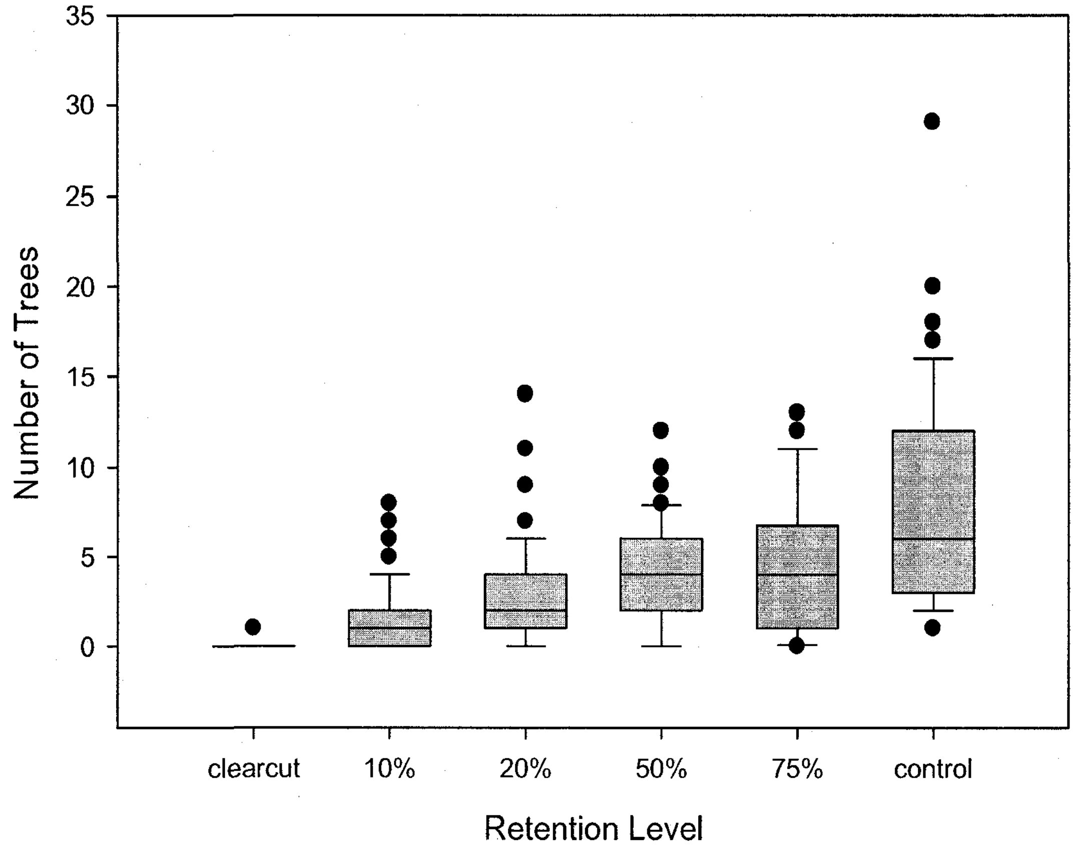

Fig. 2-1. Box plot showing the relationship between retention level and tree density per plot (trees were counted within a 5 m radius from the centre of the plot). The bottom of the box represents the 25th percentile, the line within the box is the median number of trees, and the top box is the 75th percentile. Whiskers (error bars) above the box represent the 90th percentile while whiskers below the plot represent the 10th percentile. Dots represent outliers.

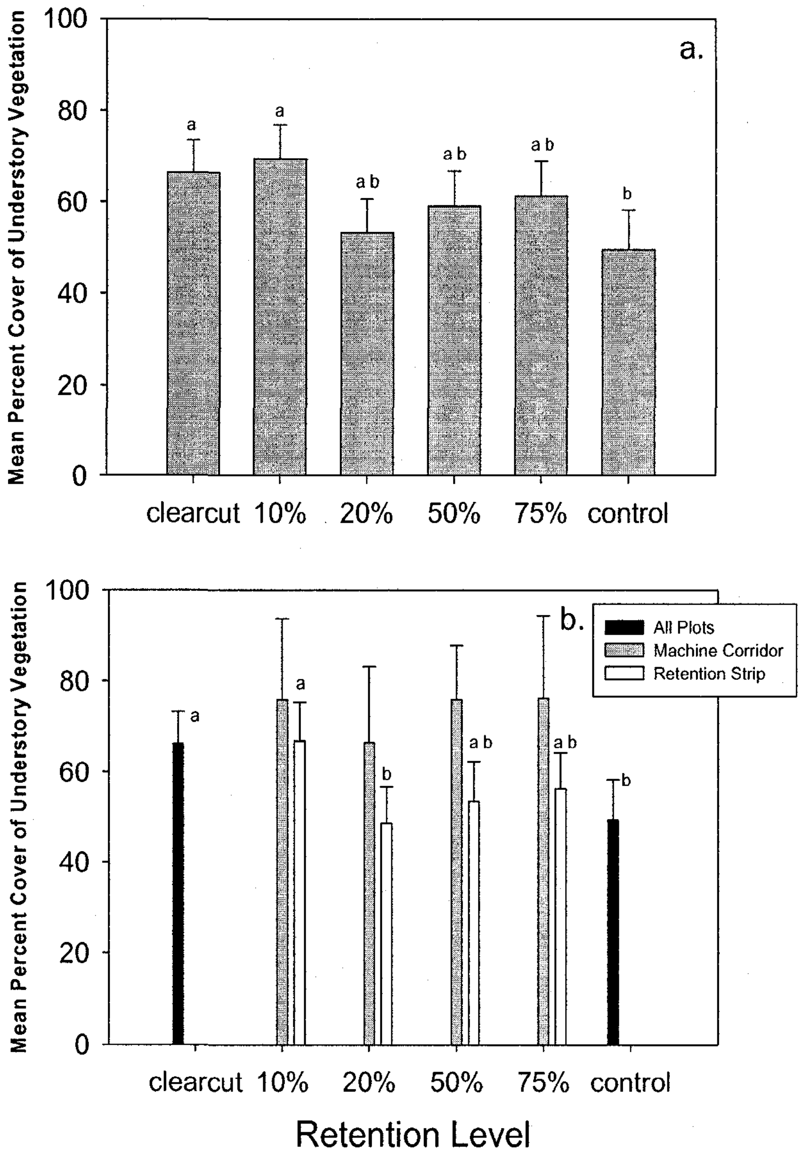

Fig. 2-2a. Mean values for percent cover (sum of individual vascular plants) for each retention level. Each bar represents 60 plots, 20 from each of three compartments: 15 plots were in retention strips and 5 plots were in machine corridors. Error bars are mean percent cover with 95% confidence intervals. Treatments with the same letter were not significantly different (Table 2-2) based on least squared means (at $\alpha = 0.0007$, overall $\alpha = 0.01$). 1b. Mean values of percent cover (sum of individual vascular plants) in retention strips only and machine corridors only. Machine corridors had significantly greater cover of understory vegetation than retention strips (Table 2-2). There was no significant interaction of retention level and plot type. Bars for machine corridors represent 15 plots, 5 from each of three compartments, while bars for retention strips represent 45 plots, 15 from each of three compartments. Bars for clearcut and control are all 60 plots (same as Fig. 2-2a).

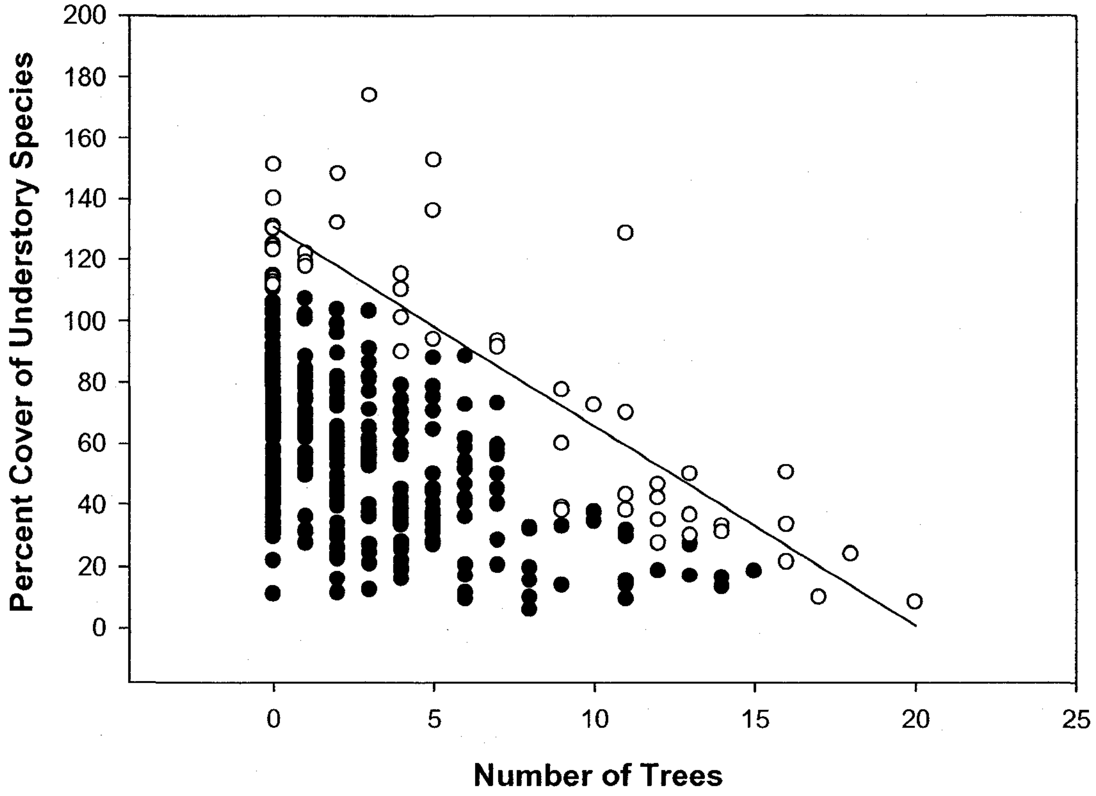

Fig. 2-3. Results of boundary line analysis of total percent cover (summed for all understory species) in plots in both machine corridors and retention strips vs. tree density (number of trees within a 5 m radius from the centre of the plot). White points (the highest 10% of responses in each of five categories of number of trees) were included in the regression, black points were not. Plots in clearcut and control compartments were included. The equation of the line was $Y = 130.72-6.5*x$. The relationship is significant at $p = 0.0001$, $R^2 = 0.7749$.

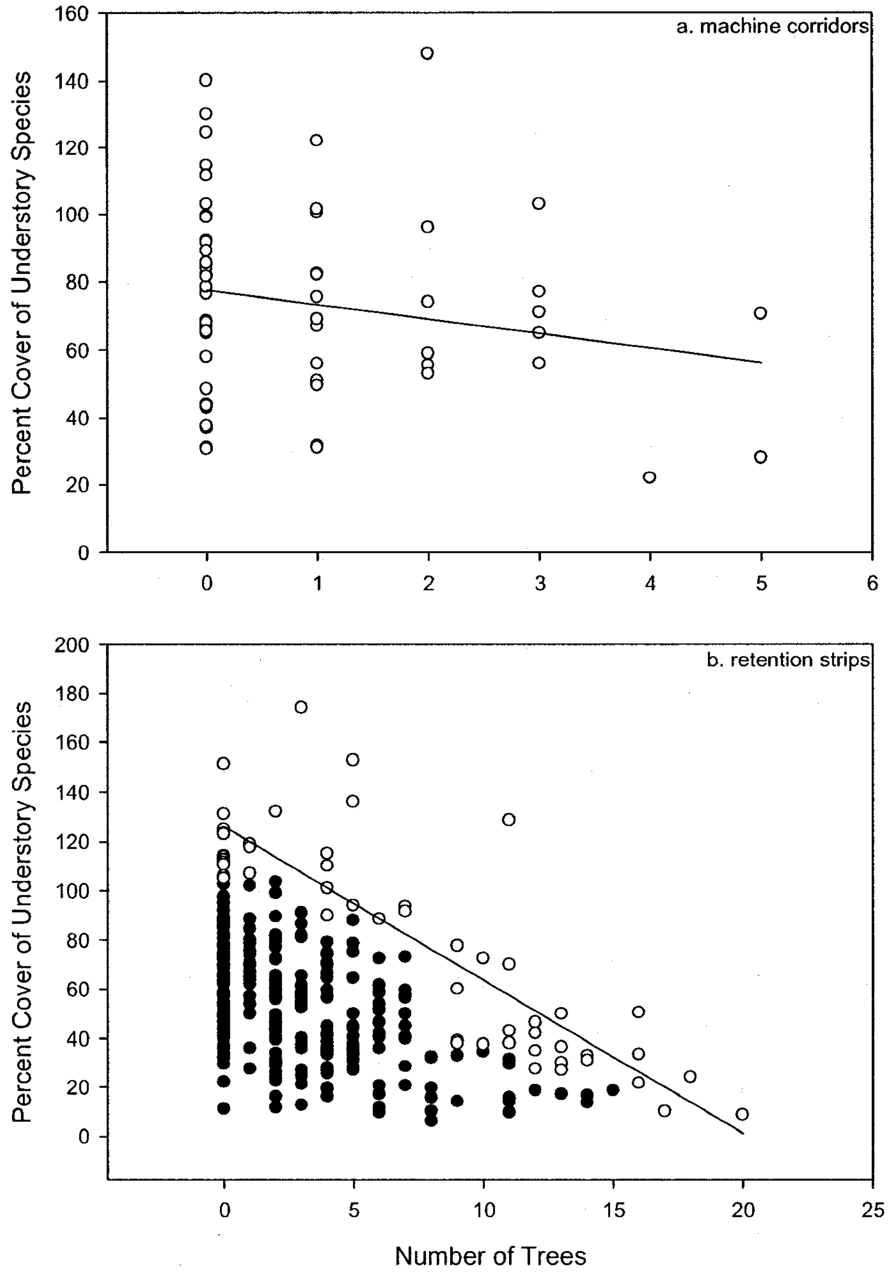

Fig. 2-4. Results of boundary line analysis of total cover of understory vegetation vs. tree density (number of trees within a 5 m radius of the centre of the plot) in a) machine corridors for which the equation of the line was Y = 77.565 – 4.225*x ($p = 0.1498$, $R^2 = 0.0354$) and b) retention strips for which the equation of the line was 126.089 – 6.248*x ($p < 0.0001$, $R^2 = 0.7526$). White points (the highest 10% of responses in each of five categories) were included in the regression, black points were not. In machine corridors all plots were included in the regression. Plots in clearcut and control compartments are not included.

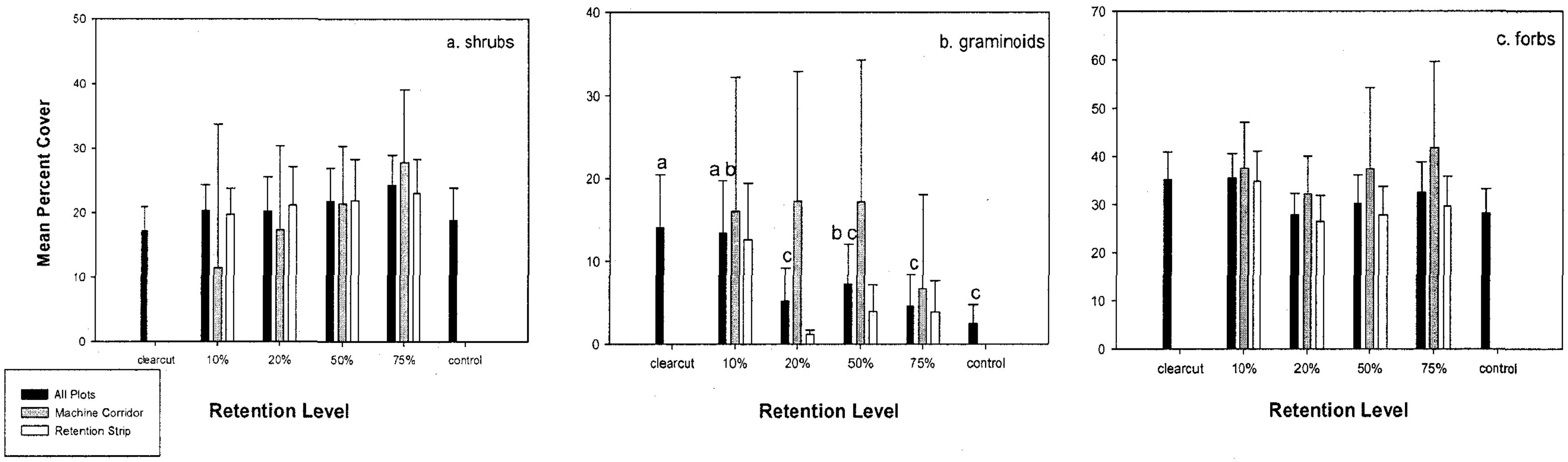

Fig. 2-5. Mean values for percent cover of a. shrubs b. graminoids c. forbs in each retention level and each plot type (all plots within a compartment, plots in machine corridors only, and plots in retention strips only). a. Percent cover of shrubs was not significantly affected by retention level, plot type, or the interaction of retention level and plot type (Table 2-2a). b. Percent cover of graminoid species was significantly affected by retention level (Table 2-2a). Percent cover of graminoids was significantly greater in machine corridors than in retention strips (Table 2-2a). There was no significant interaction of retention level and plot type. c. Percent cover of forbs was not significantly affected by retention level, plot type, or an interaction of retention level and plot type (Table 2-2a). Bars for machine corridors represent 15 plots, 5 from each of three compartments, while bars for retention strips represent 45 plots, 15 from each of three compartments. Error bars are mean percent cover with 95% confidence intervals. Treatments with the same letter are not significantly different (Table 2-2a) based on least squared means (at $\alpha = 0.0007$, overall $\alpha = 0.01$).

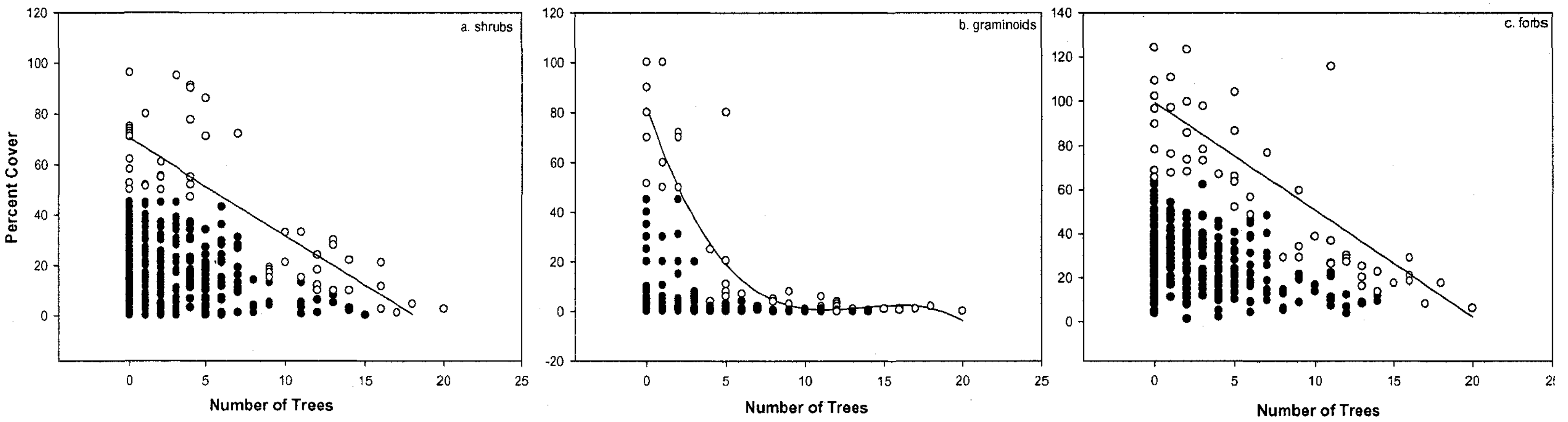

Fig. 2-6. Results of boundary line regression of percent cover of a. shrubs b. graminoids c. forbs vs. tree density (number of trees within a 5 m radius from the centre of the plot). a. shrubs: $p < 0.0001$, $R^2 = 0.6825$, $Y = 70.54-3.9*x$. b. graminoids $p < 0.0001$, $R^2 = 0.8406$, $Y = 81.99-18.885*x + 1.43x^2-0.035x^3$ c. forbs $p < 0.0001$, $R^2 = 0.6998$, $Y = 93.35-4.86*x$. White points (the highest 10% of responses in each of 5 categories) were included in the regression, black points were not. All clearcut and control plots are included.

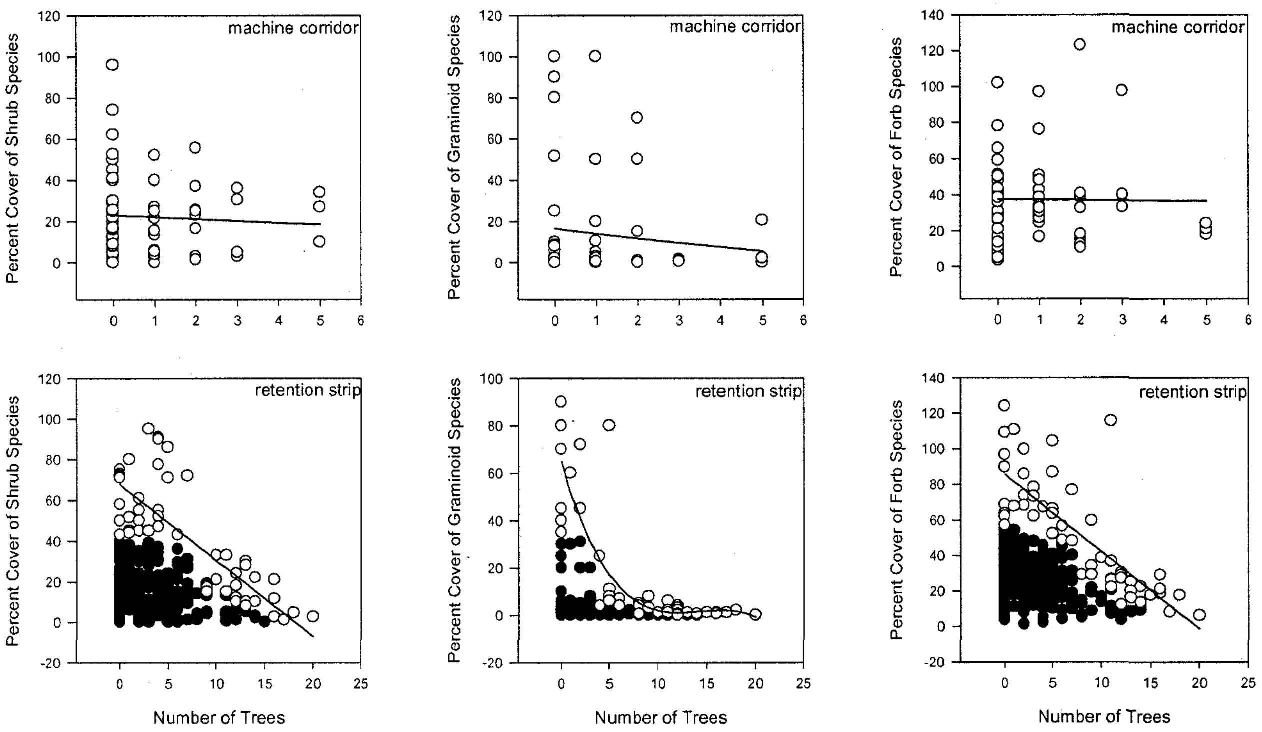

Fig. 2-7. Results of boundary line analysis of the percent cover of shrubs, graminoids, and forbs vs. tree density (number of trees within a 5m radius of the centre of the plot) in machine corridors and retention strips. White points (the highest 10% of responses in each of 5 categories) were included in the regression, black points were not. Plots in clearcut and control compartments were not included. In machine corridors all plots were included in the regression. Cover of shrubs, graminoids, and forbs in retention strips all showed a significant negative relationship with increasing tree density (Table 2-3). In machine corridors there was no significant relationship between percent cover and number of trees for shrubs, graminoids, or forbs (Table 2-3).

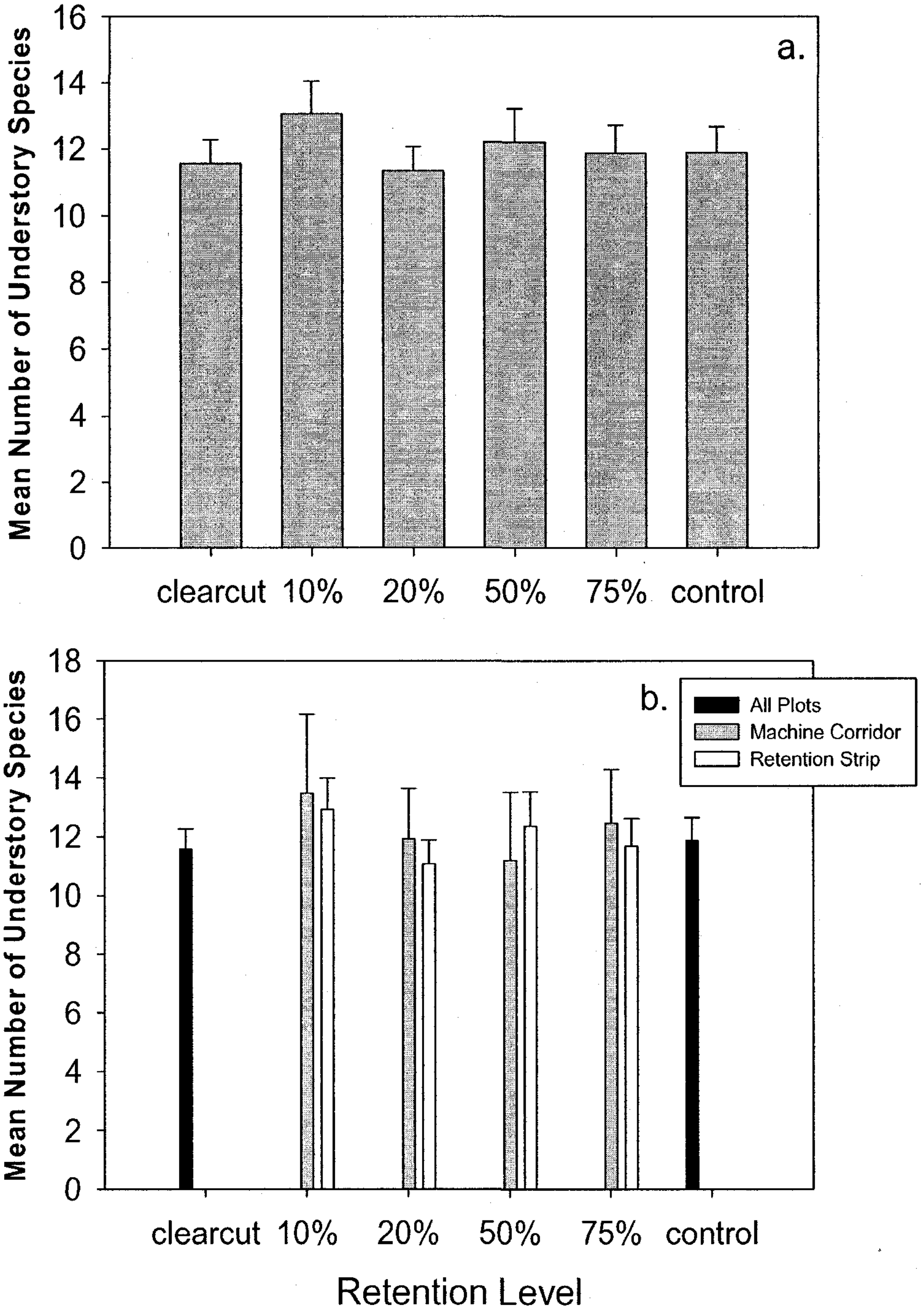

Fig. 2-8. a. Mean vascular plant species richness per plot by retention level. Species richness was not significantly affected by retention level (p = 0.0596). Bars represent mean species richness per plot for 60 plots: 3 replicates of 15 retention strip plots and 5 machine corridor plots with 95% confidence intervals. b. Mean species richness per plot for machine corridors (3 compartments, each with 5 plots) and retention strips (3 compartments each with 15 plots) separately. Species richness was not significantly affected by plot type (p = 0.4618).

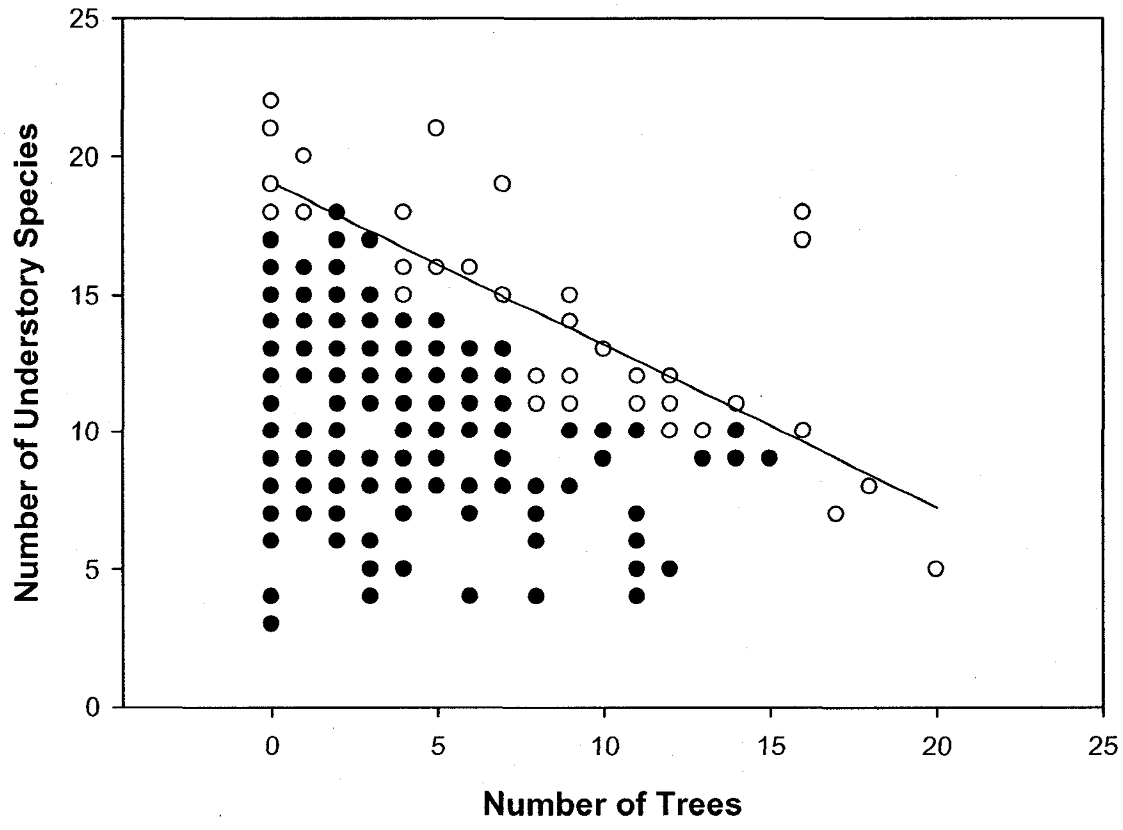

Fig 2-9. Results of boundary line analysis of total richness of understory vascular plants vs. tree density (number of trees within a 5 m radius of the centre of the plot). White points (the highest 10% of responses in each of 5 categories) were included in the regression, black points were not. Clearcut and control plots were included. The equation of the line was Y = 19.1-0.59*x. The relationship was significant at p = 0.0001, $R^2 = 0.663$.

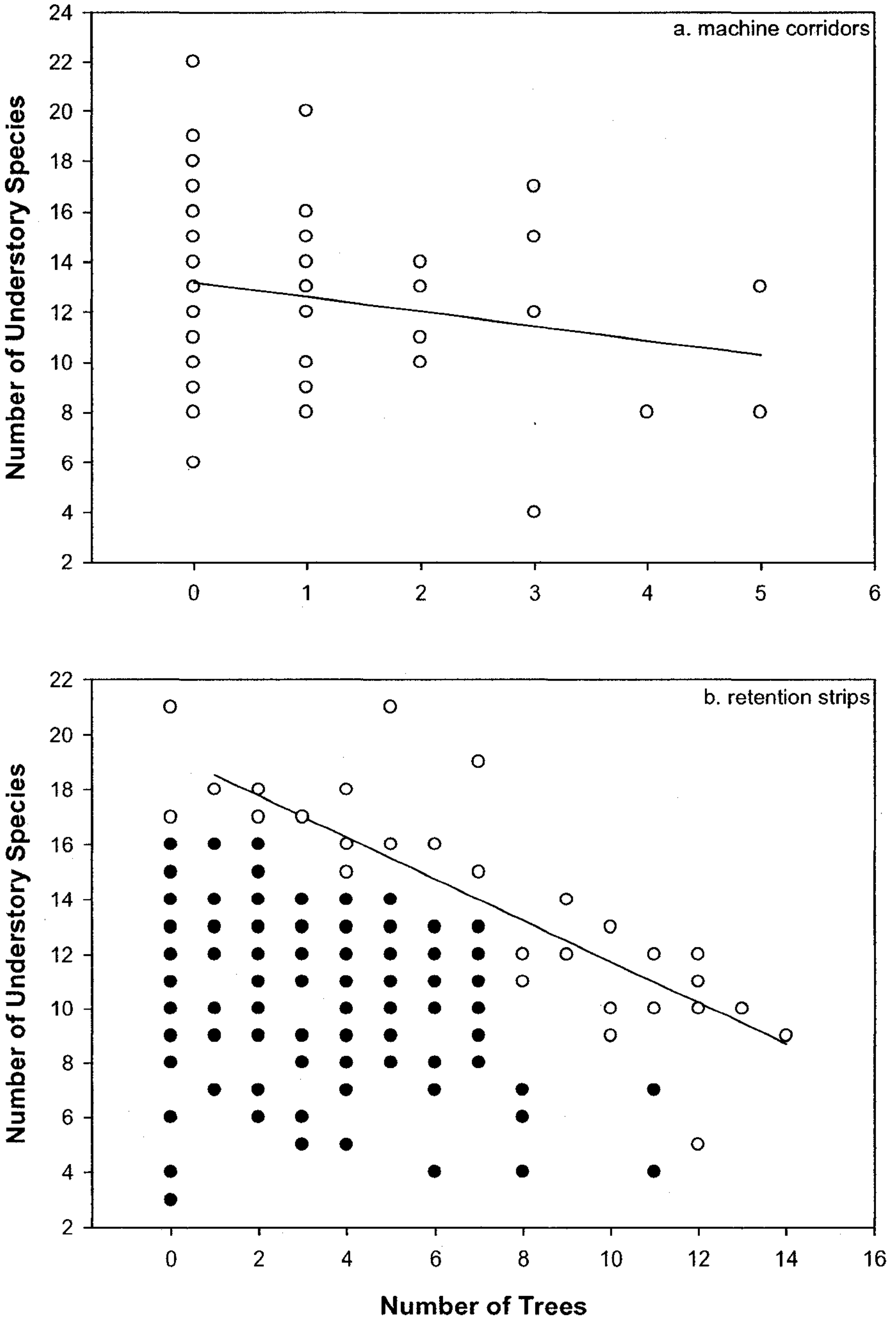

Fig. 2-10. Results of boundary line analysis of total richness of understory vascular plants vs. tree density (number of trees within a 5m radius of the centre of the plot) in a) machine corridors for which the equation of the line was Y = 13.178 – 0.576*x ($p = 0.1075$, $R^2 = 0.0440$) and b) retention strips for which the equation of the line was 19.28 – 0.755*x ($p < 0.0001$, $R^2 = 0.7428$). White points (the highest 10% of responses in each of 5 categories) were included in the regression, black points were not. In machine corridors all plots were included in the regression. Plots in clearcut and control compartments were not included.

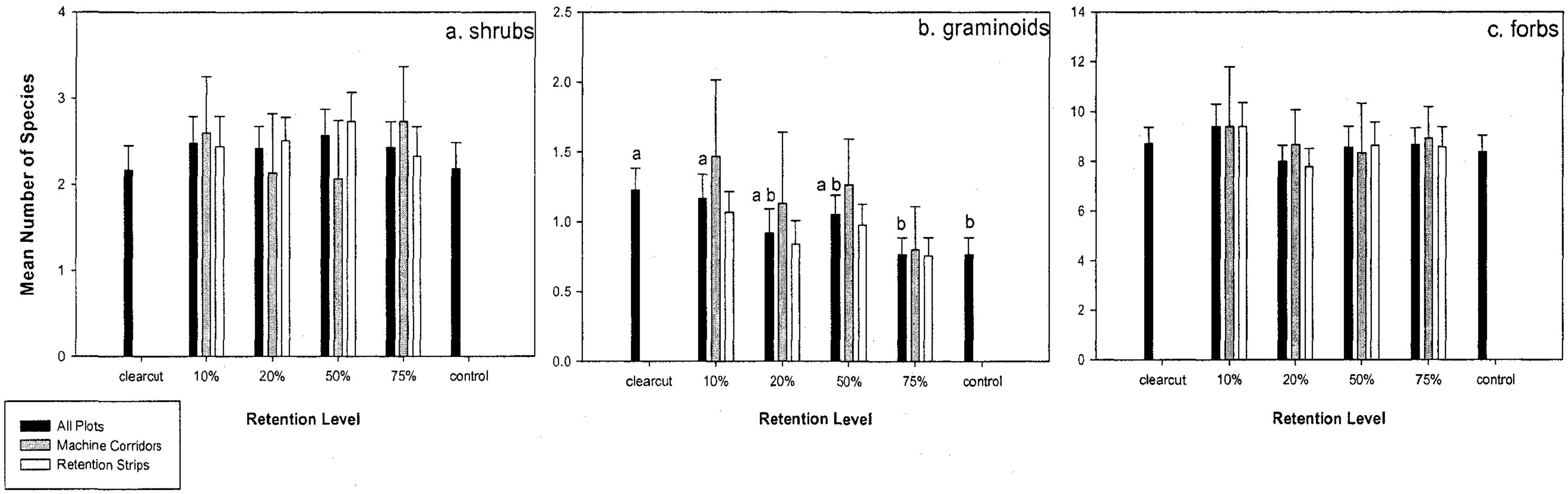

Fig. 2-11. Mean species richness of understory species by vegetation group in plots in both machine corridors and retention strips, plots machine corridors only, and plots in retention strips only for a. shrubs, b. graminoids, c. forbs. a. There was no significant effect of retention level, plot type, or an interaction of retention level and plot type on shrub richness (Table 2-2a). b. There was a significant effect of retention level on graminoid richness and machine corridors had significantly greater graminoid richness than retention strips. There was no effect of the interaction of retention level and plot type on graminoid richness (Table 2-2a). c. There was no significant effect of retention level, plot type, or the interaction of plot type and retention level on forb species richness (Table 2-2a).

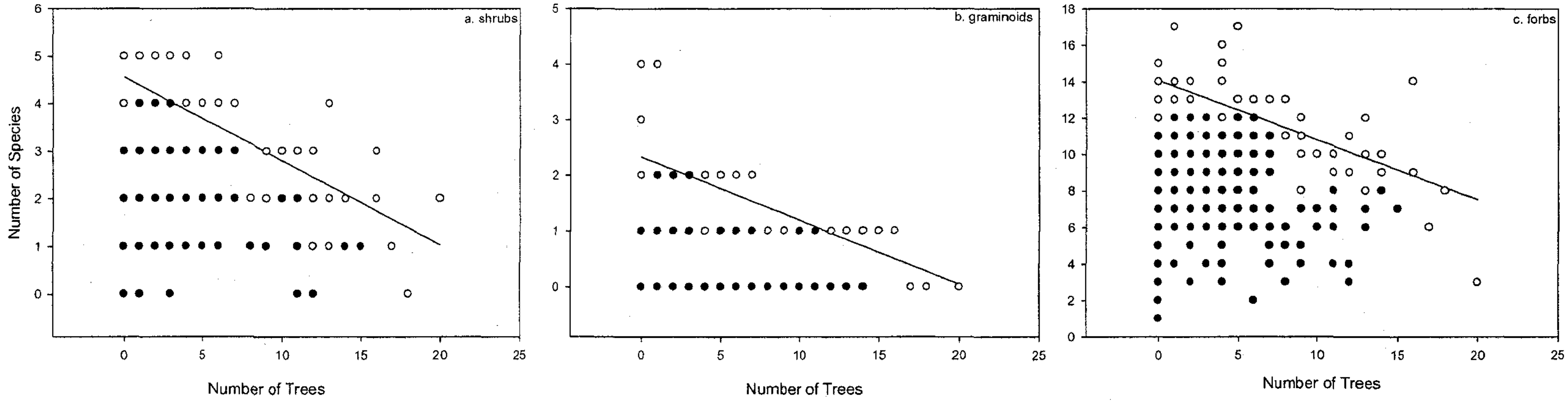

Fig. 2-12. Results of boundary line regression of richness of a. shrubs b. graminoids c. forbs vs. tree density (number of trees within a 5 m radius from the centre of the plot). a. The relationship for shrub richness and tree density was significant at p = 0.0001 with an $R^2$ of 0.6288 and represented by the equation y = 4.65-0.18*x. b. The relationship between graminoid richness and tree density was significant at p = 0.0001 with an $R^2$ of 0.6288 and represented by the equation y = 2.33-0.114*x. c. The relationship between forb richness and tree density was significant at p = 0.0001 with and $R^2$ of 0.5219 and represented by the equation y = 14.07-0.33*x White points (the highest 10% of responses in each of 5 categories) were included in the regression, black points were not. Plots in clearcut and control compartments were included.

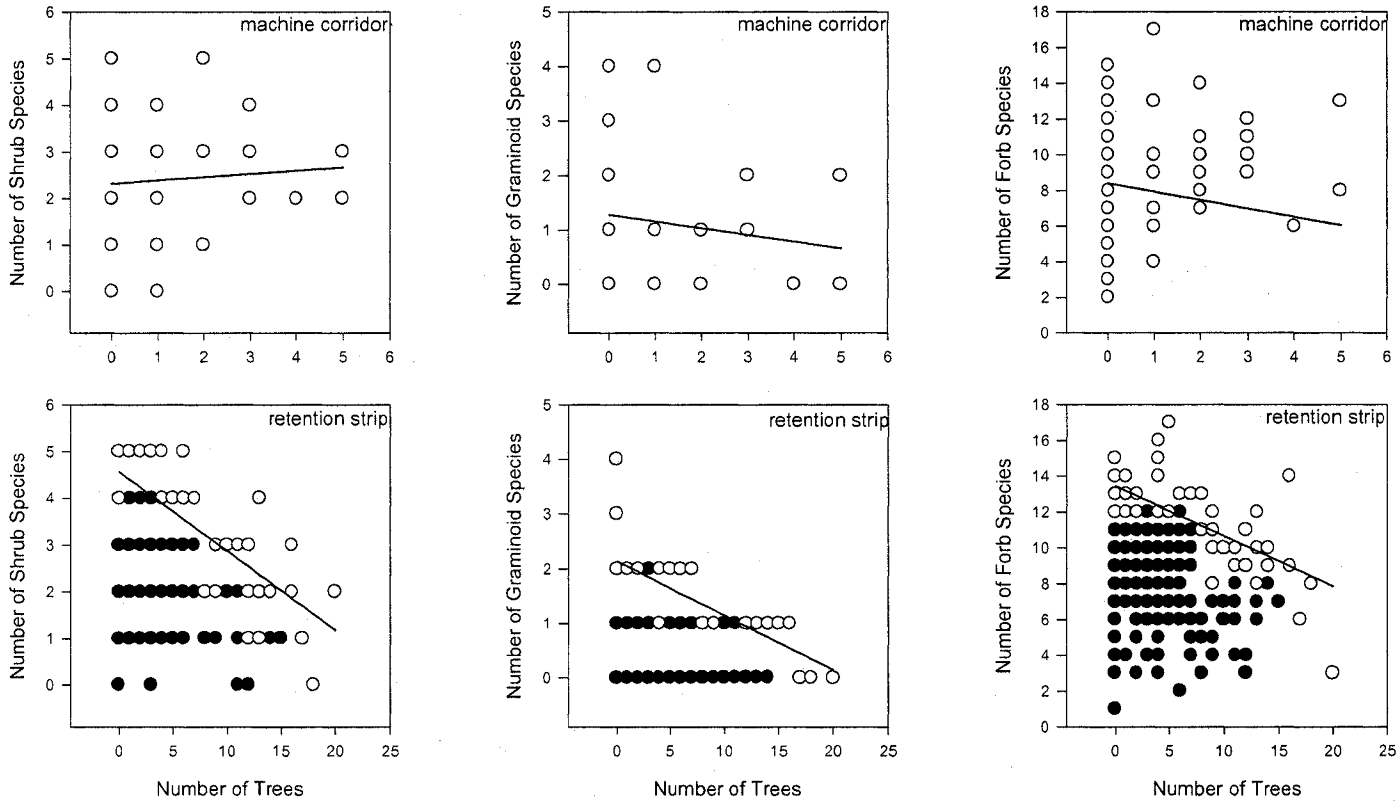

Fig. 2-13. Results of boundary line analysis of richness of shrubs, graminoids, and forbs vs. tree density (number of trees within a 5m radius of the centre of the plot) in machine corridors and retention strips. Richness in retention strips had a significant negative relationship with tree density for all vegetation groups (shrubs, graminoids, and forbs) while machine corridors did not show any significant relationships (Table 2-3). White points (the highest 10% of responses in each of 5 categories) were included in the regression black points were not. In machine corridors all plots were included in the regression. Plots in clearcut and control compartments are not included.

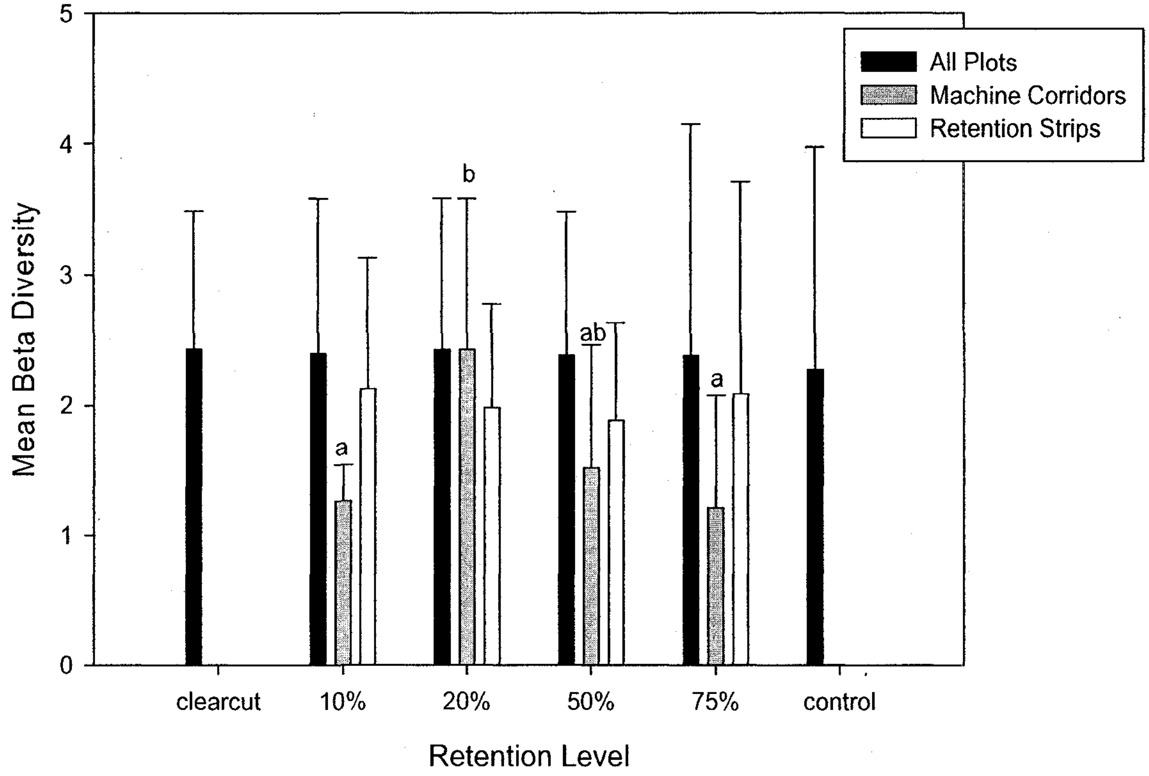

Fig. 2-14. Mean Whittaker's β diversity among plots within compartments for three compartments/treatment. No significant differences were found in species turnover among treatment for: all plots (plots in both machine corridors and retention strips, 20 plots/compartment) ($p = 0.068$) or plots in retention strips only (15 plots/compartment) ($p = 0.8963$). Plots in machine corridors only (5 plots/compartment) showed a significant difference in β diversity due to retention level ($p = 0.0096$). Values of β diversity cannot be validly compared between retention strips and machine corridors because of differences in the number of plots. Error bars represent 95% confidence intervals.

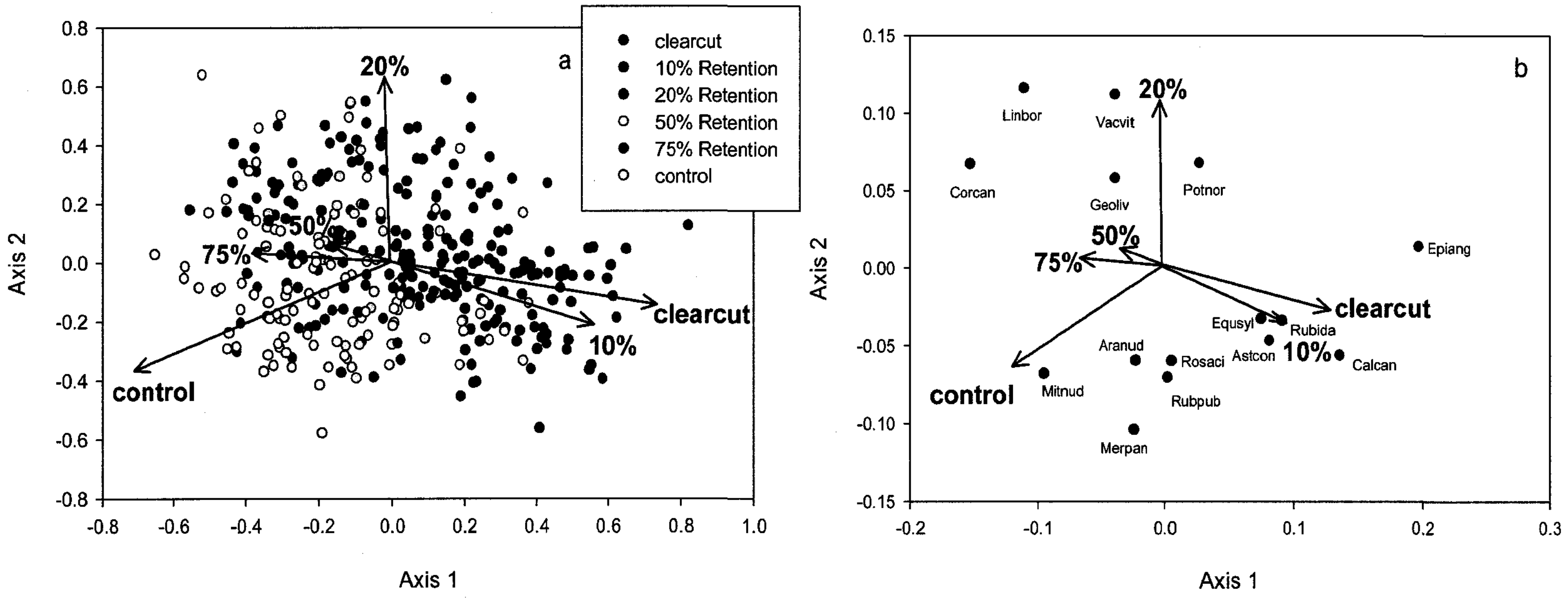

Fig. 2-15. a. Understory species composition for plots in both machine corridors and retention strips in relation to harvesting treatments as determined using distance-based redundancy analysis. Each point represents one plot. Arrows indicate the vectors for the harvesting treatments. Axis 1: λ = 0.037, Axis 2: λ = 0.015 (Table 2-4). b. Understory species that were correlated by at least 25% to at least one axis are identified by six letter codes: the first three letters of the genus name followed by the first three letters of the species name (see Appendix D).

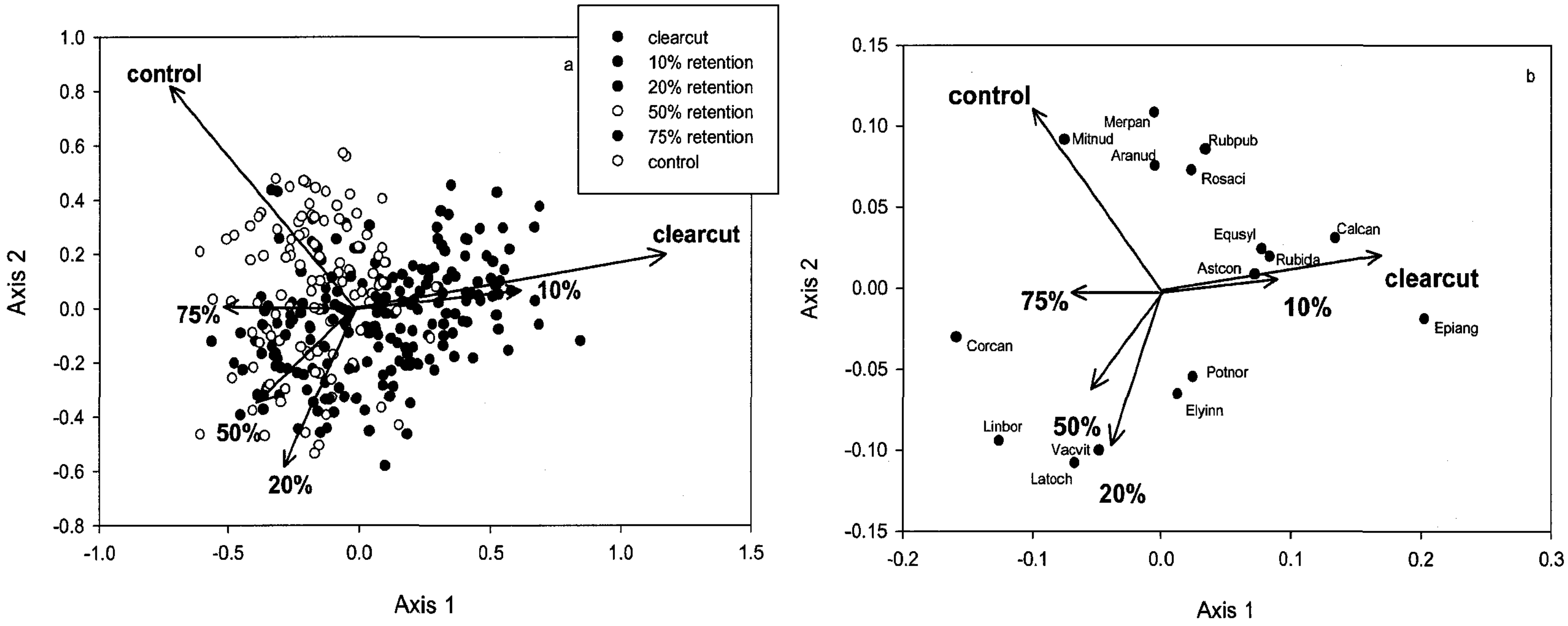

Fig. 2-16. a. Relationship of understory species composition for plots in retention strips, clearcuts, and controls to harvesting treatment as determined by using distance-based redundancy analysis. Each point represents one plot. Arrows indicate the vectors for the harvesting treatments. Axis 1: $\lambda = 0.045$, Axis 2: $\lambda = 0.021$ (Table 2-4). b. Understory species that were correlated by at least $\geq 25\%$ to at least one axis are identified by six letter codes: the first three letters of the genus name followed by the first three letters of the species name (see Appendix D).

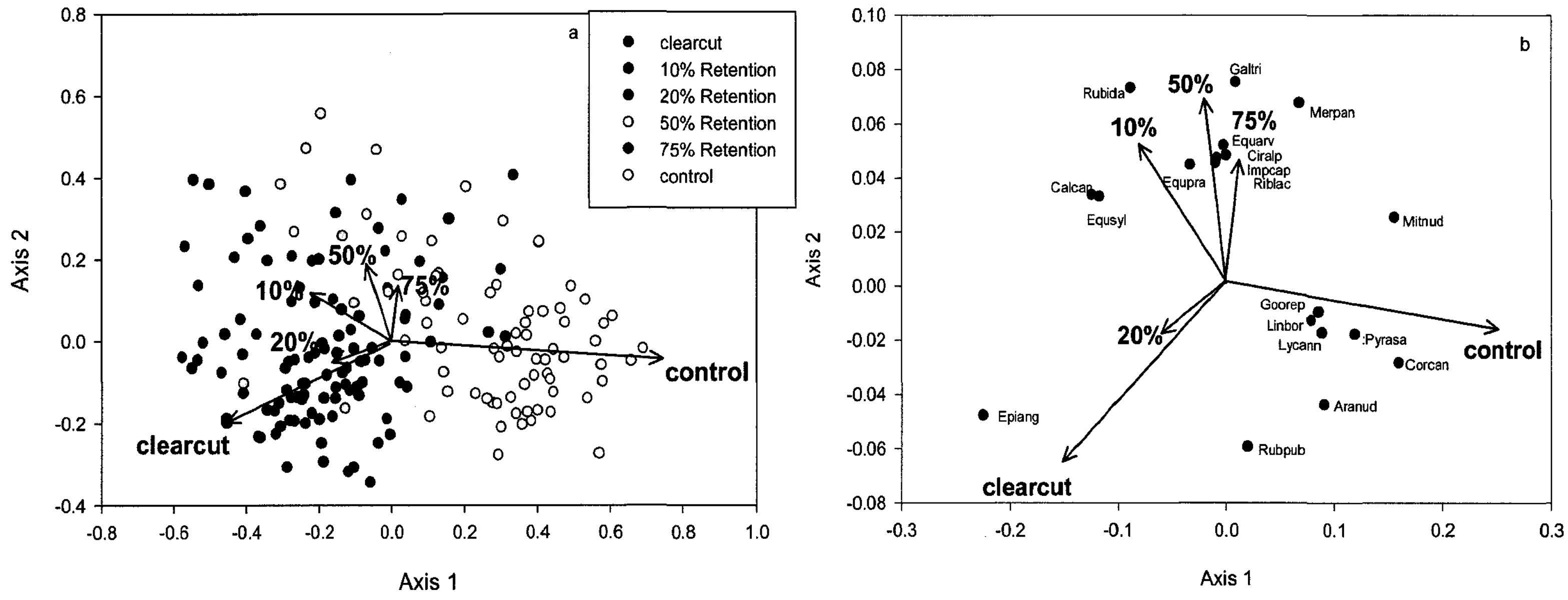

Fig. 2-17. a. Relationship of understory species composition for plots in machine corridors, clearcuts, and controls to harvesting treatment as determined by using distance-based redundancy analysis. Each point represents one plot. Arrows indicate the vectors for the harvesting treatments. Axis 1: λ = 0.068, Axis 2: λ = 0.012 (Table 2-4). b. Understory species that are correlated by at least 25% to at least one axis are identified by six letter codes: the first three letters of the genus name followed by the first three letters of the species name (see Appendix D).

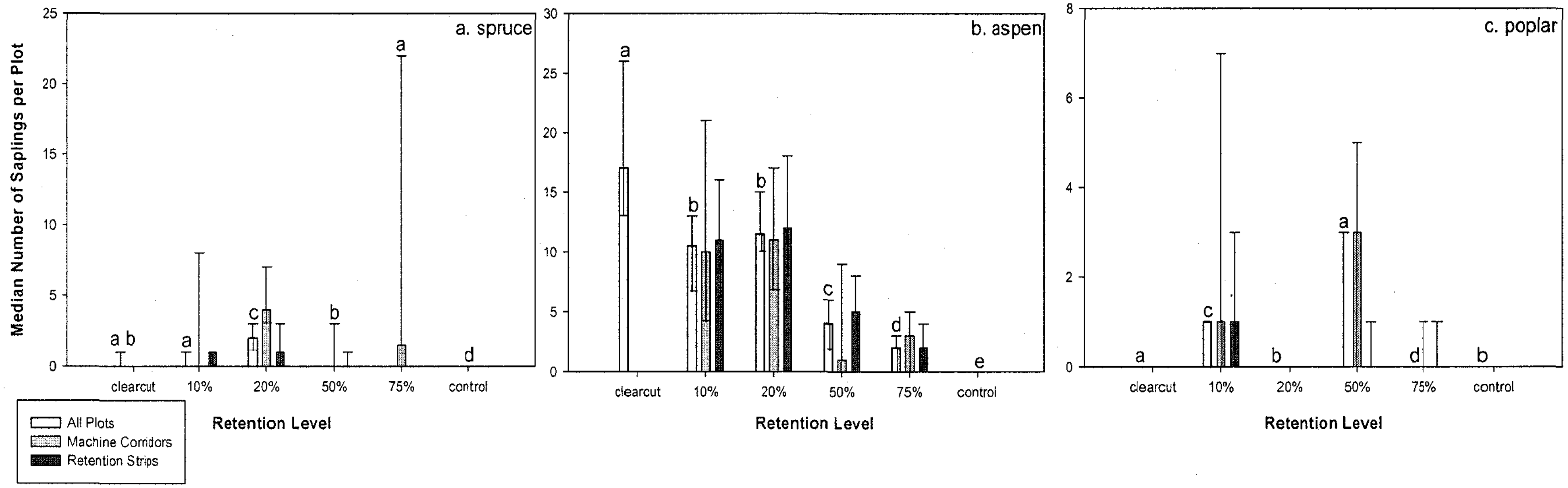

Fig. 2-18. Median number of saplings per 78.54 $m^2$ for a. spruce b. aspen and c. poplar based on all plots (both machine corridors and retention strips), plots in machine corridors only, and plots in retention strips only. a. There was a significant effect of retention level on spruce sapling density (Table 2-7a). There were significantly more spruce saplings in the retention strips than in the machine corridors and there was a significant interaction of retention level and plot type (Table 2-7a). b. There was a significant effect of retention level on aspen sapling density (Table 2-7a). The density of aspen saplings was significantly greater in retention strips than in machine corridors. There was no significant interaction of retention level and plot type on aspen sapling density (Table 2-7a). c. Poplar sapling density was significantly affected by retention level, plot type, and the interaction of retention level and plot type. Bars represent distribution-free 95% confidence intervals. Bars with the same letter are not significantly different based on least significant differences of least squared means (at $\alpha = 0.00067$, overall $\alpha = 0.01$).

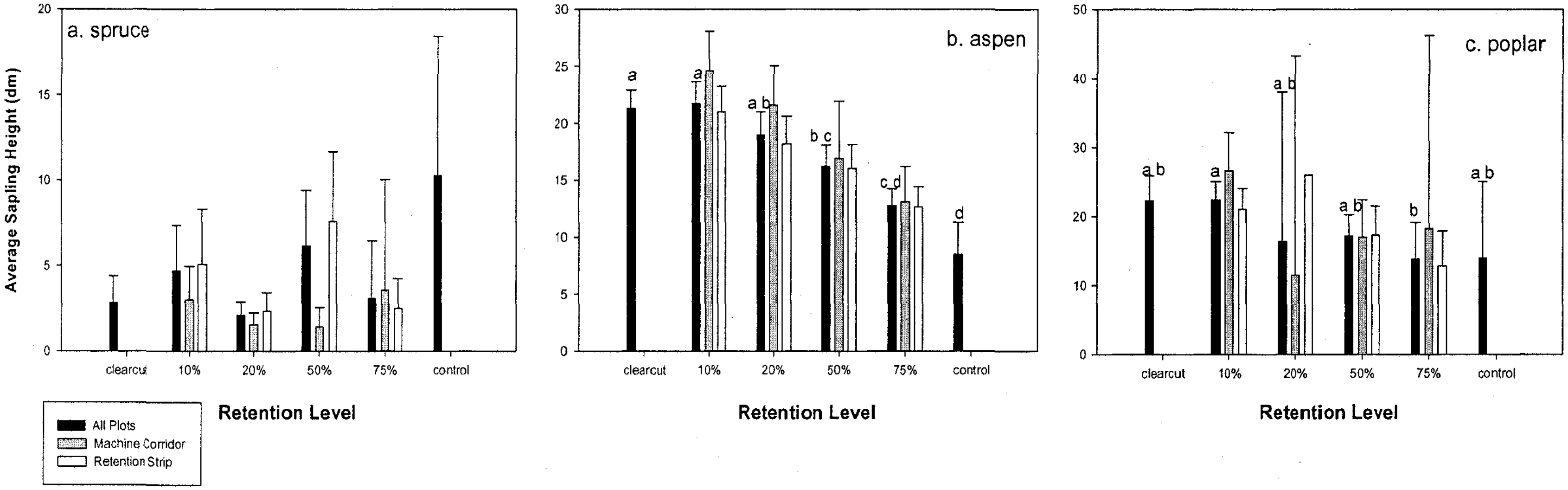

Fig 2-19. Average of the modal height (in decimeters) of a. spruce b. aspen and c. poplar saplings all plots (both machine corridors and retention strips), plots in machine corridors only, and plots in retention strips only. a. Spruce sapling height was not significantly affected by retention level, plot type, or an interaction of the two (Table 2-7a). b. The height of aspen saplings was significantly affected by retention level and plot type but not by an interaction of retention level and plot type (Table 2-7a). c. Poplar sapling height was significantly affected by retention level but not by plot type or an interaction of retention level and plot type (Table 2-7a). Bars represent 95% confidence intervals. Bars with the same letter are not significantly different based least squared means (at $\alpha = 0.00067$, overall $\alpha = 0.01$).

Table 2-1. Results of species-area curves. Average richness per compartment was the average of the total richness for each of the three compartments of a treatment. The number of species captures in 20 plots was estimated from the species-area curve. Estimated total richness per treatment is the first-order jackknife estimate.

| Retention Level | Average Richness per Compartment | Observed Total Richness per treatment | # Species Captured in 20 Plots | Estimated Total Richness per Treatment |
|---|---|---|---|---|
| clearcut | 39.67 | 62 | 42 | 79.7 |
| 10% retention | 44 | 70 | 49 | 90.7 |
| 20% retention | 38.67 | 59 | 42 | 73.7 |
| 50% retention | 40.67 | 61 | 45 | 71.8 |
| 75% retention | 39.33 | 56 | 42 | 67.8 |
| control | 39 | 63 | 45 | 78.7 |

Table 2-2. ANOVA results for cover and richness of A) plots in both machine corridors and retention strips. Analysis of 'Retention Level' and 'Block" included all plots (machine corridors, retention strips, clearcut and control) (Fig. 2-2a). Analysis of 'Plot Type' and 'Retention Level* Plot Type' did not include clearcut or control (Fig. 2-2b). B) Plots in only machine corridors or only retention strips compared to all clearcut and control plots (Fig. 2-2b).

| | | | Retention Level | | | | Plot Type | | | | Retention Level*Plot Type | | | | Block | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | N | df | F | P | N | df | F | p | N | df | F | p | N | df | F | p |
| | **Response Variable** | | | | | | | | | | | | | | | | | |
| **(A)** | **Cover: All Plots** | All Species | 360 | 5 | 4.63 | **0.0004** | 240 | 1 | 18.97 | **<0.0001** | 240 | 3 | 0.55 | 0.6469 | 360 | 2 | 24.41 | **<0.0001** |
| | | Shrubs | 360 | 5 | 0.84 | 0.5200 | 240 | 1 | 0.74 | 0.3984 | 240 | 3 | 0.65 | 0.5808 | 360 | 2 | 17.98 | **<0.0001** |
| | | Graminoids | 360 | 5 | 12.2 | **<0.0001** | 240 | 1 | 13.07 | **0.0004** | 240 | 3 | 3.55 | 0.0152 | 360 | 2 | 15.48 | **<0.0001** |
| | | Forbs | 360 | 5 | 1.82 | 0.1079 | 240 | 1 | 5.81 | 0.0167 | 240 | 3 | 0.45 | 0.7159 | 360 | 2 | 3.21 | 0.0415 |
| | **Richness: All Plots** | All Species | 360 | 5 | 2.15 | 0.0596 | 240 | 1 | 0.54 | 0.4618 | 240 | 3 | 0.51 | 0.6733 | 360 | 2 | 13.38 | **<0.0001** |
| | | Shrubs | 360 | 5 | 1.37 | 0.2345 | 240 | 1 | 0.55 | 0.4570 | 240 | 3 | 2.2 | 0.0885 | 360 | 2 | 27.08 | **<0.0001** |
| | | Graminoids | 360 | 5 | 7.29 | **<0.0001** | 240 | 1 | 8.65 | **0.0036** | 240 | 3 | 0.75 | 0.5251 | 360 | 2 | 0.49 | 0.6132 |
| | | Forbs | 360 | 5 | 2.06 | 0.0700 | 240 | 1 | 0.30 | 0.5817 | 240 | 3 | 0.37 | 0.7743 | 360 | 2 | 10.98 | **<0.0001** |

| | | | Retention Level | | | | Block | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | N | df | F | p | N | df | F | p |
| **(B)** | **Cover: Machine Corridors** | All Species | 180 | 5 | 4.02 | **0.0018** | 180 | 2 | 9.6 | **0.0001** |
| | | Shrub | 180 | 5 | 1.14 | 0.3410 | 180 | 2 | 17.96 | **<0.0001** |
| | | Graminoid | 180 | 5 | 8.81 | **0.0001** | 180 | 2 | 3.85 | 0.0232 |
| | | Forb | 180 | 5 | 1.39 | 0.2309 | 180 | 2 | 0.18 | 0.8341 |
| | **Cover: Retention Strips** | All Species | 300 | 5 | 4.69 | **0.0004** | 300 | 2 | 26.43 | **<0.0001** |
| | | Shrub | 300 | 5 | 1.93 | 0.0894 | 300 | 2 | 27.65 | **<0.0001** |
| | | Graminoid | 300 | 5 | 16.6 | **0.0001** | 300 | 2 | 21.28 | **<0.0001** |
| | | Forb | 300 | 5 | 1.85 | 0.1036 | 300 | 2 | 3.46 | 0.0327 |
| | **Richness: Machine Corridors** | All Species | 180 | 5 | 0.96 | 0.4434 | 180 | 2 | 1.86 | 0.1595 |
| | | Shrub | 180 | 5 | 1.14 | 0.3410 | 180 | 2 | 12.47 | **<0.0001** |
| | | Graminoid | 180 | 5 | 5.77 | **0.0001** | 180 | 2 | 1.91 | 0.1512 |
| | | Forb | 180 | 5 | 0.78 | 0.5635 | 180 | 2 | 2.74 | 0.0675 |
| | **Richness: Retention Strips** | All Species | 300 | 5 | 2.00 | 0.0788 | 300 | 2 | 14.56 | **<0.0001** |
| | | Shrub | 300 | 5 | 2.13 | 0.0620 | 300 | 2 | 19.28 | **<0.0001** |
| | | Graminoid | 300 | 5 | 7.35 | **0.0001** | 300 | 2 | 0.35 | 0.7029 |
| | | Forb | 300 | 5 | 2.19 | 0.0557 | 300 | 2 | 10.97 | **<0.0001** |

Table 2.3. Results of boundary line analysis of percent cover and richness vs. tree density in machine corridors and retention strips. Regressions did not include clearcut and control plots. For both percent cover and richness, plots in retention strips showed a significant negative relationship with tree density. There was no significant relationship of percent cover or richness with tree density for plots in machine corridors.

| | | **Line** | **$R^2$** | ***p*-value** |
|---|---|---|---|---|
| **Cover** | | | | |
| Machine Corridors | Shrubs | $y = 23.07816 - 0.90844x$ | 0.0035 | 0.6539 |
| | Graminoids | $y = 16.47335 - 2.26553x$ | 0.0120 | 0.4044 |
| | Forbs | $y = 37.37982 - 0.1774x$ | 0.0001 | 0.9422 |
| Retention Strips | Shrubs | $y = 67.731 - 3.74679x$ | 0.6489 | **< 0.0001** |
| | Graminoids | $y = 64.792 - 13.996x + 1.0055x^2 - 0.0235x^3$ | 0.7258 | **< 0.0001** |
| | Forbs | $y = 85.4905 - 4.34886x$ | 0.6439 | **< 0.0001** |
| | | | | |
| **Richness** | | | | |
| Machine Corridors | Shrubs | $y = 2.319 + 0.07x$ | 0.0056 | 0.5688 |
| | Graminoids | $y = 1.2798 - 0.12342x$ | 0.0392 | 0.1296 |
| | Forbs | $y = 8.40406 - 0.46803x$ | 0.0350 | 0.1525 |
| Retention Strips | Shrubs | $y = 4.564 - 0.16916x$ | 0.6098 | **< 0.0001** |
| | Graminoids | $y = 2.14 - 0.0997x$ | 0.6468 | **< 0.0001** |
| | Forbs | $y = 13.44838 - 0.2790x$ | 0.4339 | **< 0.0001** |

Table 2-4. Results of distance based redundancy analyses of the understory vegetation community composition in all plots (plots in both machine corridors and retention strips), plots in only machine corridors (including clearcut and control), and plots in only retention strips (including clearcut and control). Retention level had a significant effect on community composition in all three ordinations.

| | All Canonical Axes | | | | | Species Environment Correlations | | | |
|---|---|---|---|---|---|---|---|---|---|
| | # (Dummy) Variables | Sum of All eigenvalues | Sum of Canonical Eigenvalues ('Trace') | *F#* | *P*-value | Axis 1 | Axis 2 | Axis 3 | Axis 4 |
| **All Plots** | 5 | 0.93 | 0.069 | 5.672 | 0.0001 | 0.685 | 0.528 | 0.527 | 0.38 |
| **Machine Corridors** | 5 | 0.904 | 0.096 | 4.065 | 0.002 | 0.836 | 0.61 | 0.482 | 0.4 |
| **Retention Strips** | 5 | 0.925 | 0.085 | 5.911 | 0.0001 | 0.741 | 0.626 | 0.496 | 0.412 |

| | Cumulative % Variance of Species Data | | | | Cumulative % Variance of Species-Environment Relation | | | |
|---|---|---|---|---|---|---|---|---|
| | Axis 1 | Axis 2 | Axis 3 | Axis 4 | Axis 1 | Axis 2 | Axis 3 | Axis 4 |
| **All Plots** | 3.9 | 5.5 | 6.7 | 7.1 | 52.9 | 74.3 | 89.5 | 95.8 |
| **Machine Corridors** | 7.5 | 8.9 | 9.8 | 10.3 | 71.2 | 83.9 | 93.1 | 97.1 |
| **Retention Strips** | 4.9 | 7.2 | 8.4 | 8.8 | 53.2 | 77.9 | 91 | 96.1 |

Table 2-5. Results of pairwise contrasts of retention levels using multivariate analysis of variance and dbRDA to test for differences in composition among treatments in (a) all plots (both machine corridors and retention strips), $\alpha = 0.0006$ (b) retention strips only (including clearcut and control), $\alpha = 0.0007$ (c) machine corridors only (including clearcut and control), $\alpha = 0.0007$. Significant p values are bolded.

| | Contrast | $\sum$of all Eigenvalues | $\sum$of all Canonical Eigenvalues | F# | *P*-value |
|---|---|---|---|---|---|
| (a.) All Plots | cc vs. 10 | 0.8320 | 0.0160 | 2.3250 | 0.0013 |
| | cc vs. 20 | 0.8630 | 0.0530 | 7.5410 | **0.0001** |
| | cc vs. 50 | 0.9020 | 0.0550 | 7.5270 | **0.0001** |
| | cc vs. 75 | 0.9120 | 0.0670 | 9.1400 | **0.0001** |
| | cc vs. control | 0.8620 | 0.0890 | 13.4260 | **0.0001** |
| | 10 vs. 20 | 0.8850 | 0.0510 | 7.1360 | **0.0001** |
| | 10 vs. 50 | 0.9060 | 0.0340 | 4.5360 | **0.0001** |
| | 10 vs. 75 | 0.9080 | 0.0480 | 6.4270 | **0.0001** |
| | 10 vs. control | 0.9190 | 0.0750 | 10.3680 | **0.0001** |
| | 20 vs. 50 | 0.8740 | 0.0340 | 4.6870 | **0.0001** |
| | 20 vs. 75 | 0.8970 | 0.0340 | 4.5870 | **0.0001** |
| | 20 vs. control | 0.8830 | 0.0620 | 8.8190 | **0.0001** |
| | 50 vs. 75 | 0.8980 | 0.0180 | 2.3480 | 0.0013 |
| | 50 vs. control | 0.8980 | 0.0430 | 5.7760 | **0.0001** |
| | 75 vs. control | 0.9070 | 0.0290 | 3.7760 | **0.0001** |
| (b.) Retention Strips | cc vs. 10 | 0.8280 | 0.0190 | 2.3890 | **0.0003** |
| | cc vs. 20 | 0.8680 | 0.0550 | 6.8490 | **0.0001** |
| | cc vs. 50 | 0.8890 | 0.0820 | 10.1960 | **0.0001** |
| | cc vs. 75 | 0.8990 | 0.0800 | 9.8440 | **0.0001** |
| | 10 vs. 20 | 0.8780 | 0.0670 | 7.1110 | **0.0001** |
| | 10 vs. 50 | 0.8890 | 0.0500 | 5.1550 | **0.0001** |
| | 10 vs. 75 | 0.8920 | 0.0550 | 5.6170 | **0.0001** |
| | 10 vs. control | 0.8650 | 0.0690 | 8.8110 | **0.0001** |
| | 20 vs. 50 | 0.8460 | 0.0380 | 4.0100 | **0.0001** |
| | 20 vs. 75 | 0.8880 | 0.0390 | 4.0000 | **0.0001** |
| | 20 vs. control | 0.8780 | 0.0650 | 8.0780 | **0.0001** |
| | 50 vs. 75 | 0.8700 | 0.0250 | 2.5120 | 0.0009 |
| | 50 vs. control | 0.8860 | 0.0540 | 6.5250 | **0.0001** |
| | 75 vs. control | 0.8920 | 0.0280 | 3.2560 | **0.0001** |
| (c.) Machine Corridors | cc vs. 10 | 0.7950 | 0.0190 | 1.7260 | 0.0198 |
| | cc vs. 20 | 0.8020 | 0.0200 | 1.8420 | 0.0106 |
| | cc vs. 50 | 0.8490 | 0.0240 | 2.1000 | 0.0038 |
| | cc vs. 75 | 0.8480 | 0.0320 | 2.8130 | **0.0001** |
| | 10 vs. 20 | 0.7690 | 0.0510 | 1.8360 | 0.0258 |
| | 10 vs. 50 | 0.8710 | 0.0260 | 0.7920 | 0.6623 |
| | 10 vs. 75 | 0.8690 | 0.0570 | 1.8100 | 0.3030 |
| | 10 vs. control | 0.8520 | 0.0840 | 7.7260 | **0.0001** |
| | 20 vs. 50 | 0.8220 | 0.0600 | 2.0560 | 0.0096 |
| | 20 vs. 75 | 0.8230 | 0.0510 | 1.7280 | 0.3120 |
| | 20 vs. control | 0.8440 | 0.0720 | 6.0631 | **0.0001** |
| | 50 vs. 75 | 0.8640 | 0.0280 | 0.8730 | 0.5784 |
| | 50 vs. control | 0.8590 | 0.0470 | 4.1110 | **0.0001** |
| | 75 vs. control | 0.8640 | 0.0350 | 3.0300 | **0.0001** |

Table 2-6. Results of indicator species analysis for groups indicated by dbRDA (Figs. 2-14a, 2-15a, 2-16a). Analyses were repeated three times: once for all plots (plots in both machine corridors and retention strips), once for plots in only retention strips (including all plots for clearcuts and controls), and once for plots in only machine corridors (including all plots for clearcuts and controls). Only those species with indicator values $\geq 25$ were included. cc=clearcut

| | | **Species** | **Indicator Value** | **P** |
|---|---|---|---|---|
| **All Plots** | **Group** | | | |
| | cc & 10% | *Calamagrostis canadensis* | 31.7 | 0.001 |
| | | *Epilobium angustifolium* | 50.3 | 0.001 |
| | | *Equisetum sylvaticum* | 26.0 | 0.002 |
| | 20%, 50%, 75% | *Lathyrus ochroleucus* | 28.6 | 0.002 |
| | | *Linnaea borealis* | 32.9 | 0.004 |
| | control | *Cornus canadensis* | 31.7 | 0.001 |
| | | *Mitella nuda* | 39.5 | 0.001 |
| **Retention Strips** | cc & 10% | *Calamagrostis canadensis* | 34.0 | 0.001 |
| | | *Epilobium angustifolium* | 51.2 | 0.001 |
| | 20%, 50%, 75% | *Lathyrus ochroleucus* | 33.4 | 0.001 |
| | | *Linnaea borealis* | 40.2 | 0.001 |
| | control | *Cornus canadensis* | 37.0 | 0.002 |
| | | *Mertensia paniculata* | 30.1 | 0.009 |
| | | *Mitella nuda* | 39.1 | 0.001 |
| **Machine Corridors** | cc, 10%, 20%, 50%, 75% | *Calamagrostis canadensis* | 42.4 | 0.001 |
| | | *Epilobium angustifolium* | 69.9 | 0.001 |
| | | *Equisetum sylvaticum* | 34.7 | 0.003 |
| | control | *Cornus canadensis* | 55.8 | 0.001 |
| | | *Linnaea borealis* | 43.9 | 0.001 |
| | | *Mitella nuda* | 53.0 | 0.001 |
| | | *Pyrola asarifolia* | 34.2 | 0.001 |

Table 2-7. ANOVA results for density and height of saplings in A) plots in both machine corridors and retention strips. Analysis of ‘Retention Level’ and ‘Block” included all plots (machine corridors, retention strips, clearcut and control). Analysis of ‘Plot Type’ and ‘Retention Level* Plot Type’ did not include clearcut or control (Fig. 2-2b). B) Plots in only machine corridors or only retention strips compared to all clearcut and control plots. (Figs. 2-18 and 2-19)

| | | | **Retention Level** | | | | **Plot Type** | | | | **Retention Level*Plot Type** | | | | **Block** | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | **N** | **df** | **F** | **p** | **N** | **df** | **F** | **p** | **N** | **df** | **F** | **p** | **N** | **df** | **F** | **p** |
| | **Response Variable** | | | | | | | | | | | | | | | | | |
| **(A)** | **Density: All Plots** | Spruce | 359 | 5 | 30.68 | **<0.0001** | 239 | 1 | 138.72 | **<0.0001** | 239 | 3 | 23.23 | **<0.0001** | 359 | 2 | 10.17 | **<0.0001** |
| | | Aspen | 360 | 5 | 259.69 | **<0.0001** | 240 | 1 | 16.26 | **<0.0001** | 240 | 3 | 0.23 | 0.8785 | 360 | 2 | 6.29 | **0.0021** |
| | | Poplar | 360 | 5 | 56.41 | **<0.0001** | 240 | 1 | 13.07 | **0.0004** | 240 | 3 | 7.89 | **<0.0001** | 360 | 2 | 46.29 | **<0.0001** |
| | **Height: All Plots** | Spruce | 359 | 5 | 2.05 | 0.0753 | 239 | 1 | 0.85 | 0.3580 | 239 | 3 | 0.89 | 0.4501 | 359 | 2 | 9.35 | **0.0002** |
| | | Aspen | 360 | 5 | 21.7 | **<0.0001** | 240 | 1 | 14.76 | **<0.0001** | 240 | 3 | 0.52 | 0.6694 | 360 | 2 | 1.91 | 0.1509 |
| | | Poplar | 360 | 5 | 3.78 | **0.0036** | 240 | 1 | 0.12 | 0.7312 | 240 | 3 | 1.81 | 0.1540 | 360 | 2 | 2.95 | 0.0568 |

| | | | **Retention Level** | | | | **Block** | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | **N** | **df** | **F** | **p** | **N** | **df** | **F** | **p** |
| **(B)** | **Density: Machine Corridors** | Spruce | 179 | 5 | 97.33 | **<0.0001** | 179 | 2 | 60.87 | **<0.0001** |
| | | Aspen | 180 | 5 | 164.7 | **<0.0001** | 180 | 2 | 4.97 | **0.0080** |
| | | Poplar | 180 | 5 | 35.12 | **<0.0001** | 180 | 2 | 37.76 | **<0.0001** |
| | **Density: Retention Strips** | Spruce | 180 | 5 | 5.79 | **<0.0001** | 180 | 2 | 1.30 | 0.275 |
| | | Aspen | 180 | 5 | 223.58 | **<0.0001** | 180 | 2 | 2.42 | 0.0908 |
| | | Poplar | 180 | 5 | 37.57 | **<0.0001** | 180 | 2 | 48.97 | **<0.0001** |
| | **Height: Machine Corridors** | Spruce | 179 | 5 | 2.59 | 0.0345 | 179 | 2 | 3.30 | 0.0429 |
| | | Aspen | 180 | 5 | 18.86 | **<0.0001** | 180 | 2 | 0.78 | 0.4618 |
| | | Poplar | 180 | 5 | 2.37 | 0.0579 | 180 | 2 | 0.44 | 0.6460 |
| | **Height: Retention Strips** | Spruce | 180 | 5 | 1.48 | 0.2016 | 180 | 2 | 7.86 | **0.0006** |
| | | Aspen | 180 | 5 | 17.65 | **<0.0001** | 180 | 2 | 1.60 | 0.2038 |
| | | Poplar | 180 | 5 | 3.83 | **0.0039** | 180 | 2 | 2.40 | 0.0970 |

# Chapter 3: General Conclusions

## Understory Vegetation Community Responses to Partial Harvesting

Eight years after partial harvesting the understory vascular plant community had increased cover and different composition when compared to an unharvested control. Richness was similar across harvesting treatments. Lower retention levels lead to the greatest differences from unharvested controls. There was evidence that a threshold level for several responses appears to exist between 10% and 20% retention. Machine corridors experienced a greater degree of change than retention strips and in some ways appeared to function as clearcuts within the partially harvested areas.

### *Threshold Levels of Harvesting*

Responses to different levels of retention were different in the first growing seasons after harvesting and the 8th growing season after harvest (Fig. 3-1). Some of the responses observed by Macdonald & Fenniak (2007) may have been due to the initial disturbances caused by harvesting and may have changed over time. In the intervening years between the studies, a difference in composition between the 75% retention and unharvested control became apparent. By studying more retention levels, the current study was able to explore the response of the understory community to a gradient of harvesting intensities.

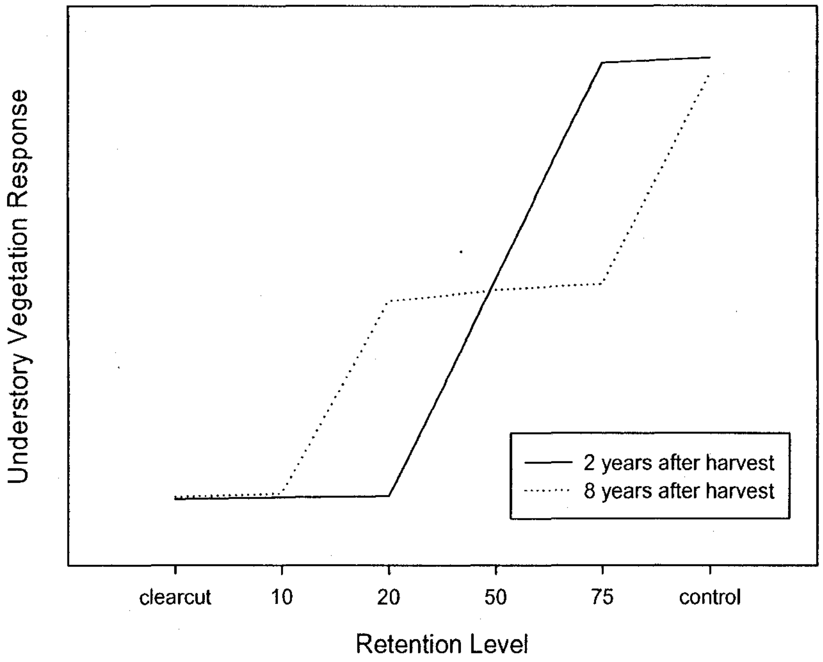

Fig. 3-1. Understory responses to varying levels of partial harvesting in the 2nd and 8th growing seasons after harvesting.

## Variable Retention Harvesting

Franklin et al. (1997) provided three purposes for variable retention harvesting. First, by creating habitat, ameliorating the microclimate, and providing substrates and energetic substances for a diversity of biota, retention provides refugia for species that might otherwise be lost. Second, retention enriches a regenerating forest with structural elements, increasing structural diversity and the potential carrying capacity. Third, retained structures can provide connectivity within a managed landscape.

The current study suggests that variable green tree retention functions best to provide refugia for plant species that might be lost through clearcutting. Also, retention prevents the establishment and increases in abundance of weedy, shade-intolerant species that are associated with clearcutting. Machine corridors, which were found to be similar to clearcuts, were also found to be significantly different from adjacent retention strips in terms of percent cover, composition, and density and height of saplings. Clearcutting leads to changes in microclimate such as increased air and soil temperatures, increased wind velocity, and lower soil and air moisture than would be found in an unharvested forest (Chen et al., 1993). By limiting the degree of some of these changes to the microclimate, green tree retention helps limit the changes in the understory community that are associated with clearcutting.

## Dispersed vs. Aggregated Retention

There are two forms of green tree retention: dispersed and aggregated. Each of these harvesting techniques has benefits and drawbacks. Dispersed retention enables a uniform distribution of structures, such as woody debris, and conditions, such as mitigating changes in microclimate, across a harvested landscape. Aggregated retention allows for the maintenance of ecological conditions that resemble unharvested forest (Franklin et al., 1997). Maintaining the same amounts of retention but altering the distribution of the retained trees can have a significant effect on the response of the forest community. Aggregated patches of retention can support late-seral species that disappear from harvested areas (Nelson & Halpern, 2005), however patches of less than 1 ha are often not effective because the entire patch is subjected to edge effects (Esseen, 1994) and does not retain any areas that are representative of the composition of understory vegetation in pre-harvested forests (Bradbury, 2004).

By leaving retained trees spread uniformly across a landscape, dispersed green tree retained may result in more homogenous landscapes after harvesting than aggregated retention. By leaving retention in patches, aggregated green tree retention results in a dichotomous harvested landscape: patches of intact or nearly intact forest surrounded by clearcuts. This effect is likely to be analogous to machine corridors within a partially harvested dispersed green tree retention landscape in that in order to assess the effect of the harvesting treatment as a whole, both harvested areas and retained patches must be considered. Ultimately it may be a combination of aggregated patches surrounded by dispersed retention that results in the most sustainable harvesting technique.

## Effects of Forest Type

Canopy composition has been found to be the greatest factor influencing understory vegetation communities (De Grandpré et al., 1993; Légaré et al., 2002). Canopy composition influences light availability in the understory (Messier et al., 1998), nutrient cycling (Côté et al., 2000), soil fertility (Paré & Bergeron, 1996), and vascular plant cover (Saetre et al., 1997; Légaré et al., 2002). It is therefore likely that canopy composition will affect how a forest will respond to partial harvesting and how it will recover. Macdonald & Fenniak (2007) found that coniferous and broadleaf forests responded differently to harvesting, with mixedwood forests being more similar to coniferous forests.

This study examined the effects of partial harvesting only in mixedwood forests. It is likely that the composition both of trees present before harvesting and of the retained trees will affect how a mixedwood forest will respond to harvesting and the long term response of the understory community. If the proportion of broadleaf and conifer trees changes after harvesting, then conditions within the understory will likely also change, potentially altering the understory community permanently. Also, aspen are able to resprout quickly due to suckering and in areas of low retention, such as clearcut and 10% retention, aspen densities were high. Spruce saplings were generally taller in the unharvested control, probably due to saplings that established before harvesting. Lower retention may lead to aspen dominated forests while higher retention may lead to spruce dominated forests or mixedwood forests with more spruce.

### Forest Management Implications

Partial harvesting shows potential as a technique to maximize the conservation of understory vascular plant species in managed mixedwood boreal forests. Leaving as many residual trees as possible within a harvested area is beneficial for the maintenance of diversity of the understory community, including species richness and abundance. Retention levels of 20% and greater appear to be the most effective for maximizing the beneficial effects of partial harvesting.

The response of the understory community in machine corridors is significantly different from responses in the retention strips; with machine corridors acting as clearcuts within partially harvested areas. Minimizing the size and number of machine corridors on a harvested landscape will reduce the overall impact of partial harvesting on the understory plant community in mixedwood boreal forests.

## Future Research

Future research should consider direct measurements of canopy cover and light in the understory after partial harvesting (Lieffers et al. 1999). Partial harvesting poses a risk of exposing trees that are not wind-hardened and subsequent loss of trees to wind-throw (Coates, 1997), thus initial retention levels may not be an accurate portrayal of tree density or canopy cover in the years following harvesting. This study, for example, found that analyses using tree density revealed a relationship (decreasing upper limit of richness with decreasing tree density) that was not apparent when retention level was used as a surrogate for actual tree density or canopy cover.

Changes in understory vegetation need to be monitored over time. Responses within harvesting treatments may converge or diverge over time. For example, although the composition of the understory vegetation in the 10% retention was not found to be different from composition in clearcuts in this study, overtime the presence of residual trees may help the understory plant community in the 10% retention to recover faster than clearcuts. Macdonald & Fenniak (2007) found that the composition of understory vegetation in retention strips in 75% retention were not significantly different from unharvested controls, while this study did find a significant difference. This lag in response time suggests potentially divergent responses among retention levels over time.

Determining the effects of time on the regeneration of the understory vegetation within partially harvested forests will be a key component of further studies on the effects of partial harvesting on understory communities. Understory plant communities may take longer to recover from disturbances than overstory cover (Robinson et al. 1994). If partial harvesting can facilitate a faster recovery of the canopy, it may also facilitate a faster response from the understory community. Clearcut Appalachian forests have been found to show significant difference from unharvested forests in terms of richness and cover for 45-87 years after harvesting (Duffy & Meier, 1992). Similarly, secondary coastal Acadian forests in Nova Scotia have been found to have compositional differences from unharvested forests for 54 years after harvesting (Moola & Vasseur, 2004). Partial harvesting may mitigate some of these long lasting effects of clearcutting, either by reducing the intensity or persistence of the changes.

## Conclusion

Partial harvesting has the potential to minimize the impact of harvesting on vascular understory plant communities. In practice, leaving as much retention as possible, especially above 20%, and minimizing machine corridors can maximize the beneficial effects of partial harvesting. Future studies should examine the effects of canopy closure and light in addition to prescribed retention levels as well as monitor the longer term effects of partial harvesting on the understory vegetation community.

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Appendix A. Description of tree removal at EMEND. Adapted from Sidders and Luchkow. The EMEND final harvest layout and extraction plan (1998, Unpublished). Available online at: http://www.emend.rr.ualberta.ca/index.asp?page=harvest_treatments

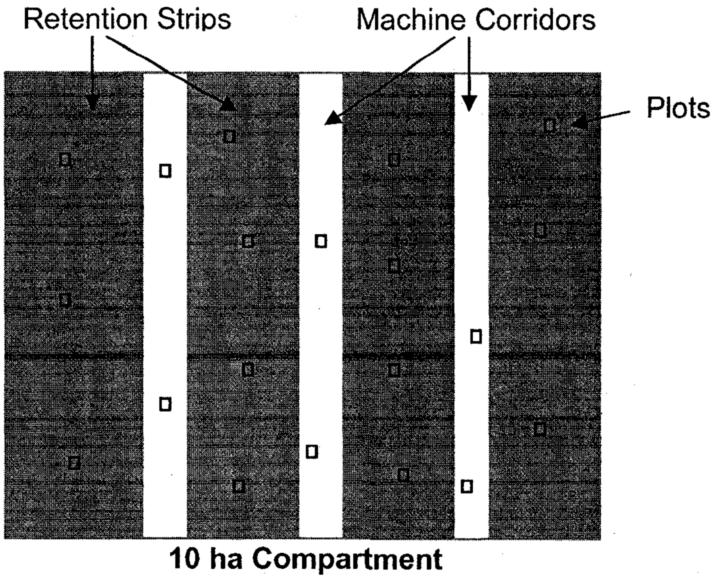
| Retention Level | Machine Corridor (% of Net Area) | Stem Removal in Retention Strips | Retention Strip (% of Net Area) |
|---|---|---|---|
| 75% | 25% | No individual tree removal | 75% |
| 50% | 25% | 1 removed of 3 | 75% |
| 20% | 25% | 3 removed of 4 | 75% |
| 10% | 25% | 7 removed of 8 | 75% |

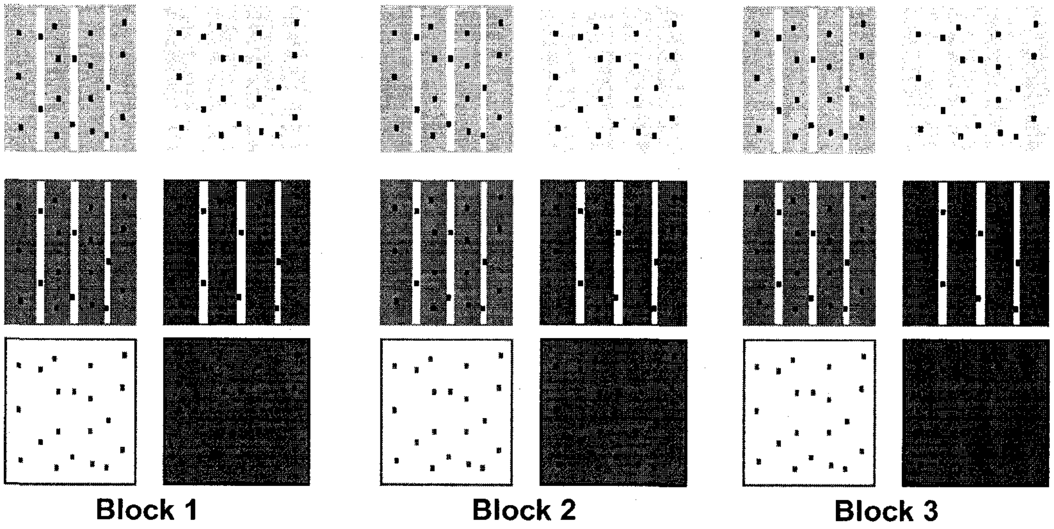
Appendix C. Tree density and basal area before (1998) and after (2003) harvesting.

| | | | 1998 | | 2003 | |
|---|---|---|---|---|---|---|
| **Compartment** | **Treatment** | **Tree Species** | **Density** | **Basal Area** | **Density** | **Basal Area** |
| 899 | Clearcut | White Spruce | 145.8333 | 12.85494449 | 20.83333 | 2.527163718 |
| | | Balsam Poplar | 20.83333 | 2.73712665 | 20.83333 | 2.777427359 |
| | | Aspen | 125 | 15.24587447 | 20.83333 | 3.372562315 |
| 868 | 10% | White Spruce | 729.1667 | 16.60587206 | 166.6667 | 3.553449177 |
| | | Balsam Poplar | 187.5 | 8.783443854 | 41.66667 | 1.809572203 |
| | | Aspen | 333.3333 | 17.21448966 | 83.33333 | 3.982996168 |
| 875 | 20% | White Spruce | 750 | 23.21219404 | 333.3333 | 11.01492178 |
| | | Balsam Poplar | 20.83333 | 0.298205613 | 20.83333 | 0.403317979 |
| | | Aspen | 312.5 | 11.31864153 | 62.5 | 2.518033473 |
| 903 | 50% | White Spruce | 416.6667 | 35.82057281 | 125 | 13.34984309 |
| | | Balsam Poplar | 62.5 | 3.720247971 | 41.66667 | 3.342929922 |
| | | Aspen | 104.1667 | 8.664407045 | 62.5 | 6.84639182 |
| 906 | 75% | White Spruce | 208.3333 | 16.55740648 | 145.8333 | 7.290452294 |
| | | Balsam Poplar | 125 | 13.63526964 | 62.5 | 5.809863469 |
| | | Aspen | 62.5 | 6.118721036 | 20.83333 | 2.264300993 |
| 867 | Control | White Spruce | 541.6667 | 10.92993522 | 541.6667 | 11.91214025 |
| | | Balsam Poplar | 104.1667 | 1.796744043 | 83.33333 | 1.858479559 |
| | | Aspen | 770.8333 | 24.44217561 | 729.1667 | 24.97118991 |
| 874 | Clearcut | White Spruce | 562.5 | 19.75153628 | 104.1667 | 2.978521844 |
| | | Balsam Poplar | 20.83333 | 1.022652995 | | |
| | | Aspen | 395.8333 | 16.70453762 | 20.83333 | 0.919062337 |
| 900 | 10% | White Spruce | 83.33333 | 13.23111717 | 41.66667 | 3.99363175 |
| | | Balsam Poplar | 41.66667 | 3.411930365 | | |
| | | Aspen | 125 | 15.14256198 | 41.66667 | 6.44974972 |
| 905 | 20% | White Spruce | 375 | 37.50237065 | 62.5 | 3.948275045 |
| | | Balsam Poplar | 41.66667 | 3.084321432 | 20.83333 | 3.537970301 |
| | | Aspen | 41.66667 | 4.297842382 | | |
| 908 | 50% | White Spruce | 62.5 | 3.24581879 | 41.66667 | 0.637350071 |
| | | Balsam Poplar | 500 | 30.44066539 | 125 | 7.395155598 |
| | | Aspen | 104.1667 | 6.110278011 | 41.66667 | 2.877500091 |
| 909 | 75% | White Spruce | 958.3333 | 38.96545165 | 770.8333 | 34.75293944 |
| | | Balsam Poplar | 166.6667 | 7.737834345 | 145.8333 | 7.463566993 |
| | | Aspen | 145.8333 | 7.650082542 | 104.1667 | 4.900896763 |
| 902 | Control | White Spruce | 270.8333 | 35.48849692 | 270.8333 | 37.02974134 |
| | | Aspen | 104.1667 | 15.54088941 | 83.33333 | 14.14150741 |
| 914 | Clearcut | White Spruce | 458.3333 | 32.56143497 | | |
| | | Aspen | 62.5 | 3.132345217 | | |
| 913 | 10% | White Spruce | 562.5 | 19.26056469 | 20.83333 | 0.293804115 |
| | | Balsam Poplar | 20.83333 | 0.77049131 | | |
| | | Aspen | 250 | 29.16751967 | 41.66667 | 4.572404258 |
| 910 | 20% | White Spruce | 583.3333 | 28.18436563 | 83.33333 | 3.927445649 |
| | | Aspen | 250 | 12.55904599 | 41.66667 | 4.100969409 |
| 911 | 50% | Aspen | 41.66667 | 2.024820205 | | |
| | | White Spruce | 833.3333 | 45.3800712 | 541.6667 | 25.78265279 |
| 912 | 75% | White Spruce | 479.1667 | 34.68245002 | 208.3333 | 13.58873483 |
| | | Aspen | 125 | 8.893694028 | 62.5 | 5.743546468 |

|  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|
| 928 | Control | White Spruce | 750 | 34.88568798 | 750 | 37.34604382 |
|  |  | Aspen | 83.33333 | 5.944117354 | 83.33333 | 6.310816175 |

Appendix C. Each treatment was applied to a 10 ha compartment and replicated in three compartments. Each group of six treatments was segregated spatially and temporally; creating three blocks.





# Appendix D. List of vascular plant species found in sample plots and their six letter codes. Nomenclature follows Moss, 1983.

| | |
|---|---|
| achmil | *Achillea millefolium* L. |
| achsib | *Achillea sibirica* Ledeb. |
| actrub | *Actaea rubra (Ait.) Willd.* |
| adomos | *Adoxa moschatellina* L. |
| agotra | *Agropyron trachycaulum* (Link) Malte |
| agrsca | *Agrostis scabra* Willd. |
| alncri | *Alnus crispa* (Ait.) Turrill |
| alnrug | *Alnus rugosa* (Du Roi) Clausen |
| amealn | *Amelanchier alnifolia* (Nutt.) Nutt. ex M. Roemer |
| aqubre | *Aquilegia brevistyla* Hook. |
| aranud | *Aralia nudicaulis* L. |
| arcuva | *Arctostaphylos uva-ursi* (L.) Spreng. |
| arespp | *Arenaria spp.* L. |
| arncor | *Arnica cordifolia* Hook. |
| astcil | *Aster ciliolatus* (Lindl.) A.& D. Löve |
| astcon | *Aster conspicuus* (Lindl.) Nesom |
| astpun | *Aster puniceus* L. |
| astalp | *Astragalus alpinus* L. |
| astame | *Astragalus americanus* Hook. M.E. Jones |
| betgla | *Betula glandulosa* Michx. |
| betpap | *Betula papyrifera* Marsh. |
| calcan | *Calamagrostis canadensis* (Michx.) Beauv. |
| caraur | *Carex aurea* Nutt. |
| carbac | *Carex backii* Boott |
| carbru | *Carex brunnescense* (Pers.) Poir. |
| cardew | *Carex deweyana* Schwein. |
| cardis | *Carex disperma* Dewey |
| carmic | *Carex microptera* Mackenzie |
| carsic | *Carex siccata* Dewey |
| ciralp | *Circaea alpina* L. |
| cortri | *Corallorhiza trifida* Chatelain |
| corcan | *Cornus canadensis* L. |
| corsto | *Cornus stolonifera* Michx. |
| delgla | *Delphinium glaucum* S. Wats. |
| elyinn | *Elymus innovatus* (Beal) Pilger |
| epiang | *Epilobium angustifolium* (L.) Holub |
| epigla | *Epilobium glandulosum* (Lehm.) Hoch & Raven |
| epipal | *Epilobium palustre* L. |
| equarv | *Equisetum arvense* L. |
| equpra | *Equisetum pratense* Ehrh. |
| equsci | *Equisetum scirpoides* Michx. |
| equsyl | *Equisetum sylvaticum* L. |
| fravir | *Fragaria virginiana* Duchesne |
| galbor | *Galium boreale* L. |
| galtri | *Galium triflorum* Michx. |
| geoliv | *Geocaulon lividum* (Richards.) Fern. |
| geumac | *Geum macrophyllum* Willd. |
| goorep | *Goodyera repens* R. Br. Ex Ait. f. |

| | |
|---|---|
| gymdry | *Gymnocarpium dryopteris* (L.) Newman |
| habobt | *Habenaria obtusata* (Banks ex s Lindl. |
| haborb | *Habenaria orbiculata* (Pursh) Lindl. |
| herlan | *Heracleum lanatum* Bartr. |
| impcap | *Impatiens capensis* Meerb. |
| latoch | *Lathyrus ochrolaeucus* Hook. |
| latven | *Lathyrus venosus* Muhl. ex Willd. |
| ledgro | *Ledum groenlandicum* Oeder |
| linbor | *Linnaea borealis* L. |
| londio | *Lonicera dioica* L. |
| loninv | *Lonicera involucrata* (Richards.) Banks ex Spreng. |
| luzpar | *Luzula parviflora* (Ehrh.) Desv. |
| lycann | *Lycopodium annotinum* L. |
| lyccom | *Lycopodium complanatum* L. |
| maican | *Maianthemum canadensis* Desf. |
| merpan | *Mertensia paniculata* (Ait.) G. Don |
| mitnud | *Mitella nuda* L. |
| monuni | *Moneses uniflora* (L.) Gray |
| osmdep | *Osmorrhiza depauperata* Phil. |
| petpal | *Petasites palmatus* (L.) Fries |
| petvit | *Petasites vitifolius* (Greene) Cherniawsky |
| picgla | *Picea glauca* (Moench) Voss |
| popbal | *Populus balsamifera* L. |
| poptre | *Populus tremuloides* Michx. |
| potnor | *Potentilla norvegica* L. |
| potpal | *Potentilla palustris* L. |
| pyrasa | *Pyrola asarifolia* Michx. |
| pyrsec | *Pyrola secunda* (L.) House |
| pyrvir | *Pyrola virens* Sw. |
| ribgla | *Ribes glandulosum* Grauer |
| riblac | *Ribes lacustre* (Pers.) Poir. |
| riboxy | *Ribes oxycanthoides* L. |
| ribtri | *Ribes triste* Pallas |
| rosaci | *Rosa acicularis* Lindl. |
| rubida | *Rubus idaeus* L. |
| rubpub | *Rubus pubescens* Raf. |
| salbeb | *Salix bebbiana* Sarg. |
| salgla | *Salix glauca* L. |
| salmyr | *Salix myrtillifolia* Anderss. |
| salpse | *Salix pseudomonticola* Ball |
| salpyr | *Salix pyrifolia* Anderss. |
| salsco | *Salix scouleriana* Barratt ex Hook. |
| shecan | *Sheperdia canadensis* (L.) Nutt. |
| smitri | *Smilacina trifolia* (L.) Sloboda |
| stelon | *Stellaria longifolia* Muhl. ex Willd. |
| symalb | *Symphoricarpos albus* Blake |
| symocc | *Symphoricarpos occidentalis* Hook |
| taroff | *Taraxacum officinale* G.H. Weber ex Wiggers |
| tribor | *Trientalis borealis* Raf. |
| urtdio | *Urtica dioica* L. |

| | |
|---|---|
| vaccae | *Vaccinium caespitosum* Michx. |
| vacmyr | *Vaccinium myrtilloides* Michx |
| vacvit | *Vaccinium vitis-idaea* L. |
| vibedu | *Viburnum edule* (Michx.) Raf |
| vicame | *Vicia americana* Muhl. ex Willd. |
| viocan | *Viola canadensis* L. |
| vioren | *Viola renifolia* Gray |

Appendix E. List of plots and their locations. Compartment refers to the identification number of the compartment at EMEND. R = retention strip, M = machine corridor. Previously sampled plots were sampled by Macdonald & Fenniak (2007) in 1998, 1999, and 2000.

| Compartment | Plot | Retention Level | Latitude | Longitude | Previously Sampled? |
|---|---|---|---|---|---|
| 928 | 1 | Control | N 56.79940 | W 118.32387 | no |
| 928 | 2 | Control | N 56.79926 | W 118.32414 | no |
| 928 | 3 | Control | N 56.79921 | W 118.32428 | no |
| 928 | 4 | Control | N 56.79891 | W 118.32445 | no |
| 928 | 5 | Control | N 56.79874 | W 118.32484 | no |
| 928 | 6 | Control | N 56.79920 | W 118.32535 | no |
| 928 | 7 | Control | N 56.79924 | W 118.32521 | no |
| 928 | 8 | Control | N 56.79916 | W 118.32514 | no |
| 928 | 9 | Control | N 56.79935 | W 118.32473 | no |
| 928 | 10 | Control | N 56.79944 | W 118.32464 | no |
| 928 | 11 | Control | N 56.79854 | W 118.32552 | no |
| 928 | 12 | Control | N 56.79842 | W 118.32519 | no |
| 928 | 13 | Control | N 56.79808 | W 118.32664 | no |
| 928 | 14 | Control | N 56.79783 | W 118.32676 | no |
| 928 | 15 | Control | N 56.79707 | W 118.32900 | no |
| 928 | 16 | Control | N 56.79720 | W 118.32910 | no |
| 928 | 17 | Control | N 56.79760 | W 118.32879 | no |
| 928 | 18 | Control | N 56.79789 | W 118.32818 | no |
| 928 | 19 | Control | N 56.79802 | W 118.32782 | no |
| 928 | 20 | Control | N 56.79859 | W 118.32635 | no |
| 914 | 1 | Clearcut | N 56.78815 | W 118.35058 | no |
| 914 | 2 | Clearcut | N 56.78797 | W 118.35074 | no |
| 914 | 3 | Clearcut | N 56.78771 | W 118.35094 | no |
| 914 | 4 | Clearcut | N 56.78756 | W 118.35126 | no |
| 914 | 5 | Clearcut | N 56.78815 | W 118.35001 | no |
| 914 | 6 | Clearcut | N 56.78832 | W 118.34890 | no |
| 914 | 7 | Clearcut | N 56.78804 | W 118.34976 | no |
| 914 | 8 | Clearcut | N 56.78809 | W 118.34938 | no |
| 914 | 9 | Clearcut | N 56.78813 | W 118.34922 | no |
| 914 | 10 | Clearcut | N 56.78813 | W 118.34893 | no |
| 914 | 11 | Clearcut | N 56.78752 | W 118.34925 | no |
| 914 | 12 | Clearcut | N 56.78739 | W 118.34935 | no |
| 914 | 13 | Clearcut | N 56.78679 | W 118.34908 | no |
| 914 | 14 | Clearcut | N 56.78672 | W 118.34895 | no |
| 914 | 15 | Clearcut | N 56.78697 | W 118.34848 | no |
| 914 | 16 | Clearcut | N 56.78785 | W 118.34847 | no |
| 914 | 17 | Clearcut | N 56.78781 | W 118.34808 | no |
| 914 | 18 | Clearcut | N 56.78765 | W 118.34764 | no |
| 914 | 19 | Clearcut | N 56.78732 | W 118.34727 | no |
| 914 | 20 | Clearcut | N 56.78719 | W 118.34752 | no |
| 913 | M | 10% | N 56.78882 | W 118.35290 | no |
| 913 | M | 10% | N 56.78855 | W118.35293 | no |
| 913 | M | 10% | N 56.78834 | W 118.35300 | no |
| 913 | M | 10% | N 56.78986 | W 118.35290 | no |

| | | | | | |
|---|---|---|---|---|---|
| 913 | M | 10% | N 56.78979 | W 118.35257 | no |
| 913 | R | 10% | N 56.79006 | W 118.35456 | no |
| 913 | R | 10% | N 56.78988 | W 118.35345 | no |
| 913 | R | 10% | N 56.78937 | W 118.35224 | no |
| 913 | R | 10% | N 56.78947 | W 118.35206 | no |
| 913 | R | 10% | N 56.78895 | W 118.35276 | no |
| 913 | R | 10% | N 56.78882 | W 118.35327 | no |
| 913 | R | 10% | N 56.78878 | W 118.35201 | no |
| 913 | R | 10% | N 56.78999 | W 118.35466 | no |
| 913 | R | 10% | N 56.79041 | W 118.35436 | no |
| 913 | R | 10% | N 56.79036 | W 118.35404 | no |
| 913 | R | 10% | N 56.78981 | W 118.35421 | no |
| 913 | R | 10% | N 56.78979 | W 118.35438 | no |
| 913 | R | 10% | N 56.79000 | W 118.35382 | no |
| 913 | R | 10% | N 56.78965 | W 118.35363 | no |
| 913 | R | 10% | N 56.78955 | W 118.35351 | no |
| 912 | M | 75% | N 56.78676 | W 118.35596 | no |
| 912 | M | 75% | N 56.78678 | W 118.35634 | no |
| 912 | M | 75% | N 56.78760 | W 118.35750 | no |
| 912 | M | 75% | N 56.78816 | W 118.35746 | no |
| 912 | M | 75% | N 56.78759 | W 118.35576 | no |
| 912 | R | 75% | N 56.78657 | W 118.35581 | yes |
| 912 | R | 75% | N 56.78796 | W 118.35736 | no |
| 912 | R | 75% | N 56.78728 | W 118.35511 | no |
| 912 | R | 75% | N 56.78785 | W 118.35471 | no |
| 912 | R | 75% | N 56.78803 | W 118.35507 | no |
| 912 | R | 75% | N 56.78823 | W 118.35572 | no |
| 912 | R | 75% | N 56.78786 | W 118.35590 | no |
| 912 | R | 75% | N 56.78683 | W 118.35615 | no |
| 912 | R | 75% | N 56.78721 | W 118.35680 | no |
| 912 | R | 75% | N 56.78745 | W 118.35702 | no |
| 912 | R | 75% | N 56.78775 | W 118.35693 | no |
| 912 | R | 75% | N 56.78762 | W 118.35781 | no |
| 912 | R | 75% | N 56.78734 | W 118.35771 | no |
| 912 | R | 75% | N 56.78858 | W 118.35807 | no |
| 912 | R | 75% | N 56.78821 | W 118.35807 | no |
| 911 | M | 50% | N 56.78485 | W 118.35870 | no |
| 911 | M | 50% | N 56.78455 | W 118.35889 | no |
| 911 | M | 50% | N 56.78566 | W 118.35739 | no |
| 911 | M | 50% | N 56.78556 | W 118.36093 | no |
| 911 | M | 50% | N 56.78611 | W 118.35925 | no |
| 911 | R | 50% | N 56.78490 | W 118.35854 | no |
| 911 | R | 50% | N 56.78531 | W 118.36153 | no |
| 911 | R | 50% | N 56.78558 | W 118.36157 | no |
| 911 | R | 50% | N 56.78616 | W 118.3579 | no |
| 911 | R | 50% | N 56.78580 | W 118.35749 | no |
| 911 | R | 50% | N 56.78559 | W 118.35773 | no |
| 911 | R | 50% | N 56.78539 | W 118.35795 | no |
| 911 | R | 50% | N 56.78533 | W 118.35899 | no |
| 911 | R | 50% | N 56.78533 | W 118.35957 | no |

| | | | | | |
|---|---|---|---|---|---|
| 911 | R | 50% | N 56.78487 | W 118.35812 | no |
| 911 | R | 50% | N 56.78437 | W 118.35895 | no |
| 911 | R | 50% | | | no |
| 911 | R | 50% | N 56.78563 | W 118.35743 | no |
| 911 | R | 50% | N 56.78578 | W 118.36128 | no |
| 911 | R | 50% | N 56.78564 | W 118.36106 | no |
| 910 | M | 20% | N 56.78443 | W 118.35335 | no |
| 910 | M | 20% | N 56.78409 | W 118.35338 | no |
| 910 | M | 20% | N 56.78416 | W 118.35327 | no |
| 910 | M | 20% | N 56.78447 | W 118.35328 | no |
| 910 | M | 20% | N 56.78481 | W 118.35335 | no |
| 910 | R | 20% | N 56.78483 | W 118.35598 | no |
| 910 | R | 20% | N 56.78517 | W 118.35279 | no |
| 910 | R | 20% | N 56.78495 | W 118.35308 | no |
| 910 | R | 20% | N 56.78463 | W 118.35343 | no |
| 910 | R | 20% | N 56.78468 | W 118.35382 | no |
| 910 | R | 20% | N 56.78572 | W 118.35407 | no |
| 910 | R | 20% | N 56.78554 | W 118.35430 | no |
| 910 | R | 20% | N 56.78562 | W 118.35470 | no |
| 910 | R | 20% | N 56.78464 | W 118.35554 | no |
| 910 | R | 20% | N 56.78460 | W 118.355908 | no |
| 910 | R | 20% | N 56.78414 | W 118.35359 | no |
| 910 | R | 20% | N 56.78412 | W 118.35354 | no |
| 910 | R | 20% | N 56.78456 | W 118.35309 | no |
| 910 | R | 20% | N 56.78484 | W 118.35275 | no |
| 910 | R | 20% | N 56.78474 | W 118.35234 | no |
| 909 | M | 75% | N 56.77306 | W 118.33833 | no |
| 909 | M | 75% | N 56.77370 | W 118.33972 | yes |
| 909 | M | 75% | N 56.77513 | W 118.34261 | no |
| 909 | M | 75% | N 56.77304 | W 118.33853 | no |
| 909 | M | 75% | N 56.77229 | W 118.33773 | no |
| 909 | R | 75% | N 56.77283 | W 118.33892 | yes |
| 909 | R | 75% | N 56.77344 | W 118.33998 | yes |
| 909 | R | 75% | N 56.77377 | W 118.33938 | yes |
| 909 | R | 75% | N 56.77361 | W 118.34011 | yes |
| 909 | R | 75% | N 56.77247 | W 118.34030 | no |
| 909 | R | 75% | N 56.77326 | W 118.33847 | no |
| 909 | R | 75% | N 56.77262 | W 118.33784 | no |
| 909 | R | 75% | N 56.77248 | W 118.33715 | no |
| 909 | R | 75% | N 56.77209 | W 118.33701 | no |
| 909 | R | 75% | N 56.77249 | W 118.33884 | no |
| 909 | R | 75% | N 56.77319 | W 118.33840 | no |
| 909 | R | 75% | N 56.77373 | W 118.33938 | no |
| 909 | R | 75% | N 56.77434 | W 118.34176 | no |
| 909 | R | 75% | N 56.77384 | W 118.34171 | no |
| 909 | R | 75% | N 56.77471 | W 118.34238 | no |
| 908 | M | 50% | N 56.77060 | W 118.33861 | no |
| 908 | M | 50% | N 56.77034 | W 118.33800 | no |
| 908 | M | 50% | N 56.76846 | W 118.33930 | no |
| 908 | M | 50% | N 56.76844 | W 118.33961 | no |

|  |  |  |  |  |  |
|---|---|---|---|---|---|
| 908 | M | 50% | N 56.76975 | W 118.33864 | no |
| 908 | R | 50% | N 56.77049 | W 118.33886 | no |
| 908 | R | 50% | N 56.76906 | W 118.33911 | no |
| 908 | R | 50% | N 56.76979 | W 118.33895 | no |
| 908 | R | 50% | N 56.76953 | W 118.33975 | no |
| 908 | R | 50% | N 56.76939 | W 118.33974 | no |
| 908 | R | 50% | N 56.76886 | W 118.33997 | no |
| 908 | R | 50% | N 56,76869 | W 118.33842 | no |
| 908 | R | 50% | N 56.77046 | W 118.33831 | no |
| 908 | R | 50% | N 56.77037 | W 118.33730 | no |
| 908 | R | 50% | N 56.77040 | W 118.77040 | no |
| 908 | R | 50% | N 56.76814 | W 118.33834 | no |
| 908 | R | 50% | N 56.76817 | W 118.33900 | no |
| 908 | R | 50% | N 56.76817 | W 118.33896 | no |
| 908 | R | 50% | N 56.76848 | W 118.33960 | no |
| 908 | R | 50% | N 56.76868 | W 118.33885 | no |
| 906 | M | 75% | N 56.77917 | W 118.38827 | no |
| 906 | M | 75% | N 56.77923 | W 118.38808 | no |
| 906 | M | 75% | N 56.77822 | W 118.38942 | no |
| 906 | M | 75% | N 56.77843 | W 118.38944 | no |
| 906 | M | 75% | N 56.77869 | W 118.38882 | no |
| 906 | R | 75% | N 56.77850 | W 118.38742 | no |
| 906 | R | 75% | N 56.77885 | W 118.38947 | no |
| 906 | R | 75% | N 56.77889 | W 118.38960 | no |
| 906 | R | 75% | N 56.77815 | W 118.38950 | no |
| 906 | R | 75% | N 56.77792 | W 118.38813 | no |
| 906 | R | 75% | N 56.77829 | W 118.38778 | no |
| 906 | R | 75% | N 56.77878 | W 118.38786 | no |
| 906 | R | 75% | N 56.77876 | W 118.38791 | no |
| 906 | R | 75% | N 56.77894 | W 118.38779 | no |
| 906 | R | 75% | N 56.77901 | W 118.38805 | no |
| 906 | R | 75% | N 56.77844 | W 118.38952 | no |
| 906 | R | 75% | N 56.77820 | W 118.38751 | no |
| 906 | R | 75% | N 56.77873 | W 118.38968 | no |
| 906 | R | 75% | N 56.77880 | W 118.38978 | no |
| 906 | R | 75% | N 56.77900 | W 118.38986 | no |
| 905 | M | 20% | N 56.77614 | W 118.39091 | no |
| 905 | M | 20% | N 56.77624 | W 118.39103 | no |
| 905 | M | 20% | N 56.77615 | W 118.39111 | no |
| 905 | M | 20% | N 56.77563 | W 118.39174 | no |
| 905 | M | 20% | N 56.77636 | W 118.39158 | no |
| 905 | R | 20% | N 56.77547 | W 118.39197 | yes |
| 905 | R | 20% | N 56.77530 | W 118.39171 | yes |
| 905 | R | 20% | N 56.77606 | W 118.39118 | yes |
| 905 | R | 20% | N 56.77576 | W 118.39110 | yes |
| 905 | R | 20% | N 56.77622 | W 118.39124 | no |
| 905 | R | 20% | N 56.77632 | W 118.39147 | no |
| 905 | R | 20% | N 56.77638 | W 118.39179 | no |
| 905 | R | 20% | N 56.77623 | W 118.39175 | no |
| 905 | R | 20% | N 56.77601 | W 118.38938 | no |

| | | | | | |
|---|---|---|---|---|---|
| 905 | R | 20% | N 56.77561 | W 118.38954 | no |
| 905 | R | 20% | N 56.77564 | W 118.39188 | no |
| 905 | R | 20% | N 56.77664 | W 118.39019 | no |
| 905 | R | 20% | N 56.77674 | W 118.39049 | no |
| 905 | R | 20% | N 56.77692 | W 118.39035 | no |
| 905 | R | 20% | N 56.77620 | W 118.39077 | no |
| 903 | M | 50% | N 56.77294 | W 118.39559 | no |
| 903 | M | 50% | N 56.77308 | W 118.39563 | no |
| 903 | M | 50% | N 56.77276 | W 118.39521 | no |
| 903 | M | 50% | N 56.77292 | W 118.39512 | no |
| 903 | M | 50% | N 56.77291 | W 118.39479 | no |
| 903 | R | 50% | N 56.77312 | W 118.39561 | no |
| 903 | R | 50% | N 56.77379 | W 118.39775 | no |
| 903 | R | 50% | N 56.77355 | W 118.39793 | no |
| 903 | R | 50% | N 56.77375 | W 118.39836 | no |
| 903 | R | 50% | N 56.77348 | W 118.39757 | no |
| 903 | R | 50% | N 56.77329 | W 118.39802 | no |
| 903 | R | 50% | N 56.77321 | W 118.39746 | no |
| 903 | R | 50% | N 56.77289 | W 118.39564 | no |
| 903 | R | 50% | N 56.77272 | W 118.39538 | no |
| 903 | R | 50% | | | no |
| 903 | R | 50% | N 56.77412 | W 118.39530 | no |
| 903 | R | 50% | N 56.77401 | W 118.39804 | no |
| 903 | R | 50% | N 56.77394 | W 118.39838 | no |
| 903 | R | 50% | N 56.77404 | W 118.39876 | no |
| 903 | R | 50% | N 56.77398 | W 118.39906 | no |
| 902 | 1 | Control | N 56.76070 | W 118.41458 | no |
| 902 | 2 | Control | N 56.76079 | W 118.41502 | no |
| 902 | 3 | Control | N 56.76086 | W 118.41502 | no |
| 902 | 4 | Control | N 56.76181 | W 118.41441 | no |
| 902 | 5 | Control | N 56.76177 | W 118.41477 | no |
| 902 | 6 | Control | N 56.76206 | W 118.41474 | no |
| 902 | 7 | Control | N 56.76193 | W 118.41520 | no |
| 902 | 8 | Control | N 56.76228 | W 118.41461 | no |
| 902 | 9 | Control | N 56.76226 | W 118.41421 | no |
| 902 | 10 | Control | N 56.76231 | W 118.41487 | no |
| 902 | 11 | Control | N 56.76221 | W 118.41506 | no |
| 902 | 12 | Control | N 56.76231 | W 118.41548 | no |
| 902 | 13 | Control | N 56.76238 | W 118.41575 | no |
| 902 | 14 | Control | N 56.76250 | W 118.41561 | no |
| 902 | 15 | Control | N 56.76270 | W 118.41548 | no |
| 902 | 16 | Control | N 56.76279 | W 118.41548 | no |
| 902 | 17 | Control | | | no |
| 902 | 18 | Control | N 56.76335 | W 118.41562 | no |
| 902 | 19 | Control | N 56.76320 | W 118.41626 | no |
| 902 | 20 | Control | N 56.76335 | W 118.41675 | no |
| 900 | M | 10% | N 56.75717 | W 118.41682 | no |
| 900 | M | 10% | N 56.75696 | W 118.41688 | no |
| 900 | M | 10% | N 56.75678 | W 118.41691 | no |
| 900 | M | 10% | N 56.75661 | W 118.41695 | no |

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|---|---|---|---|---|---|
| 900 | M | 10% | N 56.75645 | W 118.41694 | no |
| 900 | R | 10% | N 56.75596 | W 118.41595 | no |
| 900 | R | 10% | N 56.75675 | W 118.41770 | no |
| 900 | R | 10% | N 56.75705 | W 118.41804 | no |
| 900 | R | 10% | N 56.75729 | W 118.41779 | no |
| 900 | R | 10% | N 56.75740 | W 118.41736 | no |
| 900 | R | 10% | N 56.75732 | W 118.41702 | no |
| 900 | R | 10% | N 56.75701 | W 118.41674 | no |
| 900 | R | 10% | N 56.75560 | W 118.41585 | no |
| 900 | R | 10% | N 56.75544 | W 118.41585 | no |
| 900 | R | 10% | N 56.75531 | W 118.41576 | no |
| 900 | R | 10% | N 56.75493 | W 118.41565 | no |
| 900 | R | 10% | N 56.75503 | W 118.41535 | no |
| 900 | R | 10% | N 56.75516 | W 118.41528 | no |
| 900 | R | 10% | N 56.75560 | W 118.41492 | no |
| 900 | R | 10% | N 56.75592 | W 118.41461 | no |
| 899 | 1 | Clearcut | N 56.75884 | W 118.40982 | no |
| 899 | 2 | Clearcut | N 56.75862 | W 118.40955 | no |
| 899 | 3 | Clearcut | N 56.75837 | W 118.40949 | no |
| 899 | 4 | Clearcut | N 56.75825 | W 118.40947 | no |
| 899 | 5 | Clearcut | N 56.75805 | W 118.40949 | no |
| 899 | 6 | Clearcut | N 56.75754 | W 118.40949 | no |
| 899 | 7 | Clearcut | N 56.75754 | W 118.41011 | no |
| 899 | 8 | Clearcut | N 56.75743 | W 118.41034 | no |
| 899 | 9 | Clearcut | N 56.75725 | W 118.41051 | no |
| 899 | 10 | Clearcut | N 56.75808 | W 118.41187 | no |
| 899 | 11 | Clearcut | N 56.75780 | W 118.41180 | no |
| 899 | 12 | Clearcut | N 56.75774 | W 118.41172 | no |
| 899 | 13 | Clearcut | N 56.75771 | W 118.41168 | no |
| 899 | 14 | Clearcut | N 56.75736 | W 118.41163 | no |
| 899 | 15 | Clearcut | N 56.75736 | W 118.41184 | no |
| 899 | 16 | Clearcut | N 56.75733 | W 118.41205 | no |
| 899 | 17 | Clearcut | N 56.75698 | W 118.41176 | no |
| 899 | 18 | Clearcut | N 56.75627 | W 118.41343 | no |
| 899 | 19 | Clearcut | N 56.75712 | W 118.41373 | no |
| 899 | 20 | Clearcut | N 56.75692 | W 118.41354 | no |
| 875 | M | 20% | N 56.74467 | W 118.39805 | no |
| 875 | M | 20% | N 56.74527 | W 118.39782 | no |
| 875 | M | 20% | N 56.74561 | W 118.39765 | no |
| 875 | M | 20% | N 56.74630 | W 118.39701 | no |
| 875 | M | 20% | N 56.74607 | W 118.39739 | no |
| 875 | R | 20% | N 56.74693 | W 118.39878 | no |
| 875 | R | 20% | N 56.746981 | W 118.39668 | no |
| 875 | R | 20% | N 56.74657 | W 118.39660 | no |
| 875 | R | 20% | N 56.74632 | W 118.39774 | no |
| 875 | R | 20% | N 56.74662 | W 118.39959 | no |
| 875 | R | 20% | N 56.74652 | W 118.39916 | no |
| 875 | R | 20% | N 56.74620 | W 118.39877 | no |
| 875 | R | 20% | | | no |
| 875 | R | 20% | N 56.74495 | W 118.39716 | no |

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|---|---|---|---|---|---|
| 875 | R | 20% | N 56.74551 | W 118.39790 | no |
| 875 | R | 20% | N 56.74599 | W 118.39823 | no |
| 875 | R | 20% | N 56.74582 | W 118.39751 | no |
| 875 | R | 20% | N 56.74620 | W 118.39783 | no |
| 875 | R | 20% | N 56.74719 | W 118.39668 | no |
| 875 | R | 20% | N 56.74696 | W 118.39674 | no |
| 874 | 1 | Clearcut | N 56.74723 | W 118.39281 | no |
| 874 | 2 | Clearcut | N 56.74710 | W 118.39274 | no |
| 874 | 3 | Clearcut | N 56.74704 | W 118.39281 | no |
| 874 | 4 | Clearcut | N 56.74691 | W 118.39299 | no |
| 874 | 5 | Clearcut | N 56.74675 | W 118.39308 | no |
| 874 | 6 | Clearcut | N 56.74677 | W 118.39386 | no |
| 874 | 7 | Clearcut | N 56.74669 | W 118.39411 | no |
| 874 | 8 | Clearcut | N 56.74604 | W 118.39519 | no |
| 874 | 9 | Clearcut | N 56.74604 | W 118.39564 | no |
| 874 | 10 | Clearcut | N 56.74668 | W 118.39500 | no |
| 874 | 11 | Clearcut | N 56.74598 | W 118.38955 | yes |
| 874 | 12 | Clearcut | N 56.74601 | W 118.38993 | yes |
| 874 | 13 | Clearcut | N 56.74553 | W 118.39025 | no |
| 874 | 14 | Clearcut | N 56.74561 | W 118.39059 | yes |
| 874 | 15 | Clearcut | N 56.74538 | W 118.39066 | yes |
| 874 | 16 | Clearcut | N 56.74546 | W 118.39105 | no |
| 874 | 17 | Clearcut | N 56.74545 | W 118.39117 | yes |
| 874 | 18 | Clearcut | N 56.74743 | W 118.39006 | no |
| 874 | 19 | Clearcut | N 56.74746 | W 118.39083 | no |
| 874 | 20 | Clearcut | N 56.74761 | W 118.39114 | no |
| 868 | M | 10% | N 56.75731 | W 118.37987 | no |
| 868 | M | 10% | N 56.75397 | W 118.38121 | no |
| 868 | M | 10% | N 56.75378 | W 118.38137 | no |
| 868 | M | 10% | N 56.75499 | W 118.38185 | no |
| 868 | M | 10% | N 56.75919 | W 118.37704 | no |
| 868 | R | 10% | N 56.75732 | W 118.37979 | no |
| 868 | R | 10% | N 56.75745 | W 118.37961 | no |
| 868 | R | 10% | N 56.75755 | W 118.37937 | no |
| 868 | R | 10% | N 56.75772 | W 118.37869 | no |
| 868 | R | 10% | N 56.75843 | W 118.37856 | no |
| 868 | R | 10% | N 56.75877 | W 118.37864 | no |
| 868 | R | 10% | N 56.65871 | W 118.37796 | no |
| 868 | R | 10% | N 56.75766 | W 118.37971 | no |
| 868 | R | 10% | N 56.75382 | W 118.38169 | no |
| 868 | R | 10% | N 56.75379 | W 118.38114 | no |
| 868 | R | 10% | N 56.75384 | W 118.38086 | no |
| 868 | R | 10% | N 56.75426 | W 118.38179 | no |
| 868 | R | 10% | N 56.75449 | W 118.38200 | no |
| 868 | R | 10% | N56.75494 | W 118.38161 | no |
| 868 | R | 10% | N 56.75727 | W 118.37971 | no |
| 867 | 1 | Control | N 56.76279 | W 118.37476 | no |
| 867 | 2 | Control | N 56.76281 | W 118.37432 | no |
| 867 | 3 | Control | N 56.76201 | W 118.37411 | no |
| 867 | 4 | Control | N 56.76184 | W 118.37455 | no |

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|---|---|---|---|---|---|
| 867 | 5 | Control | N 56.75987 | W 118.37489 | no |
| 867 | 6 | Control | N 56.76010 | W 118.37505 | no |
| 867 | 7 | Control | N 56.76028 | W 118.37621 | no |
| 867 | 8 | Control | N 56.76018 | W 118.37580 | no |
| 867 | 9 | Control | | | no |
| 867 | 10 | Control | | | no |
| 867 | 11 | Control | N 56.75952 | W 118.37707 | no |
| 867 | 12 | Control | N 56.75936 | W 118.37675 | no |
| 867 | 13 | Control | N 56.75956 | W 118.37678 | no |
| 867 | 14 | Control | N 56.75979 | W 118.37667 | no |
| 867 | 15 | Control | N 56.75976 | W 118.37545 | no |
| 867 | 16 | Control | N 56.76054 | W 118.37552 | no |
| 867 | 17 | Control | N 56.76121 | W 118.37464 | no |
| 867 | 18 | Control | N 56.76211 | W 118.37445 | no |
| 867 | 19 | Control | N 56.76299 | W 118.37454 | no |
| 867 | 20 | Control | N 56.76303 | W 118.37423 | no |