VEGETATION COMMUNITY DEVELOPMENT EIGHT YEARS AFTER HARVESTING IN SMALL STREAMS BUFFERS AT THE MALCOLM KNAPP RESEARCH FOREST

by

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ABSTRACT

Riparian areas connect terrestrial and aquatic environments. The objectives of this research were to compare the vegetation community composition and structure eight years after harvesting and to explore successional trends among buffer widths at year eight after disturbance and in a chronosequence. A series of small clearcuts were harvested in 1998 in a 70 year old second growth stand at the Malcolm Knapp Research Forest and 0m, 10m and 30m reserve zones were established adjacent to the streams. Each treatment was replicated 3 times and 3 unharvested streams were identified as controls. Overstory and understory vegetation was measured annually from the year of harvest. Canopy density was measured using a densiometer. For comparative purposes, four vegetation plots were added in riparian areas within an 1868 and an old-growth stand during the summer of 2006. Eight years after harvesting, understory vegetation development is affected by buffer width due to higher light levels, and species richness in the 10m and 0m buffers is higher than in the 30m buffer and control. Shrubs and deciduous trees dominate the 0m and 10m buffer treatments. Proximity to the stream does not affect the composition and abundance of species with the exception of herbs and mosses. In the 10m and 30m buffer treatments, up to 15% overstory trees were windthrown in the first 2 years after harvest producing large canopy gaps. Consequently, the understory development in the 10m and 30m buffers is more like that in the 1868 and old-growth stands than in the controls, but these treatments still lack the very large trees and microsite heterogeneity of the older stands. In the unharvested controls, self-thinning continues and there has been 30% mortality of mostly smaller trees over the past 8 years. However, overstory density remains high. The 0m buffer was quickly colonized by shrubs and ferns and within the last 2 years has become dominated by juvenile deciduous trees. Overall, the 10m buffer balances timber production with the maintenance of overstory and understory structure dynamics. The combined effect of light from the edge and partial windthrow is accelerating succession towards a more mature or 'old-growth' condition.

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1 INTRODUCTION

1.1 Background

Riparian ecosystems are a transitional space between terrestrial and aquatic communities and thus they contain a set of distinct environmental factors, ecological processes and vegetation communities distributed in a complex net throughout the landscape. Due to these properties, they play an important role in maintaining landscape level ecological functions (Wyant and Ellis 1990; Naiman and Decamps 1997; Naiman et al. 2000; Rosales et al. 2001; Ward et al. 2002).

Changes in forest practices regulations in British Columbia and the northwest United States in the past two decades have lead to greater protection of small streams during timber harvesting. In addition harvesting has moved into younger forests where stands are often dense and have limited structural complexity. Retention of buffers on small streams complicates harvesting operations and the resulting strips of trees are susceptible to wind damage. At present there are different standards for riparian management in different jurisdictions and land ownerships. While the theoretical benefits to retaining riparian buffers are many, the actual short, medium term and long term outcomes of riparian management prescriptions are not clear.

1.2 Problem statement

Effective prescriptions for riparian management in production forests are necessary to maintain the ecological benefits of riparian forests while enabling sustainable timber production. Understanding riparian plant community composition and response to disturbance through time is important for designing silviculture and restoration prescriptions. Buffer width is a key consideration in riparian buffer prescriptions. In order to know whether riparian vegetation communities in managed second growth will develop 'old-forest' properties, we need to know whether successional/developmental processes in managed second growth forests are taking them toward conditions present in 'old-forests'.

1.3 Thesis objectives

The objectives of this thesis research were to: 1) *describe* the structure and floristic diversity of plant communities of riparian zones managed using different buffer width treatments at the Malcolm Knapp Research Forest, eight years after harvesting; 2) *compare* the different treatments eight years after harvesting; 3) *document* the successional trajectories of plant communities in the different treatments over the first eight years after treatment and compare these to conditions in young- mature (thrifty), mature and old-growth forests.

1.4 Approach

The thesis research is a component of the riparian buffers experiment led by Dr. John Richardson of the Faculty of Forestry, University of British Columbia. This experiment commenced in 1998 at the Malcolm Knapp Research Forest (MKRF). The broad objective of this integrated experiment is to determine the effectiveness of different widths of riparian reserves along small streams, considering both physical and biological ecosystems responses in a full ecosystem approach (Fig. 1; Richardson 2003).

This experiment uses a ´before-after, control-impact´ (BACI) methodology to better account for site-to-site and year-to-year variability in the natural processes under study. Unharvested controls, and cutblocks with 0m, 10m and 30m riparian buffers (collectively referred to as the 'treatments') were established in a 70 year old second growth stand on the Malcolm Knapp Research Forest. Each treatment was replicated 3 times.

This thesis focuses on the vegetation component of the riparian buffers experiment, reports results of monitoring from 1998 through 2006, and tests hypotheses concerning treatment effects and community development. The experimental design enables use of ANOVA to test the effect of the independent variables, stream proximity (2m and 15m), buffer width, side of the stream (right or left) and location along the stream (upstream or downstream) on the floristic composition and structure. For assessing successional trajectories under a short-term approach, I used a repeated measures ANOVA in which year was added as a fifth factor with 5 levels: 1998, 2000, 2003, 2005 and 2006.

The thesis is divided into five chapters of which this introduction is the first chapter. The second chapter is a review of the literature concerning riparian ecosystems with an

emphasis on the Pacific Northwest (PNW) of North America. In chapter 3, the condition of the vegetation communities in the various treatments eight years following treatment is described and differences between communities at year 8 are examined. In Chapter 4, successional trajectories and differences in vegetation diversity, structural complexity and abundance among treatments over time are explored using two different approaches. The first one corresponds to a short-term successional approach, which is restricted to the first eight years after harvesting whereas the second uses a chronosequence approach to explore conditions at different successional stages. The fifth chapter is an integrating discussion with conclusions and recommendations for further research and management. The appendices contain detailed results including ANOVA´s tables, graphs, and formulas.

Figure 1. Elements associated with a riparian ecosystem and the way they interact with each other. The circled component is the portion of the system on which this project focuses. Source: Richardson 2003.

2 LITERATURE REVIEW

2.1 Importance of riparian ecosystems

Riparian ecosystems have been widely recognized as being of central importance in ecology, resources management and conservation. This importance lies in the wide variety of services they provide and the complexity of interactions that take place within them. As a result, riparian ecosystems have been assigned as a priority area for conservation and for scientific investigation (Dupuis and Steventon 1999; Hibbs and Bower 2001; Ogg and Keith 2002).

Riparian ecosystems are transitional spaces between terrestrial and aquatic communities and they encompass a set of distinct environmental factors and ecological processes including complex interactions among hydrology, geomorphology, biotic and abiotic factors and disturbances. They are arranged linearly and continuously adjacent to streams and are therefore distributed in a complex network through the landscape. Due to these properties, they play an important role in maintaining landscape level ecological functions (Wyant and Ellis 1990; Naiman and Decamps 1997; Naiman et al. 2000; Rosales et al. 2001; Ward et al. 2002; Coroi et al. 2004).

Riparian ecosystems modify stream ecological processes and biological conditions by retaining nutrients such as nitrates and carbon compounds, providing materials for redistribution by streams throughout the landscape (Gregory et al. 1991; Kiffney et al. 2002; Ward et al. 2002; Richardson et al. 2005), stabilizing the soil and thus preventing erosion (Hancock et al. 1996; Kiffney et al. 2003; Lyon and Sagers 2003), and moderating stream temperature (Hancock et al. 1996; Helfield and Naiman 2001; Moore

et al. 2005). They provide inputs of organic matter, offer habitat and food for many aquatic and terrestrial species, some of which are riparian obligates, and they act as biological corridors through which plants and animals can be dispersed (Gregory et al. 1991; Naiman et al. 2000; Darveau et al. 1998; Cockle and Richardson 2003; Richardson et al. 2005).

For these reasons, riparian ecosystems are characterized by high wildlife abundance and diversity. For example, it has been estimated that 70% of all vertebrate species in the Pacific Northwest use riparian habitats in some way for at least some portion of their life cycles (Wipfli 1997; Darveau et al. 1998; Sullivan et al. 1998; Hannon et al. 2002; Cockle and Richardson 2003; Shirley 2004; Richardson et al. 2005).

The main characteristics of riparian forests, such as their diversity and structural patterns, species composition and productivity, are strongly influenced by the size and hydrology of the stream, the morphology and width of the riparian zone, and disturbance regimes including fluvial (e.g., flood and debris flow), terrestrial (e.g., fire and wind throw) and human (e.g., forest harvesting and land use), each with a particular periodicity, intensity and spatial scale. Local climate, soil and parent materials also determine physical conditions within the riparian zone (e.g. nutrient availability, wind intensity, pH, soil texture and moisture, depth to water table, among others) (Qian et al. 1997; Suzuki et al. 2002; Cockle and Richardson 2003; Richardson et al. 2005).

Disturbances produce immediate, medium term and long term changes in the structural, compositional and functional properties of riparian forests. These changes can be viewed as a set of events or stages acting in a continuum within a specific temporal and spatial

scale. They are controlled, in part, by mechanisms related to the stream dynamics derived from fluvial processes, woody debris flow, energy inputs, nutrient cycling, transport of sediments and disturbances (Hancock et al. 1996; Wipfli 1997; Pabst and Spies 1998), but also by the physical characteristics of the stream and the eco-physiological traits of dominant vegetation species. The latter includes differences in the species' phenology, shade, salinity and flood tolerance, regeneration strategy, and response to intra- and inter-specific competition (Danvind and Nilsson 1997; Kozlowski 1997; Pabst and Spies 1998; Parolin 2002; Ward et al. 2002; Rood et al. 2003; Balian and Naiman 2005; Liquori 2006; Sarr and Hibbs 2007).

In recent decades, one of the most common management strategies implemented in order to protect stream ecosystems has been the establishment of continuous unharvested buffer strips adjacent to the stream. The effectiveness and influence of the buffer strip on the stream environment are dependent on the size of the stream, the position of the stream within the drainage network, the hydrologic regime and the local geomorphology (Naiman and Decamps 1997; Hagar 1999; Blinn and Kilgore 2001; Hibbs and Bower 2001). As a result, buffer width is considered to be the main element determining the functionality of riparian zones as corridors. Pinay and Decamps (1988) studied the role of forested riparian buffers in regulating nitrogen fluxes between the alluvial aquifer and surface water in agricultural fields. They showed that all the nitrate was removed within the first 30 meters of the buffer.

2.2 The riparian habitat: concepts and processes

Riparian ecosystems are distributed in three spatial dimensions: vertical, transversal and longitudinal. As a whole, three dimension ecotone connects ecologically and physically the aquatic and terrestrial environments in a forest-stream complex (Fig. 2) (Ward 1989; Naiman et al. 1993; Stanford and Ward 1993; Naiman et al. 2000; Coroi et al. 2004).
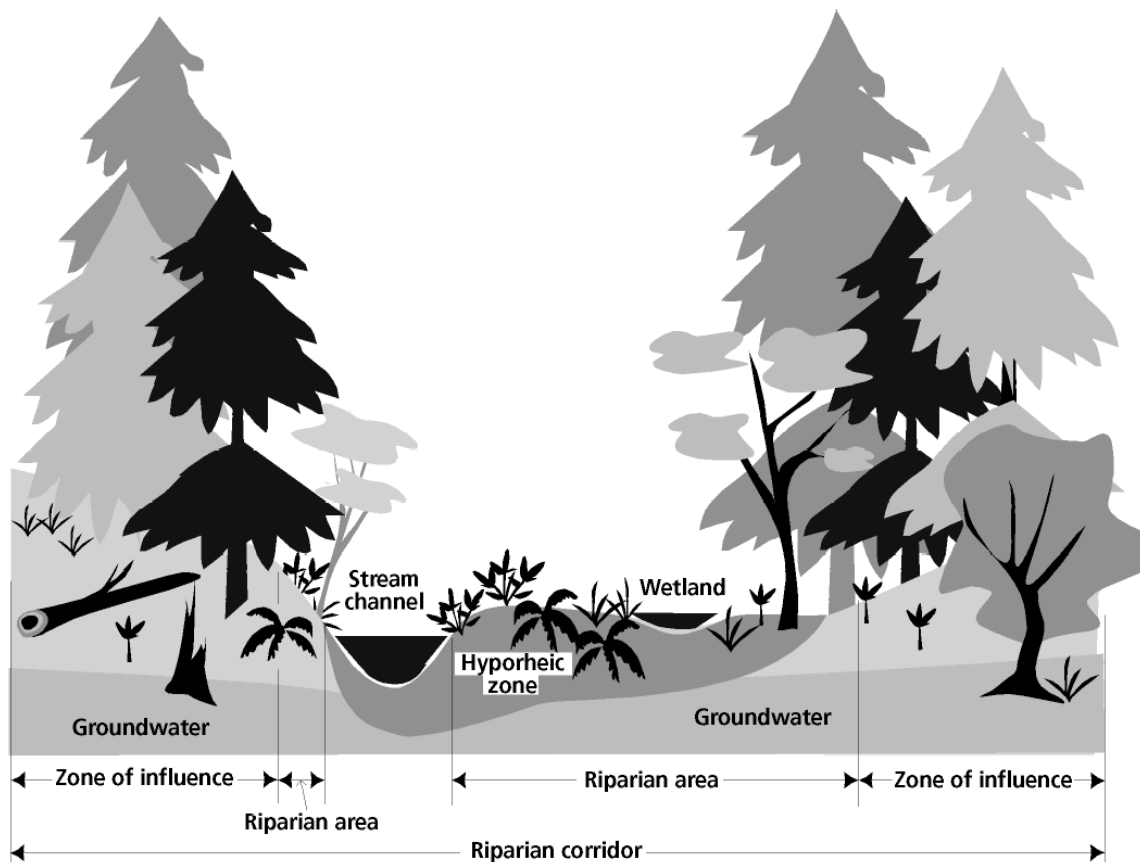
Figure 2. Representation of a riparian corridor showing its most important elements. Source: Stanford and Ward (1993).

The forest-stream complex is hydrologically connected and therefore water, solutes and organic and inorganic materials (including adapted biota), move through interstitial

pathways into the stream channel. This transitional habitat known as the 'hyporheic zone' (Fig.2) is defined physically by the degree of penetration of stream water into deposits within the active channel through floodplain substrata, and biologically by the presence of a distinct suite of flood tolerant or flood requiring species. Floodplains are typical in medium and larger sized streams with low gradients that are bounded by terraces of fluvial deposits. In the case of small headwater streams however, streams are typically higher gradient and channels are constrained by hillslopes or by a combination of hillslope and narrow fluvial terraces. This results in a narrow hyporheic zone and restricts or eliminates the habitat for floodplain specialist species.

As corridors within watersheds, riparian forests display a unique longitudinal pattern that exerts substantial control on the movement of water, nutrients, sediment, organic matter, fauna and flora (Naiman et al 2000; Coroi et al. 2004). Additionally, riparian forests modify the climate at a local and regional scale by reducing wind speed, air temperature range, and regulating surface soil and water temperatures thus moderating the harmful effects of sun, wind and floods (Tilman 1988; Gregory et al. 1991; Naiman et al. 1993; Naiman and Decamps 1997; Helfield and Naiman 2001; Lyon and Sagers 2003; Kiffney et al. 2003; Shirley 2004). Moreover, they perform an array of important ecosystem functions, including stream bank stabilization (Hancock et al.1996), thermal regulation of streams, filtering and retention of nutrients (Gregory et al. 1991), supply of organic matter to aquatic consumers, provision of animal and wildlife habitat and migration corridors (Darveau et al. 1998; Hannon et al. 2002; Coroi et al. 2004).

In recent years, stream ecologists have investigated organic-matter inputs for stream ecosystems and in general have highlighted the role of riparian plant communities as a

source of litter and woody debris (Cummins et al. 1980; Melillo et al. 1982; Gregory et al. 1991; Prescott 1995; France 1998; Simard et al. 1998; Ellis et al. 1999; Beach and Halpern 2001; Helfield and Naiman 2001; Chen et al. 2002; Fraver et al. 2002; Lavery et al. 2004; Prescott et al. 2004; O´Keefe and Naiman 2006). Decomposition of organic matter, mainly litter, is an important and critical component of forest and stream ecosystems. Vegetative litter in the form of leaves, reproductive parts, needles and woody debris, affects nutrient cycling (basically nitrogen and carbon) and the exchange of heat and water between the soil and the floor forest. It also alters the light and precipitation regimes at the soil surface affecting the overall plant community dynamics and organization (Gessner and Chauvet 1994; Wipfli 1997; O'Keefe and Naiman 2006). Coarse woody debris in the form of standing dead trees, downed boles and large branches is a major feature in many natural forests and stream ecosystems (Harmon et al. 1986). CWD is biologically important to the freshwater and estuarine ecosystems serving as an energy and nutrient source, a site for nitrogen fixation, and habitat for organisms such as fish, birds, small mammals and plants (Naiman and Decamps 1997; Naiman et al. 2000; Beach and Halpern 2001; Balian and Naiman 2005). In Pacific coastal forests of North America, coniferous species are superior to hardwoods as sources of woody debris because of their larger size and longer persistence within stream channels (Beach and Halpern 2001).

2.3 Measures of vegetation species diversity, structural complexity and abundance

The composition, vertical and horizontal distribution and abundance of living and dead plants are referred to as 'vegetation community structure' (Brassard and Chen 2006). Understanding the processes which determine this structure is a central issue in forest ecology. At the local scale, community ecologists have viewed plant species composition and diversity as being strongly dependent on resource availability and disturbance. Plant communities encompass some attributes or emergent properties which reflect the interaction of a huge array of biotic and abiotic conditions that vary both spatially and temporally (Whittaker 1972; Peet 1974; Crawley 1986; Magurran 1988; Schoonmaker and McKee 1988; Pueyo et al. 2006).

Plant community ecologists have developed a set of concepts to help characterize and understand structural patterns. Measures of diversity are frequently seen as indicators of the well-being of ecological systems. Whittaker (1975) distinguished three levels or spatial scales of species diversity. The alpha diversity (α) makes reference to the local number of species. This is the intra-community or habitat level diversity and can be reported as the total number of species or 'species richness' (S) within a site. The beta (β) diversity, as the second level of diversity is defined, is the change in species composition along environmental gradients or between site pairs. Beta diversity is a reflection of the heterogeneity of the different communities. In other words, it is the spatial turnover in the identities of species and it captures a fundamental facet of the spatial pattern of biodiversity. Koleff et al. (2003) summarized the current availability of beta diversity measures and identified at least 20 different ways it could be measured.

Finally, the third level is the gamma (γ) or 'landscape diversity' which is the total species richness across all study plots and represents a composite of both the alpha and beta diversities.

Additionally, the use of similarity coefficients and indexes such as Jaccard´s or other diversity expressions based on species frequencies such as the Simpson´s heterogeneity index (D) and the Shannon-Wiener (H´) index can be helpful in comparing vegetation types and elucidating the degree of change among communities along a gradient. It could be said then that both alpha and beta diversity are consequences of niche diversification of species, but on different spatial scales (Appendix 1) (Peet 1974; Whittaker 1975; Crawley 1986; Schoonmaker and McKee 1988; Huston 1994; Lande 1996; Lahde et al. 1999; Decocq 2002; Clark et al. 2003; Koleff et al. 2003; Chao et al. 2004; Varga et al. 2005; Brassard and Chen 2006; Goettsch and Hernández 2006).

The Shannon-Wiener index takes into account not only the number of species present in a community, but also, the relative abundance of each species. This index takes the highest values when the relative abundance of each species in a community is the same (Appendix 1). Therefore, the Shannon-Wiener index is perhaps the most extensively used index by ecologists (Whittaker 1975; Magurran 1988; Lande 1996; Jost 2006; Pueyo et al. 2006).

An equally important index is the Simpson index which expresses concentration of dominance. It is based on the probability that two randomly chosen individuals from a given community are the same species. The inverse of Simpson (1/D) concentration, is often employed to measure species diversity, and for a given number of species, S, in a

community it has a maximum value equal to S when all species are equally frequent. Simpson´s index is heavily weighted towards the most abundant species in the sample and is less sensitive to species richness (Appendix 1) (Whittaker 1975; Magurran 1988; Lande 1996; Jost 2006).

Forest structure has become a focus for research because of its significance for ecosystem function and as an indicator of biodiversity (Daubenmire 1968; Whittaker 1975; Crawley, 1986; DeVries et al. 1997; Kimmins 1997; Frazer et al. 2000; Brassard and Chen 2006). Neither Shannon-Weiner nor Simpson's indices account for variability in the size of different species or individuals of a species. Staudhammer and LeMay (2001) proposed an index derived from the Shannon-Wiener to represent stand structural heterogeneity. This index takes into account variables such as height and diameter as well as species. The equation then calculates a single index from a DBH-height-species combination (Appendix 1). The gross aspect of vegetation structure can be indicated by a description of its physiognomy, including the mean height and degree of development of any layer, foliage persistence, dominance, basal area, density and life-forms that make up the community. The kinds of life-forms present in the community are related to the environment and tell a lot about how ecosystems function. They reflect the physiological ecology, growth strategies and life-history traits of species (Daubenmire 1968; Whittaker 1975; Crawley 1986; DeVries et al. 1997; Kimmins 1997; Frazer et al. 2000; Brassard and Chen 2006; Dorrepaal 2007).

Plant communities show both vertical stratification meaning that different species occur at different heights above the ground, and horizontal organization, which refers to the horizontal distribution and arrangement of the individuals of a community. These spatial

attributes reflect the initial and subsequent disturbances, microsite variability, establishment patterns, and differences in species shade-tolerance and response to interspecific and intraspecific competition (Whittaker 1975; Franklin and Hemstrom 1981; Crawley 1986; Oliver and Larson 1990; Decocq 2002; Kimmins 2004; Brassard and Chen 2006).

Forest structure reflects a combination of growth-forms and life stages that are adapted to the gradient of light intensity from the top of the canopy to the ground and which function ecologically in the community in a similar way (Specht 1970; Dorrepaal 2007). Both vertical and horizontal structure are important components in forest ecosystems (Zhan et al. 2007). Variation in vertical structure is expressed by multiple plant canopy levels (tree, shrubs, herbs, bryophytes, epiphytes), snags and decomposing logs (CWD) which can be distinguished at different heights above the ground. Horizontal structure refers to the horizontal distribution and arrangement of the individuals of a community.

2.4 Succession in coniferous forests of the Pacific Coast of North America

Disturbances such as wildfires, windthrow, insect and disease outbreaks, floods and debris flows are considered to be of great importance in controlling the dynamics in forested and lotic ecosystems (define as the biotic and abiotic interactions within flowing continental waters) by changing tree composition, age structure and fuel conditions at various temporal and spatial scales (White and Pickett 1985; Kimmins 1990, 1997; Oliver and Larson 1990; Kozlowski 1997; Naiman and Decamps 1997; Swanson et al. 1998; Mailly et al. 2000; Naiman et al. 2000; McCarthy 2001; Valett et al. 2002; Wei et al. 2003). Following these disturbances, plant communities reconfigure through the process of succession (Finegan 1984).

Succession is a multi-phased process of continuous colonization and extinction on a site by populations of various species, that collectively form communities. Following a stand-destroying event such as a storm or timber harvesting, the vegetation community passes through a series of seral stages, each one comprising a characteristic type of plant diversity and percentage of tree cover (Klinka et al. 1985; Qian et al. 1997; Kimmins 1990, 1997, 2004; Yang et al. 2005). Patterns of forest succession reflect a variety of processes including differences in species life histories such as migration and dispersal rates, growth rates, mode of reproduction, lifespan, growth forms, competition, disturbances and other environmental changes (Bazzaz 1979; Schoonmaker and McKee 1988; Oliver and Larson 1990; Huston 1994; Elliott et al. 1998; Pabst and Spies 2001; Valett et al. 2002; McEwan and Muller 2006).

The mechanisms of succession and vegetation dynamics have been studied extensively. One of the most influential works on succession is the description provided by Clements (1916). He regarded succession as 'the growth or development and the reproduction of a complex organism' in which sequential dominance arises from dominant species modifying their environment (particularly soil and light) making it less favorable to themselves, and perhaps more favorable to new invaders (Egler 1954; McCook 1994; Vandermeer et al. 1995). Egler (1954) critized Clements´ facilitation based succession or 'relay floristics' and came up with a different hypothesis of succession: the 'Initial Floristics Composition' (IFC by its acronym). According to the IFC, development unfolds after abandonment from the initial flora without additional increments by further invasion. This means that both pioneer and shade-tolerant species are present, in active or dormant form, in the first phase of vegetation development and most species that will

later dominate the community are already present at the onset of succession (Bormann and Likens 1979; McCook 1994; Van Breugel et al. 2007).

Other theories and models attempt to explain the causal forces driving sequential succession as correlations with plant life-history traits and strategies (Grime 1974; Huston and Smith 1987), resource allocation and growth rates (Tilman 1985) and species interactions (e.g. facilitation, tolerance, inhibition) (Connel and Slatyer 1987). In reality, forest succession proceeds along multiple pathways determined by initial conditions and subsequent shifts in the disturbance regimes. The rates and specific trajectories of succession can also vary from site to site. Moreover, different vegetation strata can have very different patterns of diversity over the course of succession (Yang et al. 2005; Van Pelt et al. 2006).

To understand successional pathways and to predict future changes in canopy composition, it is feasible to analyze the species composition of different structural layers (Peña-Claros 2003), every layer being adapted to different levels of light availability and microclimate conditions (Liira et al. 2002). During the early stages of succession, species diversity of herbs, grasses and shrubs increases. The open stage lasts until the largest and most shade-tolerant functional types dominate. Their high leaf area reduces light availability and shade-intolerant functional types become suppressed (Huston 1994; Elliott et al. 1998; Kimmins 2004; Yang et al. 2005). Shade-tolerant species form a much larger species pool than pioneer species, though they tend to be more widely distributed and occur at much lower densities (Van Breugel et al. 2007).

2.5 Protection and management of stream systems in the Pacific Coast of North America

The coastal temperate rain forest region extends from northern California to south-central Alaska and east to the crests of the Cascade Mountains in the south and the Coastal Mountains in the north. Due to its proximity to cool and moist oceanic air, the subdued range of extreme temperatures, and a high frequency of clouds, fog and precipitation, the temperate rainforest of North America encompasses an abundance of rivers and streams and supports some of the most extensive temperate rain forests in the world (Kimmins 1990; Schoonmaker et al. 1997; Naiman et al. 2000; Kiffney et al. 2002; Richardson and Milner 2005).

The rivers within the Pacific coastal rain forest are linked by an intricate network of stream channels connected to the surrounding terrain. Approximately 80% of the connecting channels are less than 2 meters wide and are classified as first- or second-order streams (Naiman et al. 1992); however, many of them do not appear on management maps and others are not even known. In general, small streams show physical and ecological differences compared to larger rivers (Table 1). For example, small streams lack floodplains and alluvial benches and therefore are considered colluvial, with steeper hillslopes and a closed canopy cover. They typically experience infrequent but intense disturbances such as flooding and geophysical responses including landslides, erosion, and debris flows (Swanson et al. 1998; Richardson et al. 2005).

Table 1. Comparison of some important ecological and functional riparian attributes between small and large streams in the Pacific Coast of North America.

Attribute	Small streams	Large streams
Widths of hydrophyte vegetation	Narrow	Narrow to wide
Canopy	Closed	Partly to fully open
Frequency of intense disturbances	High	Low to intermediate
Slide slope angles	Steep	Usually low
Alluvial development	More colluvial	Extensive alluvial areas
Water velocity	Low to high	Low to high
Microclimate	Cool, dark, humid	More open

Small headwater streams in forested areas have been shown to be strongly dependent on the input of coarse woody debris (CWD), which includes snags, logs and branches, as an energy source. The addition of CWD also modifies the morphological features of streams, ultimately slowing the movement of water and transport of dissolved solutes, thus increasing the potential for biological uptake (Swanson et al. 1978; Bilby and Likens 1980; Robinson and Beschta 1990). In addition to removing an important source of CWD, the removal of riparian vegetation can dramatically increase air, soil and water temperatures, direct solar radiation, air turbulence and wind speeds. Therefore, the density of the riparian canopy and the size and species of trees for ongoing CWD recruitment are critical factors to be taken into account for management purposes (Gregory et al.1991; Osborne and Kovacic 1993; Brosofske et al. 1997; Moore et al. 2005).

In the Pacific Northwest of the United States of America, 30m buffers are commonly used and have been found to be effective in maintaining salmonid habitat as well as preventing population declines in fish and other species (Metzger et al. 1997; Cockle and

Richardson 2003; Shirley 2004; Richardson et al. 2005). In British Columbia, 'The Forest Practices Code of British Columbia Act' came into effect in June 1995. This Act introduced new protection requirements for small streams in areas of public forest land in British Columbia designated for timber harvesting. Streams are divided into 4 classes of fish bearing streams and 2 classes of non-fish bearing streams according to the width of the active channel. Riparian management zones are required for all streams with continuous sediment lined channels. Unharvested buffers at least 20 meters wide are required on each side of streams greater than 1.5 meters wide if they are fish bearing or in community watersheds. On fish-bearing streams less than 1.5 meters wide, and non-fish bearing streams less than 3 meters wide, use of ground-based machinery is restricted within these management zones, but timber harvesting is permitted right to the stream.

Small streams occur at relatively high densities in the forests of coastal British Columbia, and this level of stream protection represents a compromise between making an area available for timber management and protection of riparian and aquatic ecosystems and water quality. While much is known about riparian communities and disturbance regimes of large rivers (order $>$ 6) (Vannote 1980; Naiman et al. 1992) and medium-sized streams (orders 4 to 6), knowledge is scarce regarding communities and processes associated small headwater streams (Richardson et al. 2005). Specifically, little information is available on the effect of different buffer widths on the vegetation component of riparian systems where adjacent timber has been removed during harvesting (Moore et al. 2005; Richardson et al. 2005). This basic knowledge about the structure, dynamics and function of small streams and their associated riparian zones is of great importance for designing conservation and management plans (Pabst and Spies 1999; Naiman et al. 2000;

Richardson et al. 2005). The goal of this thesis is to document and interpret the development of understory and overstory vegetation under different riparian buffer widths and place this in the context of successional trajectories.

Small headwater streams receive little protection under forest practices guidelines. However, they exert great importance in maintaining the productive capacity of fish habitat by processing and exporting nutrients, organic matter and stream invertebrates (Beese et al. 2003). Currently, little is known about vegetation patterns through succession in riparian ecosystems along small streams. The importance of establishing proper riparian buffers for protecting these ecosystems requires a detailed approach which takes into account the change of both understory and overstory vegetation under different riparian buffer widths during successional time. This is the overall aim of my thesis.

3 COMPARISON OF THE LIGHT ENVIRONMENT, UNDERSTORY AND OVERSTORY COMPOSITION AND STRUCTURE AMONG TREATMENTS EIGHT YEARS AFTER HARVESTING

3.1 Introduction

Forest policy in British Columbia states the mandatory retention of standing trees (buffer strips) along larger stream channels with significant populations of fish (Wang et al. 2002). However, buffer strips are not mandatory along stream whose bankfull width is less than 1.5 m and, therefore, less protection is affordable under forest practices guidelines (Beese et al. 2003; Moore et al. 2005). Shirley (2004) investigated the role of different buffer widths in explaining species richness and abundance in coastal riparian areas of British Columbia. She found that some aspects of vegetation structure such as diversity change with buffer width.

In their study on the distribution of herbs and shrubs in riparian forests of coastal Oregon, Pabst and Spies (1998) found that vegetation patterns are highly variable and sometimes indistinct, but that the vegetation composition is ordered along a complex environmental gradient (i.e. landforms, microsites and cover of coniferous tree canopies) running from streamside to lower hillslope. They suggested that hydrological disturbance, including periodic floods, erosion and alluvial deposition is the primary driver of vegetation composition; however, this would be more applicable to large streams with fluvial terraces than small hillslope constrained streams. On the other hand, plant species diversity usually increases with increasing soil nutrients, moisture and light (Decocq 2002; Suzuki et al. 2002) and would accordingly be expected to vary with proximity to the stream, particularly in hillslope constrained streams.

Moreover, it has been suggested that in order to understand the basic processes behind the formation of community structure it is useful to analyze the dynamics of functionally similar species groups rather than individual species (Liira et al. 2002). For example, competitive interactions among species of the same functional type may be stronger than between species of different functional types; thus, patterns of species richness along gradients may be more interpretable by considering species richness of the different functional types (Bonet and Pausas 2004).

The objectives of this study were: 1) to describe structurally and floristically the riparian plant communities among riparian buffer treatments of different widths; 2) to compare the light environment, the condition (dead, live, windthrown), the dynamics and dominance of overstory trees, and the composition and structure of the understory vegetation among different treatments; 3) to analyze how understory vegetation species diversity, structural complexity and abundance vary in response to buffer width and stream proximity following harvesting; 4) to determine which buffer treatment produces characteristics most like those in old-growth forests within eight years after harvesting.

The following hypotheses were tested: *i)* light levels, as indicated by canopy openness, will not be affected by stream proximity and will increase with decreasing buffer width; *ii*) measures of vegetation species diversity, structural complexity and abundance will increase with increasing buffer width and closer to the stream; *iii*) eight years after harvesting, the understory composition and structure in the 30m buffer treatment will be more similar to that in the old-growth stand; *iv*) measures of tree mortality will increase with decreasing buffer width and DBH; *v*) measures of tree growth will be higher closer

to the stream and; *vi*) measures of overstory structural complexity will increase with increasing buffer width.

3.2 Methods

3.2.1 Study area

This experiment was conducted in the UBC Malcolm Knapp Research Forest which is located in the foothills of the Coast Mountains, approximately 60 km east of Vancouver, British Columbia (122º 34'W, 49º 16'N) (Fig.3.1). This potion of the forest where the study takes place lies in the Submontane (10 to 500m in elevation) very Wet Maritime Coastal Western Hemlock biogeoclimatic variant (CWHvm), influenced by a perhumid cool mesothermal climate (Pojar et al. 1991; Green and Klinka, 1994; Kiffney et al. 2002; De Groot et al. 2007).

The Research Forest comprises 5,157 hectares and receives abundant precipitation, mostly in the form of rain. Total precipitation ranges from about 2200 mm per year at the southern end of the forest to about 3000 mm per year at the northern end. Precipitation occurs primarily from October to March. Snow is rare at the south end of the forest, while the higher elevations to the north are typically snow covered for about four months of the year. Soils are shallow and composed of glacial till and some glacio-marine deposits (De Groot et al. 2007).

The dominant forest tree species that characterize the maritime subzones are coniferous and include: western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), amabilis fir (*Abies amabilis* (Douglas ex Louden) Douglas ex Forbes), western redcedar (*Thuja plicata* Donn ex D.Don), Sitka spruce (*Picea sitchensis* (Bong.) Carriére) and yellow cedar

(*Chamaecyparis nootkatensis* D.Don). Deciduous tree species including paper birch (*Betula papyrifera* Marsh.), red alder (*Alnus rubra* Bong.), and big-leaf maple (*Acer macrophyllum* Pursh) are frequent in open spaces (Feller et al. 2000).

The natural disturbance regime for this area is classified as Natural Disturbance Type 2 (NDT2). These are ecosystems with infrequent stand-initiating events (British Columbia Ministry of Forests and B.C. Ministry of Environment, Land and Parks 1995). Windthrow and wildfires are expected in this area. Much of the research forest is comprised of second growth stands that originated from logging and fires. Major fires occurred in 1868, 1925, 1926, 1931 and 1957 and were sufficiently hot and frequent to have burnt much of the logging debris. The riparian buffers experiment is located in relatively contiguous young-mature conifer dominated stands that initiated following the 1931 fire.
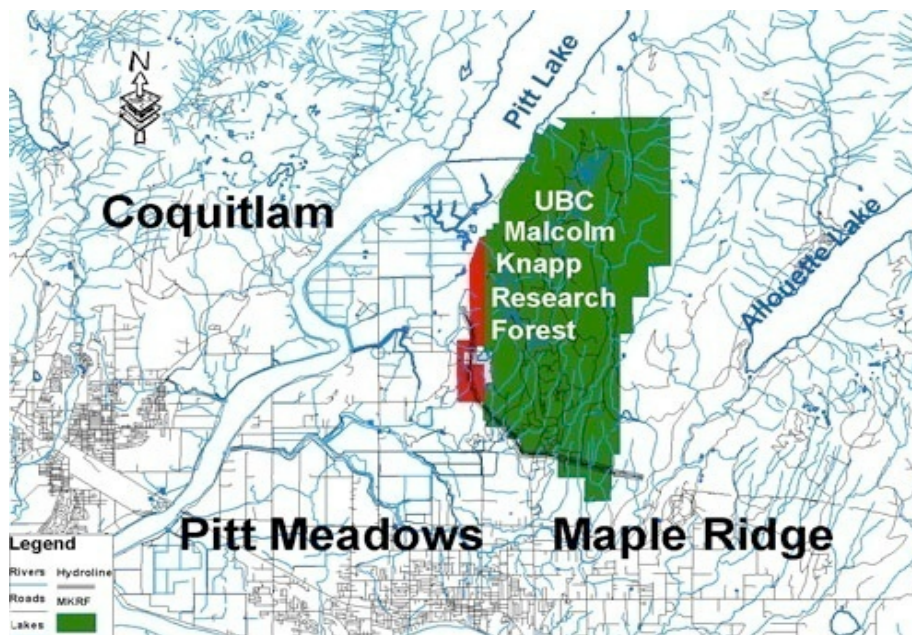
Figure 3.1. Location of the Malcolm Knapp Research Forest. Source:
http://www.mkrf.forestry.ubc.ca/general/ecology.htm

3.2.2 Experimental design

In 1998, a set of comparable small perennial streams in the southeast corner of the MKRF were identified by the integrated research team led by Dr. Richardson. These streams were primarily hillslope constrained with some portions constrained by terraces on one side. For the experiment, portions of these streams were assigned to one of four treatments: unharvested controls; 30m buffer width on each side; 10m buffer width on each side; and 0m buffer clearcuts where trees were felled right up to the stream banks. In the latter treatment, the trees were felled and then yarded away from the stream banks to minimize direct damage to the bank and channel. Each treatment was replicated 3 times on different streams, producing a total of 12 treatment units. Characteristics for the 12 treatment units are summarized in Table 3.1. Within each treatment unit, two sets of line transects were established. Each set included 15m long transects located parallel to the stream at a distance of 2m and 15m from the stream on each side (Fig.3.2). In each 15m long transect, the species name and height of each understory species that touched a vertical pin was recorded every 1m along the transect (the point method). For moss species, identification was limited to those species included in Pojar and MacKinnon (1994). Subsequently, species were assigned to 5 main functional groups related to vegetative attributes (i.e. growth form, life history strategies, litter similarities), ecophysiological traits and community responses (Liira et al. 2002; Rundel et al. 2005; Bloom and Mallik 2006). These groups were: coniferous trees, deciduous trees, shrubs, herbs, ferns and mosses.

Plot establishment and pre-harvest measurements were completed in 1998-1999. The blocks were harvested in the summer and fall of 1999 and were remeasured in the

summers of 2000, 2001, 2002, 2003, 2004, 2005 and 2006. In 2002, the forest overstory density (canopy openness) was estimated using a convex mirror densiometer. Measurements were taken for each of the four cardinal directions at each end of the transect and then averaged to produce a single value for the transects. Canopy openness was used as an indirect measure of light levels. In addition, hemispheric images were acquired with a Nikon Coolpix 990 digital camera and they were analyzed with WinSCANOPY to determine openness and calculate photosynthetically active photon flux density (PPFD). From this information, it was possible to detect a near linear relationship between canopy openness and PPFD. Therefore, the use of canopy openness as a indirect measure of the light environment was supported. For more details refer to Figures A2-2a,b and c.

Trees within 2m on each side of each transect (producing a $60m^2$ strip plot) were tagged and the DBH (diameter at breast height), DSH (diameter at stump height), height and condition were recorded. Tree condition was monitored in the summer of 1998, 1999, 2000, 2002, 2003, 2004, 2005 and 2006 and DBH measurements were taken in 1998, 2002 and 2005. The DBH measurements for the years 1998 and 2004 were used to calculate pre and post harvest basal area and stems per hectare. Only living trees with a pre-harvest DBH greater than 7.5cm were retained and used for these calculations. The formula for obtaining basal area per hectare was:

(1) **Tree Basal Area** (TBA) (m^2) = π (DBH/200)^2 for DBH in cm

(2) **Stand Basal Area** (m^2/ha) = (Sum of TBA in the plot) / (area of the plot)

Additionally, the species´ importance values were calculated. The importance value (IV) measures the relative dominance of species in a forest community and ranks species within a site based on its relative frequency, relative density, and relative dominance. The maximum importance value for any species is 300 (Curtis and McIntosh 1951).

In 2006, to provide context for the results of the buffers experiment, four plots were added adjacent to small perennial streams in older stands. Two of these plots were in a 140-year-old (1868 origin 'mature stand') and two in old-growth stands (OG). In each plot, the clusters of transects were set up following the same methodology as the original treatment units. However, the new plots were only replicated two times due to the difficulty of finding small streams in older stands within the MKRF. The same variables were measured. The data for the new plots were not analyzed together with the rest of the treatments when running the ANOVA; however, they are included in the graphical results to enable comparison with the results for the buffers experiment. The rationale behind this was the recognition that vegetation communities undergo changes over time represented by a series of seral stages which culminate in a final climax seral stage: the old-growth phase. This climax seral stage provides an indication of the direction and degree of vegetation development of a region. Because of this, it is possible to construct the probable seral sequence for any region and make comparisons between seral stages (Kimmins 1997, 2003).

Table 3.1. Physical characteristics of the riparian buffers experiment treatment units.

Treatment	Treatment Unit	Watershed Area (ha)	% BA removed	Channel length (m)	Drainage density (m/ha)	Stream flow direction	Average stream slope (%)	Fish Presence
	East Ck.	44.0	0	855	30	NNE→SSW	8	Yes
Control	Spring Ck.	111.0	0	-	-	-	-	Yes
	Mike Ck.	29.7	0	1200	-	-	-	-
	B	13.5	24.4	765	57	NNW→SSE	10	-
Om buffer	E	12.2	53.3	805	66	N→S	12	No
	I	12.6	21.4	570	45	S→N	6	No
	C	89.1	25.8	2015	55	N→S	7	Yes
10m buffer	F	11.5	24.3	605	109	N→S	14	No
	G	83.5	18.3	1935	42	N→S	4	Trans.
	SK	18.6	20.4	1105	59	NNE→SSW	10	No
30m buffer	D	43.3	21.9	1180	47	N→S	8	Yes
	H	55.4	16.1	1440	48	ENE→WSW	5	Trans.

3.2.3 Analytical approach

The experimental design corresponded to a split-plot design with four factors: buffer width with four levels (control, 0m, 10m and 30m), location of the plot with two arbitrary levels (upstream and downstream), side of the stream with two levels (left or right, looking upstream) and distance from the stream with two levels (2m or 15m). This experimental design is appropriate for ANOVA.
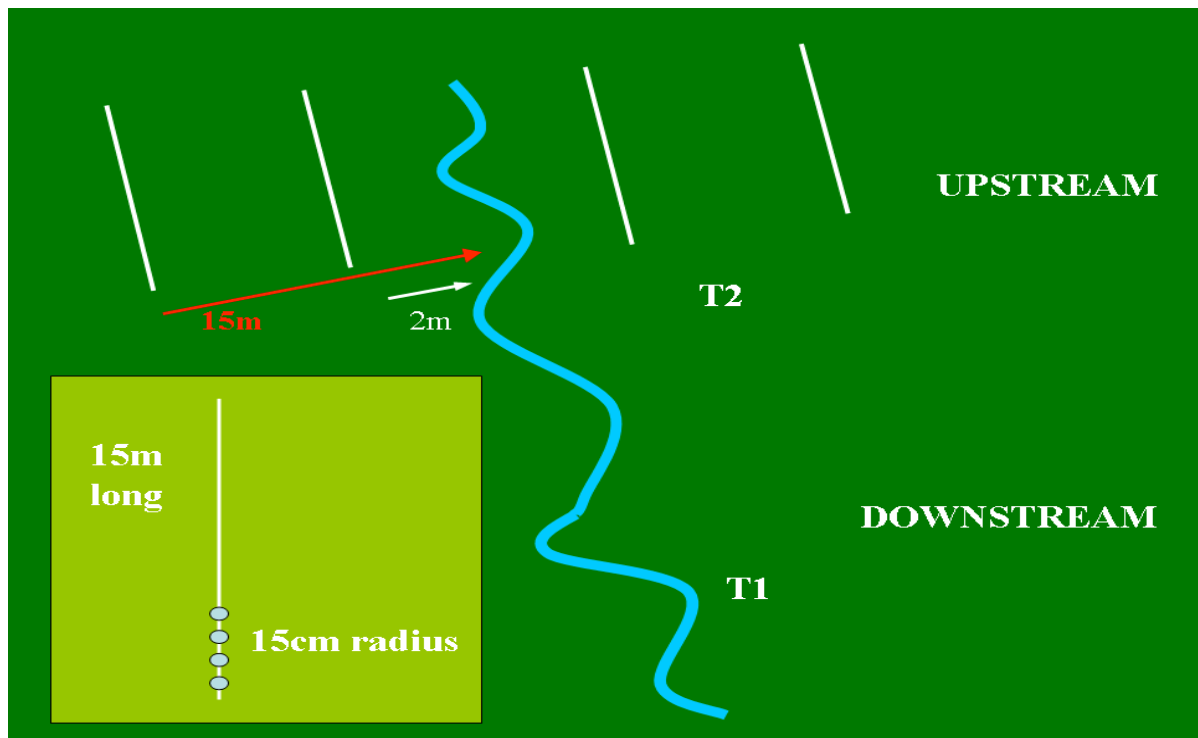
Figure 3.2. Transect cluster layout showing how the experiment was designed and its basic features. The light green square depicts one of the 8 transects which were set up in each cutblock. The little circles represent the small circular plots used in the sampling methodology.

Before running the ANOVA, I tested the significance of light levels as a covariate. Although the assumptions of the analysis of covariance were met (equal slopes and linear regression between x and y), the result was non-significant. I then ran ANOVAs using pre-harvest (1998), and year eight post-harvest (2006) data for each of the following variables: light levels, overstory basal area, overstory stems per hectare, total species richness, total cover (%), shrub, fern, moss, herb, deciduous and coniferous tree richness and cover, Shannon-Wiener Index (H') and the inverse of Simpson Index (1/D). Differences between means were tested using a Bonferroni multiple comparison test. The p-values obtained in each ANOVA were compared with the corrected split alpha (Kutner

et al. 2005). In the case of total cover, and shrub, fern, moss, herb, deciduous and coniferous tree cover, I used the arccosine transformations prior to the analysis to normalize the values.

The general model with all of the sources of variation, the degrees of freedom of each factor or interaction, the mean square formulas, and the corrected error terms used for testing the significance of a particular factor is given in Table 3.2. Due to the physical design of the plots, the upstream-downstream location as well as the side of the stream are considered fixed factors which must be included in the ANOVA; however, they are not taken into account in the ecological interpretations.

Table 3.2. General model for the ANOVA split-plot experimental design

Source	df formula	Df	MS	F ratio
T	(T-1)	3	MS(T)	MS(T)/MS(E1)
U	(U-1)	1	MS(U)	MS(U)/MS(E1)
T*U	(T-1)(U-1)	3	MS(TU)	MS(TU)/MS(E1)
Error 1	(T)(U)(R-1)	16	MS(E1)	MS(E1)/MS(E2)
S	(S-1)	1	MS(S)	MS(S)/MS(E2)
D	(D-1)	1	MS(D)	MS(D)/MS(E2)
S*D	(S-1)(D-1)	1	MS(SD)	MS(SD)/MS(E2)
T*S	(T-1)(S-1)	3	MS(TS)	MS(TS)/MS(E2)
U*S	(U-1)(S-1)	1	MS(US)	MS(US)/MS(E2)
T*U*S	(T-1)(U-1)(S-1)	3	MS(TUS)	MS(TUS)/MS(E2)
T*S*D	(T-1)(S-1)(D-1)	3	MS(TSD)	MS(TSD)/MS(E2)
T*D	(T-1)(D-1)	3	MS(TD)	MS(TD)/MS(E2)
U*D	(U-1)(D-1)	1	MS(UD)	MS(UD)/MS(E2)
T*U*D	(T-1)(U-1)(D-1)	3	MS(TUD)	MS(TUD)/MS(E2)
U*S*D	(U-1)(S-1)(D-1)	1	MS(USD)	MS(USD)/MS(E2)
T*U*S*D	(T-1)(U-1)(S-1)(D- 1)	3	MS(TUSD)	MS(TUSD)/MS(E2)
Error 2	(R-1)(S*D-1)(T*U)	48	MS(E2)	-
Total	R(T*U)(S*D)-1	95	-	-

Note: T, Treatment ; U, location of the plot; S, side of the stream; D, distance from the stream, R, replication=3.

3.3 Results

3.3.1 Light environment

The light environment was evaluated by subtracting the overstory canopy cover from 100%. There were substantial differences in post-harvest light environment among treatments and distances from the stream (p<0.0001). As expected, the 0m buffer at both 2m and 15m from the stream and the 10m buffer at 15m had the highest light levels followed by the 30m buffer at 15m, 2m and finally the control (Fig. 3.3). These differences are primarily due to light coming from the edge in the 10m and 30m buffers, however loss of overhead trees due to post-harvest tree mortality and windthrow is also a factor. The light levels in the 1868 and old-growth stands are most similar to those in the 70 year old control stand.
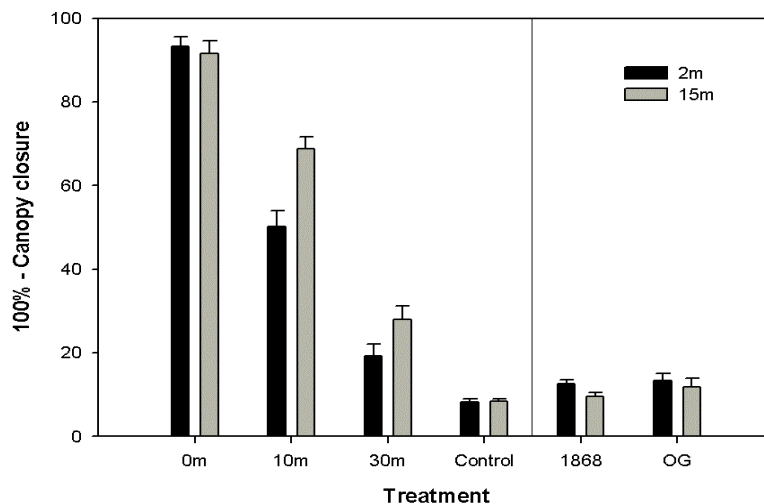
Figure 3.3. Canopy openness for 2002 (mean ± SE) (100% - % canopy closure) by treatment and distance from the stream. '1868'=Mature stand, 'OG'=old-growth stand.

3.3.2 Measures of understory vegetation species diversity and abundance eight years after harvesting

Eight years after harvesting, a total of 63 understory species belonging to 35 plant families were observed in the pooled dataset for all treatments. The best represented families were Rosaceae with 8 species (12.6%) and Ericaceae with 6 species (9.5%), followed by Betulaceae (4.8%), Dryopteridaceae, Polytrichaceae and Salicaceae with 3 species each (Fig. 3.4).

In general, the species found were native. However, the invasive species such as Canada thistle (*Cirsium arvense* (L.) Scop.), English holly (*Ilex aquifolium* L.), and Himalayan blackberry (*Rubus* discolor Weihe & Nees) were also found although their cover was very low (Table A4-1). A few pre-harvest species disappeared, were not found, or were reduced dramatically in abundance in the plots after harvesting. These species were dominated by mosses and included: racomitrium moss (*Racomitrium lanuginosum* (Hedw.) Brid.), isothecium moss (*Isothecium myosuroides* Brid.), bottle moss (*Amphidium lapponicum* (Hedw.) Schimp)., tree climacium moss (*Climacium dendroides* (Hedw.) F.Weber & D.Mohr), along with bull thistle (*Cirsium vulgare* (Savi) Ten.), showy aster (*Aster conspicuus* Lindl.).

Overall species richness was highest in the 0m and 10m treatments and declined in the 30m buffer and Control (Fig.3.7). When organized by functional groups, it is apparent that the shrubs were well-represented among all treatments; however, shrub diversity was higher in the 0m and 10m buffer treatments with averages of 4.3 and 3.9 species, respectively, which accounted for 34% and 38% of the total richness in these treatments.
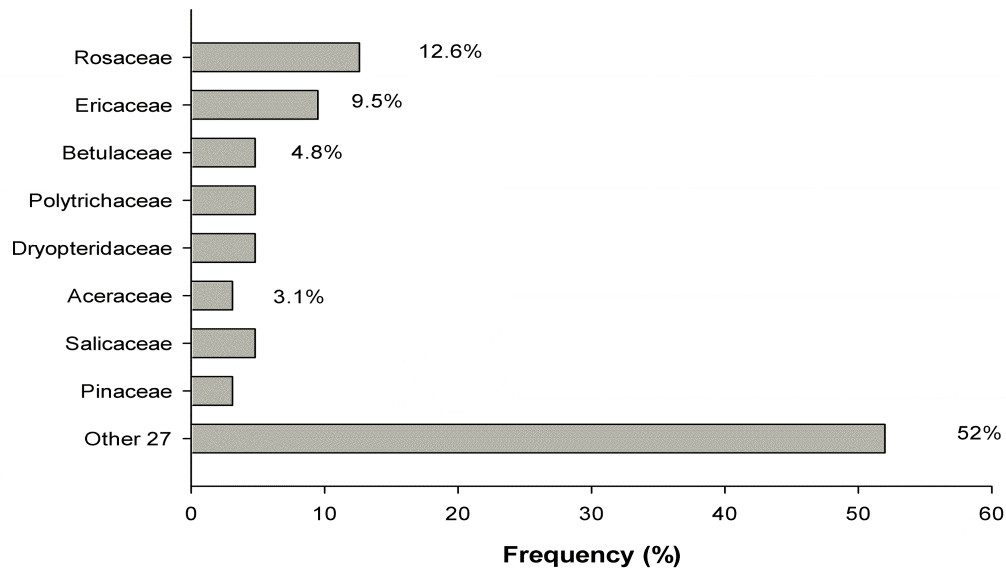
Figure 3.4. Understory plant families frequencies distribution eight years after harvesting, plots for all treatments pooled.

The 30m, control, and 1868 stand had similar patterns of shrub, fern, herb and moss richness. The control and 1868 stand had the lowest values of shrub richness at 1.3 and 1.6 species, respectively. The old-growth stand had a similar pattern of richness, but had more species in each of the categories than the 30m, control and 1868 stands. Despite the differences in the number of shrub species among treatments, the shrub richness in all treatments accounted for more than 30% of the total (Fig.3.5). Understory tree richness of both deciduous and coniferous species was not very high in general, and these species were absent in the understory in the 1868 and old-growth plots. Levels were highest in the 0m and 10m treatment, with 20% and 9% respectively of the total richness belonging to deciduous trees, and 12% and 9% of the total to coniferous trees.

Ferns were almost equally diverse in all treatments with a richness ranging between 0.96 and 2.41 species on average or in other words around 19% to 39% of the total species diversity (Fig.3.5). Herbs had low values of richness (less than other species on average) in all treatments and accounted for 1% to 3% of the species richness in each treatment. Finally, mosses were found in all treatments but diversity was highest in the old-growth stand with likely more than 2.5 species on average.
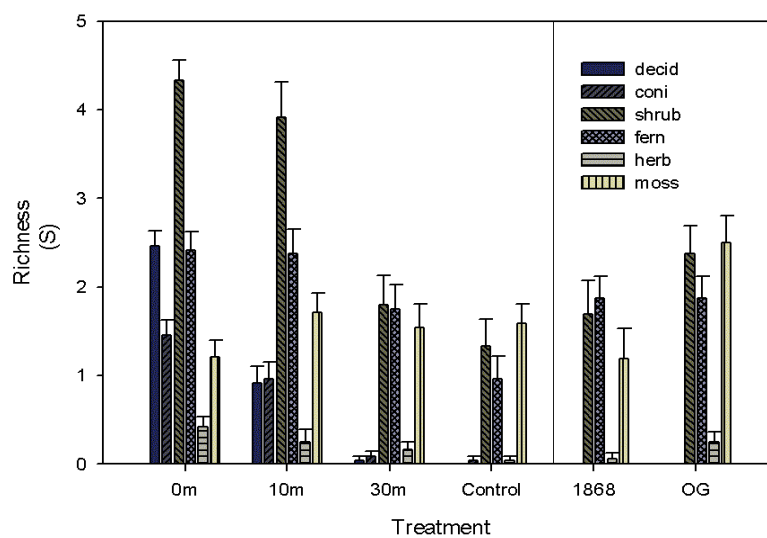
Figure 3.5. Mean number (± SE) of understory species by functional group among treatments. '1868'=Mature stand, 'OG'=old-growth stand.

Table 3.3. Measures of community diversity eight years after harvesting. Bold numbers correspond to the higher values whereas underlined numbers represent the lower ones.

	Treatment					
Diversity measures	**0m**	**10m**	**30m**	**control**	**1868**	**OG**
Species richness (S)	**12.41**	10.16	5.37	3.95	4.81	7.37
Shannon-Wiener (H´)	**2.20**	1.93	1.31	1.06	1.19	1.75
Exp H´	**9.02**	6.94	3.70	2.88	3.28	5.75
Simpson (1/D)	**7.67**	6.63	3.80	3.09	3.34	5.52
% Cover	**99.50**	87.13	58.50	43.49	64.11	73.04

As far as the diversity indexes are concerned, both the Shannon-Wiener (H´) and the inverse of Simpson (1/D) were affected by treatment levels (p=0.0024 and p=0.0001 respectively) and increased with the increase in light level (Fig. 3.6). Shannon-Wiener (H´) decreased with increasing buffer width (Fig. 3.6). However, according to the Bonferroni multiple comparison test using an α =0.05, the significant differences were found only between the 0m buffer and the control. The control showed the lowest plant diversity and dominance of all. The control and mature (1868) stand were similar in terms of plant diversity and dominance. The diversity of the old-growth stand was intermediate between the harvested treatments and the control and 1868 stand. The pattern was similar for the 1/D index (Table 3.3, 3.4b , Fig. 3.6).
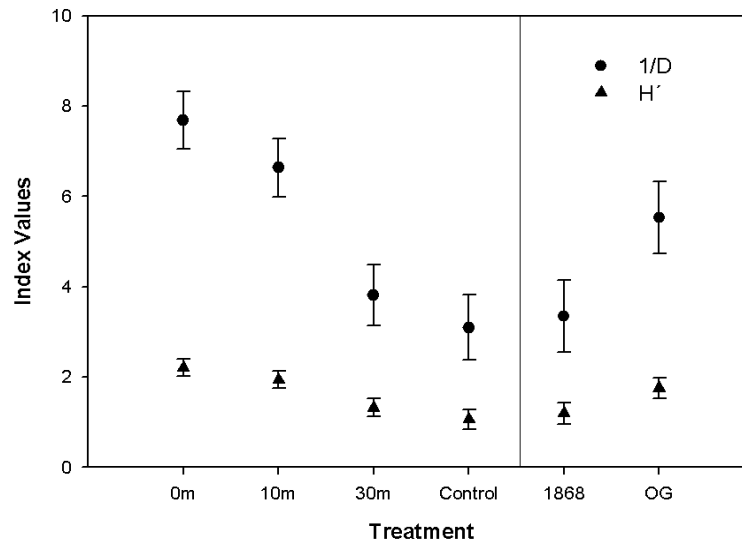
Figure 3.6. Diversity index values (mean ± SE) by each treatment eight years after harvesting. 1/D is for the reciprocal of Simpson´s index and H' is for Shannon-Wiener. '1868'=Mature stand, 'OG'=old-growth stand.
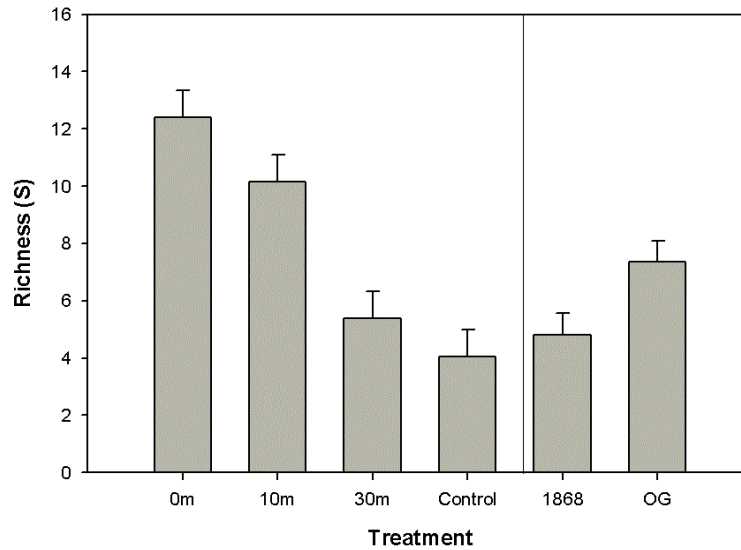
Figure 3.7. Effect of treatment levels on the total number of understory species (mean ± SE) eight years after harvesting. '1868'=Mature stand, 'OG'=old-growth stand.

These effects are due to post-treatment rather than pre-treatment differences since, the ANOVA with the 1998 pre-harvest dataset reveals that none of the main experimental factors had any significant effect on 13 out of 14 of the variables measured (Table 3.4a). The exception was for stem/ha in the case of buffer width (p=0.0074). However, there was a significant two-way interaction effect between buffer-width and distance from the stream on the shrub richness (p=0.0375). In contrast, eight years after harvesting, there was a strong effect of buffer width on all the variables except for moss and herb richness and moss cover (Table 3.4b, Fig.A2-2a-f, Fig. A2-3b). The total richness of understory species was highly affected by buffer width (p< 0.0001) (Fig. 3.7).

Table 3.4. Analysis of variance results for treatment (T), location of the plot (U), side of the stream (S) and distance from the stream (D) effects and interactions. Bold letters means significant results using an α =0.05. +Transformed prior to analysis using an arcsin function.

a) Pre-harvest (1998) analysis of variance results (*p values*)

Variable	T	U	T*U	S	D	S*D	T*S	U*S	T*U*S	T*S*D	T*D	U*D	T*U*D	U*S*D	T*U*S*D
Sumspp	0.8859	0.6638	0.9929	0.8661	0.4861	0.3500	0.2810	0.4284	0.9416	0.6367	0.5502	0.6476	0.9036	0.0692	0.9888
Sumshrub	0.9725	0.6013	0.8624	0.9505	0.8523	0.9505	**0.0195**	0.7564	0.3967	0.4367	**0.0375**	0.4959	0.9528	0.1584	0.8326
Summoss	0.8796	0.5807	0.9302	0.8454	0.6682	0.6682	0.4913	0.1541	0.5387	0.6594	0.6594	0.3720	0.5124	0.4146	0.8903
Sumfern	0.3380	0.4198	0.9827	0.5353	0.2182	0.2182	0.9119	0.7095	0.5626	0.7918	0.6364	0.8038	0.3652	0.2182	0.7918
Sumherb	0.2298	0.1567	0.3222	0.9084	0.1400	0.7301	0.4631	0.5659	0.9526	0.7365	0.5361	0.9084	0.4631	0.3035	0.9094
Cover+	0.9794	0.5629	0.9708	0.6177	0.7054	0.6502	0.0962	0.9734	0.6657	0.4821	0.9778	0.8646	0.7431	0.5298	0.3418
Covshrub+	0.9063	0.7368	0.9229	0.5415	0.9492	0.7878	0.1236	0.5438	0.6674	0.8396	0.3446	0.5842	0.5312	0.2318	0.8691
Covmoss+	0.9991	0.3315	0.9562	0.7187	0.4263	0.3361	0.0852	0.4602	0.3220	0.3932	0.8668	0.5320	0.7130	0.7249	0.7844
Covfern+	0.7264	0.5000	0.9603	0.2842	0.5675	0.9106	0.6131	0.6895	0.8573	0.6214	0.7814	0.3407	0.1281	0.8794	0.5049
Covherb+	0.4498	0.3759	0.1830	0.8033	0.0664	0.9382	0.3288	0.1700	0.6837	0.7983	0.4757	0.8046	0.6614	0.1267	0.5541
H´	0.6293	0.9366	0.9995	0.4024	0.9503	0.2619	0.1234	0.5565	0.5638	0.3449	0.8071	0.6696	0.2632	**0.0314**	0.9457
1/D	0.8399	0.7965	0.9137	0.1354	0.2518	0.2197	**0.0129**	**0.0189**	0.2036	0.1729	0.4091	0.6005	0.2154	**0.0126**	0.7373
Basal area	0.4544	0.2167	0.5217	0.6894	0.5869	0.3969	0.4122	0.3406	0.5230	0.3778	0.4426	0.4341	0.5669	0.2869	0.5751
Stems/ha	**0.0074**	0.1788	0.9693	0.0675	0.0569	0.0798	0.5271	0.7515	0.7047	0.0954	0.5799	0.3723	**0.0025**	0.2640	0.9663

b) Year eight (2006) analysis of variance results (*p values*)

Variable	T	U	T*U	S	D	S*D	T*S	U*S	T*U*S	T*S*D	T*D	U*D	T*U*D	U*S*D	T*U*S*D
Canopy closure	**<0.0001**	**0.0307**	0.7176	**0.0219**	**<0.0001**	0.7204	**0.0010**	**<0.0001**	**0.0034**	0.1683	**<0.0001**	0.4269	0.8089	0.5680	0.5695
Sumspp	**<0.0001**	0.5749	0.8007	**0.0031**	0.1019	0.9425	0.2134	0.0561	0.6844	0.6151	0.0537	0.9425	0.1604	0.7185	0.3659
Sumshrub	**<0.0001**	0.7151	0.6885	**0.0274**	0.0727	0.3448	0.1328	0.1696	0.7381	0.2721	**0.0317**	0.9418	0.6883	0.9418	0.4361
Summoss	0.7691	0.1969	0.3961	0.0684	0.3560	0.6433	0.1126	0.2497	0.9831	0.7294	0.4282	0.2497	0.6918	0.4879	0.3716
Sumfern	**0.0284**	0.8649	0.9021	**0.0026**	0.7737	0.7737	**0.0361**	**0.0486**	0.3297	0.9687	0.2627	0.9236	0.3029	0.1079	0.2412
Sumherb	0.0985	0.5404	0.3029	0.8357	0.1509	0.5346	0.8429	0.1509	0.9878	0.7598	0.2442	0.0667	**0.0284**	0.3024	0.9231
Sumconi	**<0.0001**	0.6642	0.9360	0.3437	**0.0007**	0.8491	0.2023	**0.0061**	0.3544	0.1806	**0.0038**	0.8491	0.0727	0.0916	0.5452
Sumdeci	**<0.0001**	1.0000	0.7393	0.6717	0.2070	**0.0382**	**0.0006**	0.3980	0.6143	0.3876	0.1679	1.0000	0.0670	1.0000	0.4743
Cover+	**<0.0001**	0.1635	0.6078	**0.0210**	**0.0050**	0.5729	0.1008	0.7958	0.6937	0.1179	**<0.0001**	0.0517	0.9093	0.5991	0.0828
Covshrub+	**<0.0001**	0.5792	0.6352	**0.0222**	0.1615	0.6081	0.5706	0.4621	0.4977	0.9747	**0.0043**	0.0603	0.7027	0.9707	0.4992
Covmoss+	0.9694	0.2070	0.8066	0.7039	0.0796	0.2878	0.3968	0.9839	0.1493	0.7272	0.3422	0.9749	0.8164	0.6381	0.2636
Covfern+	**0.0138**	0.7408	0.7635	**0.0169**	0.7680	0.5870	**0.0023**	0.6820	0.2631	0.4327	**0.0049**	0.6665	0.1163	0.6597	**0.0310**
Covherb+	**0.0207**	0.1634	0.1679	0.4865	0.1365	0.2194	0.4785	0.1365	0.7277	0.3221	0.8897	0.0806	0.1088	0.1362	0.3423
Covcon+	**0.0001**	0.5782	0.9655	0.8170	0.0587	0.4737	0.0595	0.3259	0.8138	0.5570	**0.0316**	0.7587	0.5417	0.2188	0.6666
Covdec+	**<0.0001**	0.1584	0.4825	0.2816	0.2143	0.8952	0.0824	0.8881	0.9176	0.7359	**<0.0001**	0.2238	**0.0134**	0.5057	0.1993
H´	**0.0024**	0.5009	0.7431	0.2333	0.0808	0.4191	0.6403	0.2705	0.6225	0.8514	0.5139	0.6713	0.3087	0.8141	0.2780
1/D	**0.0001**	0.9482	0.8872	0.2199	0.2677	0.8430	0.4970	0.2628	0.8829	0.9827	0.7256	0.4097	0.1335	0.9833	0.6210
Basal area	**<0.0001**	0.1213	0.7717	0.1333	**0.0002**	0.2849	0.5398	0.7075	0.9136	0.9318	**0.0087**	0.3546	0.8417	0.1462	0.1546
Stems/ha	**<0.0001**	0.3444	0.8293	0.2925	**0.0001**	0.5643	0.2614	0.6308	0.6574	0.1396	**0.0119**	0.7729	0.4232	0.3381	0.8744

There was a significant interaction between treatment levels and distance from the stream for coniferous trees species richness, the total percent cover of understory species, the percent cover of shrubs, ferns, coniferous and deciduous trees, and the overstory basal area per hectare and stems per hectare (Table 3.4b).

Eight years after harvest, there was an increase in understory cover further from the stream in the 10m buffer and control, but the Bonferroni multiple comparison test using a split α =0.0016 did not detect significant differences among means (Fig. 3.8). For the 0m and 30m buffer, the percent cover was similar between distances. The pattern in percent cover of ferns, shrubs, coniferous and deciduous trees, was similar. Significant differences were found in the 10m buffer at 2m and 15m from the stream. In all cases, except for the 10m buffer treatment 15, the percent cover was higher closer to the stream (Fig. 3.9) (Fig. A2-3a-e). For the 10m buffer, percent cover was higher at 15m, and this is logical since for this treatment, the 15m transect falls within the harvested area.
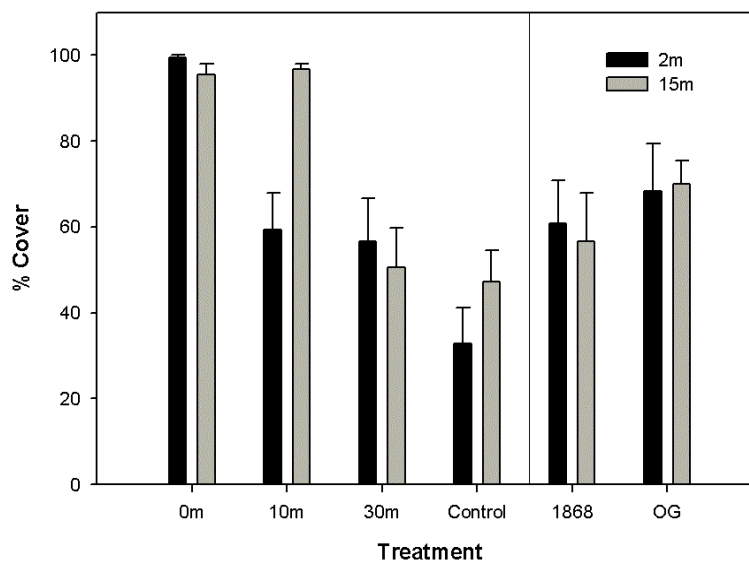
Figure 3.8. Effect of treatment levels and distance from the stream on the total percent cover (%) (mean ± SE) eight years after harvesting. '1868'=Mature stand, 'OG'=old-growth stand.
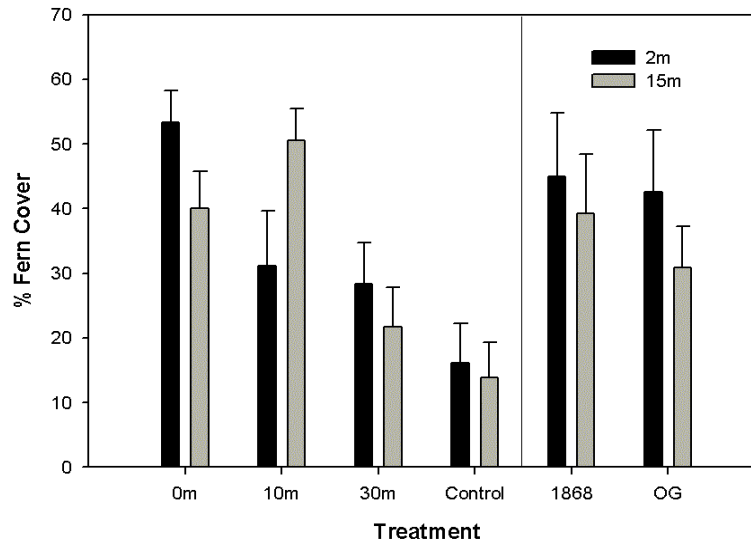
Figure 3.9. Effect of treatment levels and distance from the stream on the total percent cover of ferns (%) (mean ± SE) eight years after harvesting. '1868'=Mature stand, 'OG'=old-growth stand.

None of the factors in this experiment affected the percent cover of mosses eight years after harvesting (Table 3.4b, Fig. A2-3b). The number of moss species did not change with buffer width (Table 3.4b, Fig. A2-2b). This suggests a widespread and even distribution of this functional group among treatments.

3.3.3 Measures of overstory composition and structure eight years after harvesting

The overstory structure and composition in the Malcolm Knapp Forest included a mixture of living, dead and blown down trees with DBH ranging from 4 to 52cm. Three fast-growing coniferous tree species dominated the overstory canopy: western redcedar (Cw), western hemlock (Hw) and Douglas-fir (Fd) (Table 3.5). Changes in the condition of trees eight years after harvesting were observed in all treatments (Fig. 3.10). The first year after harvesting, up to 11% of the initially standing live trees in the 10m buffer were blown down and little wind damage occurred during the following years. By 2006, 15.2%

of the trees in the 10m buffer treatment had died standing, leaving only 70% of trees that were alive in 1998 remaining in the same condition. Windthrown trees were larger than average (Fig. 3.13), leaving relatively large canopy gaps.

In the 30m buffer, tree mortality was more uniformly distributed over the monitoring period after a small initial pulse of windthrow. By 2006, 80% of the trees in this treatment were still alive. In the unharvested controls, self-thinning continues, with substantial mortality of small trees over the past 8 years likely due to competition. While only 60% of pre-harvest live trees remain, the dying trees create small gaps that become occupied by neighbours, thus maintaining relatively high canopy cover.

The pre-harvest ANOVA for the overstory basal area showed no significant differences between treatments or distance from the stream (Table 3.4.a). However, eight years after harvesting, the overstory basal area was affected significantly by the treatment-distance-from- the stream interaction (p=0.0087) (Fig 3.11,Table 3.4a). In the 30m buffer and control, the basal area was slightly higher closer to the stream, but this was not observed in the 1868 or old-growth stands. The old-growth and mature (1868) stands had much higher basal areas compared to the rest of the treatments (150 to 211m^2/ha) (Table 3.5).
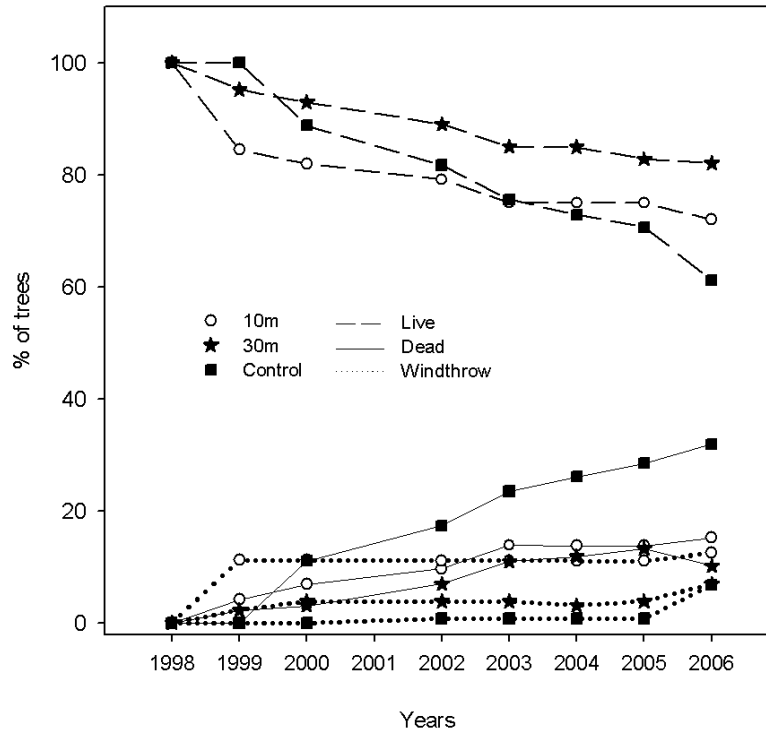
Figure 3.10. Percentage of trees by status and treatment for 1998 to 2006.
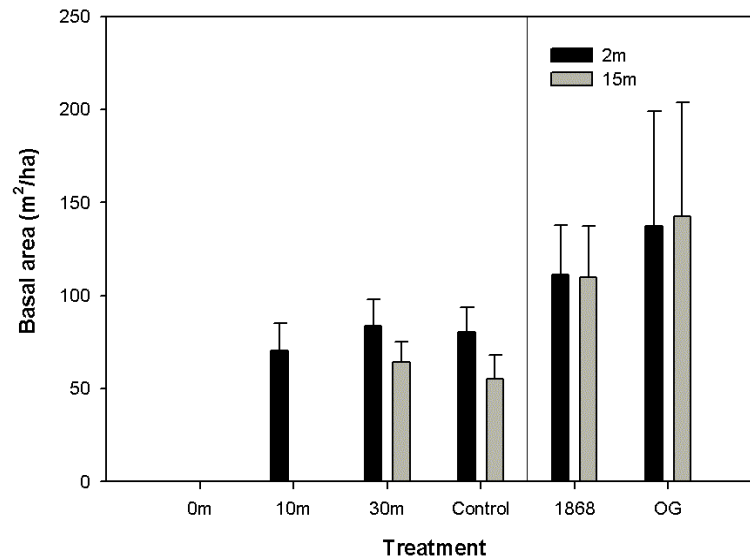
Figure 3.11. Effect of treatment levels and distance from the stream on the overstory basal area eight years after harvesting (mean ± SE). '1868'=Mature stand, 'OG'=old-growth stand.
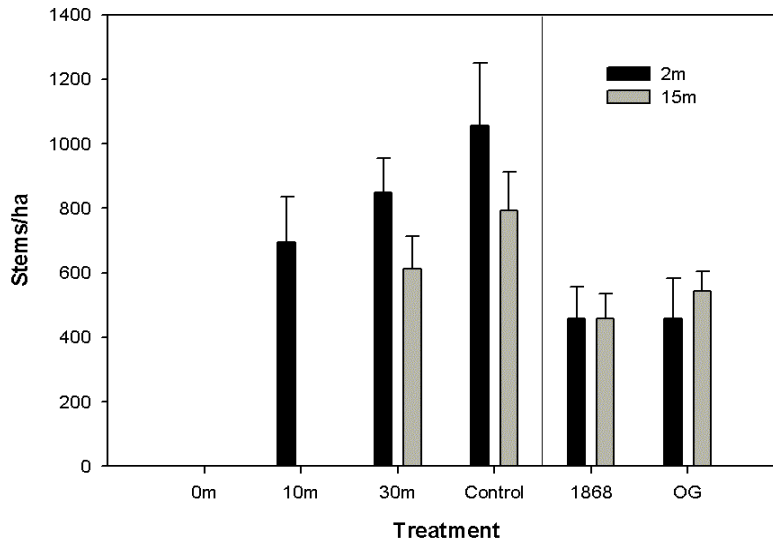
Figure 3.12. Effect of treatment levels and distance from the stream on stem density eight years after harvesting (mean ± SE). '1868'=Mature stand, 'OG'=old-growth stand.

The pattern in stems per hectare was similar to that for basal area. The average number of stems per hectare for all trees was higher in the control (second-growth) than in both the mature and old-growth stands (Fig. 3.12). Western hemlock and western redcedar were similar in abundance, with western hemlock dominating the control, mature and old-growth stands, and redcedar dominating the 10m and 30m buffer. Douglas-fir was present and, because of its large size and canopy dominance, was an important structural species (Table 3.5). Deciduous overstory trees were rare. Western redcedar and western hemlock were well represented in all diameter class sizes. Douglas-fir was more abundant in larger DBH classes (28 to 52 cm) (Figs. 3.15, A2-4a-h). As seen in Table 3.5 the control treatment contained the highest basal area for Douglas-fir (62.50 ± 31.42 m^2/ha) followed by western hemlock and western redcedar. The 10m buffer contained the greatest basal area for western hemlock (30.98 ± 9.80 m^2/ha) and the OG stand for western redcedar (64.16 ± 34.77 m^2/ha). In terms of basal area, the control and the 1868

stand were the most similar treatments. The importance value was relatively high for the three species in the 30m buffer. However, it was particularly high for Douglas- fir in the 30m buffer and for western hemlock in the control and old-growth stand.

Table 3.5. Measures of overstory composition and structure by treatment and species.

Treatment	Species code	Basal area/ha (mean ± SE)	Stems/ha (mean ± SE)	IV
10m	Hw	30.98 ± 9.80	333.33 ± 110.47	150.313
	Cw	34.53 ± 11.77	291.66 ± 77.10	166.013
	Fd	0.69 ± 0.69	13.88 ± 13.88	11.324
30m	Hw	26.42 ± 4.90	284.72 ± 56.28	145.591
	Cw	31.86 ± 7.03	333.33 ± 52.12	180.448
	Fd	12.06 ± 3.96	69.44 ± 22.24	194.723
Control	Hw	34.53 ± 11.77	555.55 ± 108.82	194.723
	Cw	22.21 ± 7.52	243.05 ± 56.73	117.371
	Fd	62.50 ± 31.42	62.50 ± 31.42	36.567
1868	Hw	25.04 ± 6.75	229.16 ± 47.81	143.497
	Cw	25.58 ± 8.67	166.66 ± 48.11	115.458
	Fd	55.32 ± 18.10	93.75 ± 30.30	112.573
OG	Hw	47.51 ± 29.91	364.58 ± 77.90	201.017
	Cw	64.16 ± 34.77	62.50 ± 20.83	97.014
	Fd	28.18 ± 21.19	31.25 ± 22.66	39.469

The 10m buffer closer to the stream experienced major windthrow events affecting mainly medium redcedar trees (DBH class size 20) (Fig 3.13, Fig. A2-6 a-c), whereas the highest number of dead trees was found in the control closer to the stream (Fig. 3.14). In general, mortality affected slender western hemlock trees (DBH class size 4 and 12). However, western redcedar trees (DBH class 12) also faced significant mortality rates (Figs. 3.14, A2-5a-h). The 30 m buffer was dominated by live medium-sized trees with a DBH ranging from 28 to 52 cm and by a high frequency of standing dead trees within small DBH classes (class size of 12 cm). Proximity to the stream did not affect this overall structure, but did affect the species-level structure (Fig. 3.15).
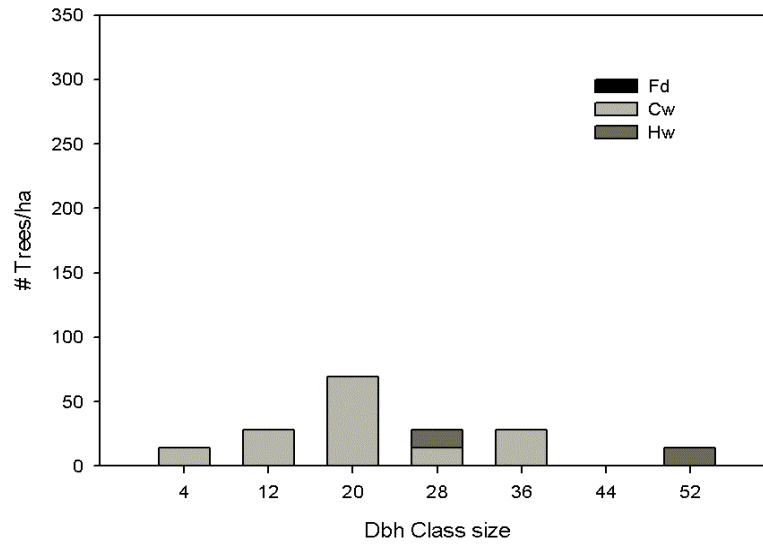
Figure 3.13. Average number of wind-blown trees per hectare in the 10m buffer 2m from the stream by DBH size class and by species.
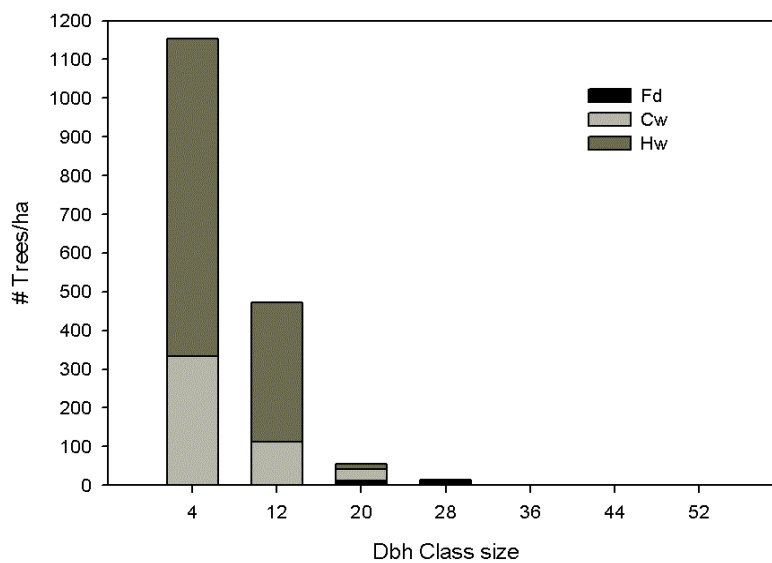
Figure 3.14. Average number of dead trees per hectare in the control 2m from the stream by DBH size class and by species.
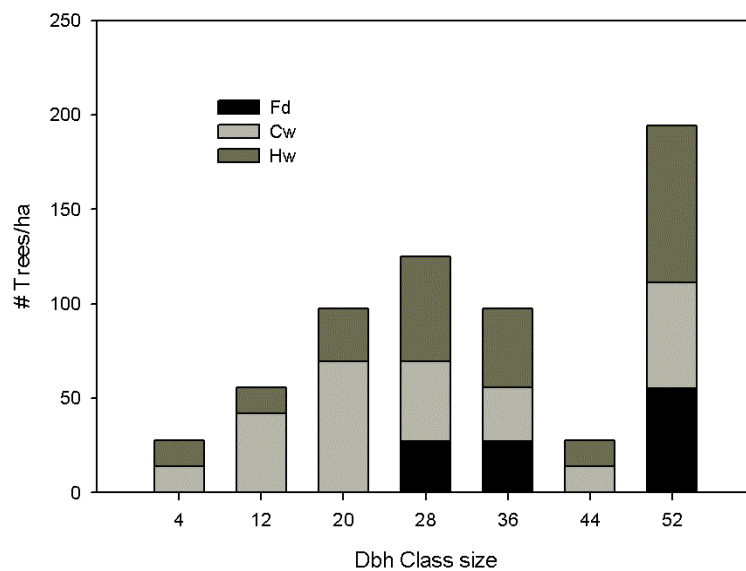
Figure 3.15. Average number of living trees per hectare in the 30m buffer 15m from the stream by DBH size class and by species.

3.4 Discussion

3.4.1 Light environment

The treatment by distance differences in light levels detected by the ANOVA are probably due to tree mortality, thinning and windthrow but mostly because light is coming from the edge in the 10m and 30m buffers further from the stream. Light levels reached up to 80% in the 0m buffer at both distances. In the 10m buffer the 15 meter transect is significantly different from the 2m transect. Much of the variation in species richness and percent cover is due to the change in the light environment, however, other factors such as reduced competition for moisture and mineralization of organic matter in the clearings may also be important.

Solar radiation at the stream surface is primarily affected by overstory canopy cover, tree height and distance from the stream (Brosofske et al. 1997; Frazer et al. 2000; Chan et al. 2004). Studies have shown that the removal of riparian trees results in increased solar radiation that penetrates into the stream environment affecting it dramatically. Brosofske et al. (1997) and Harper et al. (2005) show that the riparian forest edge at both sides of the buffer experience additional solar input which may also affect stream microclimate. Along with light level changes, the air and stream temperature, humidity, wind speed as well as the stream biota and riparian vegetation are modified after logging (Brosofske et al. 1997; Kiffney et al. 2003; De Groot et al. 2007).

The differences in light levels found in the study appear to be having an effect on stream temperature. De Groot et al. (2007) reporting on results from the riparian buffers study, found that during the summer, the maximum temperatures four years after logging were

5-8°C higher at the downstream end of the 0m treatments than at the upstream end. Over time, the light environment changes as a result of vegetation development, mainly as a consequence of invasion by fast growing deciduous trees which progressively developed a closed canopy.

3.4.2 Measures of understory cover and species diversity and structural complexity

Percent cover represents indirectly how 'favorable' the environment is for a particular species. In addition, plant cover allows a rapid assessment of plant community health (Whittaker 1975; Pueyo et al. 2006). However, where competition occurs plant cover may remain constant but species composition may change or vice versa (Merlos et al 2005). In this study, the area occupied by understory vegetation increases as light levels increases and is unaffected by stream proximity. The latter is consistent with the relatively continuous overstory in the unharvested treatments and the lack of a distinctive riparian zone adjacent to these small hillslope constrained streams. In spite of the relatively dense overstory, the understory percent cover of between 40-60% in the 30m buffer and control indicates sufficient light for persistence of many shrub, herb, fern and moss species at the MKRF. These light levels are maintained over time through canopy gap dynamics (Steward 1986; Hennon and McClellan 2003; Van Breugel et al. 2007). After disturbance such as harvesting or creation of windthrow gaps, understory percent cover tends to increase rapidly for some years due to increases in light, nutrient availability, moist soil conditions and changes in the pattern of nutrient delivery and the capacity of plants to acquire nutrients (Dyrness 1973; Pabst and Spies 1998; Schoonmaker and McKee 1988; Coroi et al. 2004; Wijesinghe et al. 2005).

Species richness is a direct measure of how diverse a stand is and also provides a description of the individual plants that comprise the site (Coroi et al. 2004; Merlos et al. 2005). Plant species richness varied with light level. The average number of species and distribution by functional group was similar in the 0m and 10m buffers, and was substantially higher than in the 30m buffer and control. In spite of this, the composition of the dominant species was relatively similar in the control and the old-growth stand and between the latter and the 0m and 10m buffer treatments. For example, there was widespread dominance of salmonberry (*Rubus spectabilis* Pursh). Aiba et al. (2001) studied regeneration patterns between secondary and old-growth stands in temperate forest southern Japan and concluded that most species characterizing old-growth stands also appear in secondary stands. Given the potentially long intervals between stand replacing disturbances, and the short duration of open conditions following disturbance in the CWHdm, it is not surprising that many understory species are capable of persistence in shade.

The type of plant cover yields important information about the habitat type and its functional state (Merlos et al. 2005). One group of species that were rare in the control, 1868 and old-growth forests was deciduous trees. In this experiment, the post-harvest ANOVA showed much higher values of deciduous tree cover in 0m treatment and in the 15m transect in the 10m treatment. This group of fast-growing shade-intolerant species, including red alder (*Alnus rubra* Bong), birch (*Betula papyrifera* Marsh) and cottonwood (*Populus balsamifera* L.), play a pioneer role in temperate forests (Darveau et al. 1998; Beach and Halpern 2001; Rood et al. 2003; Shirley 2004). Although the deciduous tree cover is very high, the species richness of this functional group is not, and

red alder is clearly the dominant species. By year eight, the red alder was the tallest component of the understory vegetation and was beginning to affect the light environment of the other understory species. Resulting differences in light environment along with chemical properties of the litter and soil may ultimately favor certain understory species and will likely result in further shifts in richness and cover (Pabst and Spies 1998).

Riparian trees are reliant on groundwater that originates from stream water during dry periods but are opportunistic and might take up water from local precipitation when available (Rood et al. 2003). While it has been shown that proximity to the stream affects the survival of cottonwood along streams of semi-arid regions, in this study, there were no differences in hardwood diversity or cover with proximity to the stream.

Shirley (2004) concluded in her study that seven years after cutting, the density of coniferous saplings increased in all forest strips and clearcuts and that this variable was influenced by soil conditions, disturbance history, and slope along stream reaches. Coniferous percent cover eight years after harvesting in this study was enhanced by light availability. The 10m buffer at 15m had the greatest increase in coniferous understory, reaching a percent cover of almost 35%. The dominant understory conifer, western hemlock is well known for its ability to establish in canopy gaps formed by windthrow (e.g. Sinton et al. 2000).

Eight years after harvesting, the shrub layer has developed strongly creating a thick layer on sites where solar radiation is greater. This is consistent with the results of Weber et al. (2003) who found that the forest edge has a more vigorous shrub layer than the interior

with an understory of salal (*Gaultheria shallon* Pursh), oval-leaf blueberry (*Vaccinium ovalifolium* Sm.) and salmonberry. Pabst and Spies (1998) found in a study conducted in coastal Oregon, that the distribution of shrub species is related to their tolerance to shade and saturated soils. It is clear that the effect of light on shrub richness is strong, as evidenced by the increase in richness on sites with greater canopy openness. Proximity to the stream is not affecting significantly the cover of shrubs. This result for shrubs is consistent with Macdonald et al. (2004) who concluded that there is little influence of proximity to streams on forest composition and successional development in moist environments. These results are also consistent with those found in Shirley (2004) in which species richness of shrubs in riparian strips in coastal British Columbia, decreases with increasing buffer width. The pre-harvest effect of treatment by distance on shrub richness is presumably to moisture and nutrient gradients. Light coming from the edge of the buffer and the intermixing of windthrow, disturbed and non-disturbed habitats leads to the presence of pioneer species such as red alder, salmonberry, sedges, bracken fern (*Pteridium aquilinum* (L.) Kuhn), and herbs such as aster (*Aster spp.*), and species more commonly associated with late-seral communities such as devil´s club (*Oplopanax horridus* (Sm.) Miq.), false azalea (*Menziesia ferruginea* Sm.) and cascara (*Rhamnus purshiana* (DC.) Cooper). In addition, salmonberry is the dominant shrub in all treatments and is likely to persist for a long time after the initial disturbance.

Salmonberry appears to be particularly well adapted to disturbance and edaphic conditions in Pacific Northwest forests. Pabst and Spies (1998, 2001) and Minore and Weatherly (1994) found that in riparian areas of Oregon, salmonberry was most abundant 10m away from the stream and that canopy openings creating by the death of ovestory

trees were filled by salmonberry stems. Salmonberry is able to invade openings, displace other shrub species and colonize valley floors and many lower slopes. This is perhaps due to the capacity of this species of rapidly spreading rhizomes and its early phenology which allows it to persist even under canopies of red alder. In contrast, salal tends to occur farther away from the stream on higher, drier microenvironments. Competition from salal does not seem to be as severe as that created by abundant salmonberry, so conifers tend to dominate the upper slopes where salal occurs (Pabst and Spies 1988; Minore and Weatherly 1994). However, competition is intense during seedling establishment (Mallik and Prescott 2001).

In contrast to the results for shrubs, herbaceous cover and richness increased significantly closer to the stream. This suggests that the limiting factor for herb establishment and growth is water availability and soil and air humidity. Other authors have found that herbaceous richness shows a strong positive relationship with water availability in terms of stream surface flow permanence and groundwater depth. Thus, they can be bioindicators of ground water decline. Species such as yellow-flowered sedge (*Carex anthoxanthea* J. Presl & C. Presl), is an herbaceous indicator species for wet soils (Vellend et al. 2000; Bagstad et al. 2005). Gutiérrez et al. (2000) observed that seasonal rains can increase abundance of annual plants in riparian zones. The complete removal of the overstory in wet-mesic habitats also promotes growth of many herbaceous species with rapid clonal expansion and large number of seeds (Fraterrigo et al. 2006).

Herbs are not the dominant functional group and their overall cover is very low. The mature (1868) stand had a similar herb cover as the control. The percent cover of herbs ($\approx 4\%$) in the old-growth stand suggests that environmental heterogeneity and

microhabitat preferences are important factors in maintaining the diversity of herbs in the understory of old-growth forests (Vellend et al. 2000). According to Pojar et al. (1991), the herb layer of the CWH biogeoclimatic zone is poorly developed, particularly in the dry maritime (dm) and very wet (vm) subzones. Herb species are usually confined to depressions and include bunchberry (*Cornus canadensis* L.), foamflower (*Tiarella trifoliata* L.) and skunk cabbage (*Lysichiton americanum* Hultén & H. St. John).

Fern richness and percent cover vary along an environmental gradient related to light levels and soil moisture. The 10m buffer 15m away from the stream contained the highest fern percent cover and richness. These results suggest that the 0m buffer and the 10m buffer 15 meters away from the stream exhibit similar growing conditions for ferns. The fern cover in the 30m buffer and control are not significantly different, in spite of their differences in light levels. This suggests that there are other environmental factors apart from light that might influence fern distribution and abundance such as soil moisture, soil nitrate concentration, topographic position and disturbance (Pabst and Spies 1998; Karst et al. 2005).

Minore and Weatherly (1994) also stated that riparian areas often differ on opposite sides of the same stream and also vary along the stream as it undercuts banks at some points and creates flood plains at others. In particular, the 15m transect within the 10m buffer lies just outside the buffer; thus, it is exposed to higher levels of sunlight and desiccation as is the case for the 0m buffer. This is translated into a warming up of air and water temperature in the 15m transect which ultimately has an effect on understory vegetation development. The transition from the forest interior to edge in the 10m buffer appears to create an ecotone which is more abrupt at the right side of the stream. Because of that,

species with more shade and moisture affinities are overlapping with those species with drier affinities, commonly found in open areas, and thus species richness is increased.

The old-growth forest and the mature (1868) stands display intermediate values for fern richness and cover which means that the condition offered by the 0m and 10m buffers is temporary and sooner or later both variables might reach a middle and almost stable point.

There are not discrete groups according to the Bonferroni test which can allow us to differentiate particular groups except for the 10m buffer. On the contrary, in the case of ferns, the results point in the direction of having a gradient pattern with a complex overlapping. It is important to point out that two out of the three fern species found in the 10m buffer are very common and distributed widely and that they account for almost all the percent cover: sword fern (*Polystichum munitum* (Kaulf.) C. Presl) and bracken fern (*Pteridium aquilinum* (L.) Kuhn). Bracken fern is found in open forests and is considered to be pioneer species. In general, bracken fern becomes more abundant in disturbed areas and basically after a fire event. This is due to its capacity of resprouting rather than germinating from spores. This species has long underground rhizomes that are resistant to fires and that store carbohydrates and also a large number of dormant buds. Additionally, it has been reported that where bracken fern is dense, other vegetation is often degraded or even disappear (Le Duc et al. 2003; Silva and Matos 2006). These characteristics explain the absence of this species in the control, the 1868 and old-growth stand.

However, the higher percent cover of sword fern in the 1868 stand at the 2m transect suggests the affinity of this species to relatively moist soils and to moderate disturbances.

It is worth pointing out that I found a few disturbed patches in the 1868 stand where sword fern was highly abundant.

None of the independent variables seemed affect moss richness and percent cover although there was a tendency to have greater abundance and diversity in the old growth stand. This lack of response suggests that mosses are apparently very sensitive to microenvironmental and microtopographic conditions rather than coarse scale variations associated with buffer treatments. Many bryophytes and lichens are dependent on old trees and old-growth forests (Qian et al. 1997). The importance of a microclimate with moist air as well as the substrate form (convex or concave) is determinant for bryophyte growth. Moist and nutrient-rich sites are species-rich habitats for bryophytes (Hylander et al. 2005; Nelson and Halpern 2005). The indifferent response of number of bryophyte species and cover to buffer widths has been reported in other studies carried out in boreal riparian sites in which mosses had a higher survival rate and higher establishment rate after logging (Hylander et al. 2002, 2005).

Generally, changes in plant species composition are characterized by an increasing dominance of fast-growing, shade-tolerant species reflected in an increase in the Shannon-Wiener index, which is based on the relative abundance of the species, and the reciprocal of Simpson index, which increases when diversity increases (Risser and Rice 1971; Magurran 1988). Results show that the understory richness, percent cover, Shannon-Wiener index and the reciprocal of Simpson index are different in every treatment and there is a strong effect of buffer width reflected as the light environment on the majority of the variables measured. The greater the dominance in the community, the greater the differences between richness and H´. In all treatments there is a medium

degree of dominance, however, the plant community in the old-growth forest as well as in the control is almost even. This result is interesting because it demonstrates that the community in a 70 year old forest is indeed moving toward a similar species distribution and dominance found in an old-growth forest.

3.4.3 Measures of overstory condition, composition and structure

The influence of forest edges on forest structure is widely recognized. In forests, a major response to edge creation is the damage to trees which leads to reduced canopy cover and greater abundance of snags and logs at edges (Harper et al. 2005). Edge-related tree mortality including windthrow has occurred in the 10m and 30m buffers and this is consistent with reports that edge effects may penetrate 10-30 meters further into the forest interior (e.g. Mesquita et al. 1999; López et al. 2006). Interestingly, the highest mortality in terms of stems per hectare is in the 70 year old control stand, due to continuing self-thinning. It is not surprising that the rate of blown down trees was particularly intense in the 10m buffer during the first years after harvesting, specifically the first year. Rowan et al. (2003) studied the effectiveness of stand edge treatments in reducing windthrow in coastal British Columbia. They found that most tree damage occurred during the first year after harvesting. This result is validated by other studies that showed that windthrow damage is greatest in the first few years following logging (Coates 1997). In coastal British Columbia, winter storms often cause windthrow (uprooting and stem breakage) along new stands exposed by clearcutting (Rowan et al. 2003). Wind damage in forest stands is affected by stand characteristics such as age, species composition, diameter and height distributions as well as by stand treatment history (i.e. percent of stand removed during cutting), site conditions and storm

characteristics (i.e. season, wind direction, gust wind speed) (Coates 1997). Windthrow seems to be a less important mortality force in the 30m buffer than it is in the 10m buffer. In the 30m buffer and control, dead standing and uprooted trees are frequent structural attributes and indicate a continuous recruitment of dead stems. Slender western hemlock and redcedar have higher mortality rates in the 30m buffer and control suggesting that natural self-thinning is ongoing. This finding is supported by Kobe and Coates (1997), who found that the more shade tolerant species (western red cedar and western hemlock) exhibit rapid decreases in the probability of mortality with increased radial growth. Simard et al. (2004) found that neighbor competition on conifers differ with stand age. Conifer mortality peaks in young stands (25-50 years old) which have reached full site occupancy but still have high stocking density.

An important finding of this study is that the number of stems per hectare and basal area per hectare of live trees in the 10m buffer are not different from the values found in the control and in the 30m buffer and that the frequency of trees tends to be greater as DBH increases. In contrast, the mature and old-growth stands have substantially more basal area and lower number of stems per hectare, which means low densities and bigger trees. This result was also found by Keeton et al. (2007) in which they concluded that old-growth riparian forest exhibit greater accumulations of aboveground tree biomass. Red cedar and western hemlock represent most of the basal area of older stands > 400 years old. It has been also demonstrated by long-term successional studies that low stand densities are more likely to produce large-diameter old-growth trees (Poage and Tappeiner 2002), and that direct competitive interaction between coniferous species decline with increasing stand age (Getzin et al. 2006)

3.5 Conclusions

The results of this experiment support the practice of riparian buffers along small streams for maintaining vegetation compositional and structural diversity, and potentially accelerating development of old-growth stand characteristics. The increased light associated with harvesting is the major factor influencing changes in cover and diversity. The 10m buffer offers a wide array of microenvironments for structural retention and understory establishment and growth and appears to accelerate gap formation more typical of old-growth forests. Proximity to the stream has an influence on some species, mainly herbs and mosses, which are important components of the temperate rain forest of coastal British Columbia, but appears to have little effect on shrubs and tree recruitment. The influence of stream proximity likely becomes more important in drier environments where soil moisture is less available or where streams flow through fluvial terraces.

4 SUCCESSIONAL TRAJECTORIES

4.1 Introduction

Ecological succession is a key concept in understanding ecological dynamics and it may be observed at a broad range of scales, from the microscopic to the continental (McCook 1994). The development of some community characteristics such as productivity, biomass, composition and abundance can be followed through succession (Whittaker 1975). Vegetation development proceeds along multiple pathways determined by initial conditions and subsequent shifts in disturbance regimes (Van Pelt et al. 2006).

The underlying mechanisms and forces driving succession are of utmost importance if we want to understand how natural communities are organized. Scientists and theoreticians have come up with several models and hypotheses which help in explaining succession (McCook 1994). Egler's (1954) "Initial floristic Composition" model offered an alternate view of how succession proceeds. In this view, succession is very heterogeneous, since the vegetation development of any site depends on which species get established first (Wilson et al. 1992; Vandermeer et al. 1995).

Egler (1954) also criticized Clements' hypothesis of succession in terms of what he chose to designate as "Relay floristics" model of succession (successive appearance and disappearance of groups of species) in which a given species invades the site at a certain stage of development, making the habitat's condition more suitable for subsequent species but unsuited for themselves. In that sense, successive dominants arrive later than the pioneers (Egler 1954; Wilson et al. 1992; McCook 1994; Vandermeer et al. 1995).

Other models and theories of succession take into account life-history traits (Huston and Smith 1987), resource supplies (Tilman 1985), and species interactions (Connell and Slayer 1987).

Since forest succession proceeds slowly in human terms, communities that initiated at different times are often studied in lieu of following an individual community over time. There are limitations of studying succession using this 'chronosequence' approach. As stated in Schoonmaker and Mckee (1988), in order to consider a group of stands of different ages as a true chronosequence, they should have similar characteristics in terms of climate, climatic histories and disturbance regimes. These stands should be on similar soils and sites and have similar species and spatial and age distributions. There have been few studies in British Columbia that focus on changes in plant diversity through succession, and these studies have typically used site-specific chronosequences (Brulisauer et al. 1996; Clark et al., 2003). As a result, site-specific diversity patterns following disturbance are not known in depth (Qian et al. 1997).

In this study, community-level dynamics in the initial years of secondary succession in different riparian buffer widths (treatments) was evaluated. Vegetation development was repeatedly measured over eight years following harvesting (referred to in text as the short-term approach). To provide a longer term successional context for this short-term response, conditions in the riparian buffers treatments and 70 year old controls were compared with stands that initiated in 1868 and with an old-growth stand using a chronosequence approach (referred to in text as the long-term approach).

The objectives of this experiment were to: 1) evaluate how successional trajectories vary following harvesting in response to buffer width and stream proximity; 2) determine how dominance of indicator groups and selected species (representative of seral stage) change with time; 3) compare vegetation species diversity, structural complexity and abundance in response to buffer width and stream proximity over time and 4) identify successional trends in species dominance.

The hypotheses tested were: *i*) buffer width will affect successional trajectories; *ii*) stream proximity will affect successional trajectories; *iii*) eight years of successional change will result in the shift to deciduous dominance (% cover) in the 0m and 10m buffer treatments; *iv*) changes in species dominance will be more rapid as light levels increase; *v*) in the early years after disturbance, the species richness will increase faster than structural complexity, later on, this will reverse and structural complexity will change faster than species; *vi*) although their abundance will vary, most species will be present in all successional stages.

4.2 Methods

4.2.1 Study area

This experiment was carried out in the Malcolm Knapp Research Forest. The details are given in Chapter 3.

4.2.2 Experimental design

The experimental layout, measurements and sampling intervals were the same as described in Chapter 3.

In order to explore successional trajectories using a short-term approach, plant functional groups or 'indicator groups' were defined using species that show a similar response to variation in environmental conditions or have a similar effect on ecosystem processes (Dorrepaal 2007). These indicators groups incorporate responses to certain perturbations (Skov 2000), and summarize ecological attributes, site characteristics as well as patterns of distribution and abundance (Liira et al. 2002; Keith et al. 2007).

Nine indicator groups (IG) were created and their total richness and total percent cover per measurement year were calculated. The percent cover of each indicator group was transformed using the arcsin function and then analyzed using an ANOVA. Responses to light availability and soil moisture were used as the main criteria for grouping species, under the logic that these are the most important limiting resources in forested ecosystems that affect the performance and competitive ability of species (Daubenmire 1968; Royo and Carson 2006). Therefore, aggregating IG in this way will enable us to identify patterns of responses to changes and to measure indirectly the quality of the sites

in terms of light and moisture and the change of these environmental factors along succession.

Species were assigned to these groups based on ecophysiological characteristics reported in the literature (Table A4-1) (Pojar and MacKinnon 1994). The indicator groups and the species comprising each group are as follows:

1. *Woody shrubs* (shrubs with woody stems) salal, Alaskan blueberry, oval-leaved blueberry, black blueberry, red huckleberry and false azalea.

2. *Light shrubs* (shade-intolerant species): salmonberry, thimbleberry, devil´s club.

3. *Early ferns* (early-seral fern species): bracken fern.

4. *Late ferns* (late-seral fern species): sword fern, spiny woody fern, deer fern.

5. *Dry shrubs* (low-moisture indicator species): salal, dull-oregon grape.

6. *Wet shrubs* (high-moisture indicator species): salmonberry, thimbleberry, devil´s club, stink currant.

7. *Mineral mosses* (indicators of mineral soils): red bryum moss, juniper haircap moss, common haircap moss, large hair moss, false polytrichum, dusky fork moss.

8. *Wet mosses* (high-moisture indicator species): fan moss, flat moss, coastal leafy moss, menzies´tree moss, clear moss.

9. *Feather mosses* (late-seral mosses): step moss, oregon beaked moss, electrified cat´s tail moss, cat-tail moss, lanky moss, tree moss.

For the chronosequence comparison, four stands were selected based on the disturbance history of the Malcolm Knapp Research Forest. Each stand was assigned to a seral stage

based on its age, structure and dominant developmental processes. The 0m buffer was selected as the 'early growth', the control as the 'second growth', the 1868 stand as the 'mature' and the Knapp Reserve old-growth as 'old-growth'. The information collected in 2006 was used to plot the percent cover of shrubs, ferns, herbs, mosses, deciduous and coniferous trees. In addition, several species were selected according to their dominance and ecological importance to distinguish seral stages (Table A4-1), and their percent cover was plotted. Since no statistical analysis was run for the chronosequence component, further interpretations are discussed just as 'trends' based on inspection of graphs.

4.2.3 Analytical approach: short-term study

The hypotheses were tested using a split-split plot for repeated measures experimental design with two factors (treatment and location of the plot) in the main plot, two factors (side and distance from the stream) in the first subplot and one more factor (year) in the second subplot. The number of levels within each factor was the same as in the experimental design explained in detail in Chapter 3. However, the year (Y) as a repeated measure was added as a new factor with 5 levels (1998, 2000, 2003, 2005 and 2006). This experimental design is also appropriate for ANOVA (Kuehl 1994).

The response variables were: total species richness, total cover (%), shrub, fern, moss, herb, deciduous and coniferous tree richness and cover, Shannon-Wiener (H'), the inverse of Simpson (1/D) and the richness and percent cover of each of the nine functional groups aggregated (Table A3-1). However, only the abundances were used for interpreting successional trends. Measurements for all variables for 1998 (pre-harvest) and for the ongoing years 2000, 2003, 2005 and 2006 (post-harvest) were used in the

ANOVA. Differences among means were tested using a Bonferroni multiple comparison test. The *p*-values obtained in each ANOVA were compared with the corrected split alpha when making conclusions (Kutner et al. 2005).

The analysis of variance table (Table 4.1) shows all the sources of variation taken into account in this experiment, the degrees of freedom of each factor or interaction, the mean square formulas and the corrected error terms used for testing the significance of a particular factor.

Table 4.1. General model for the ANOVA split-split plot experimental design.

Source	df formula	Df	MS	*F* ratio
T	(T-1)	3	MS(T)	MS(T)/MS(E1)
U	(U-1)	1	MS(U)	MS(U)/MS(E1)
T*U	(T-1)(U-1)	3	MS(TU)	MS(TU)/MS(E1)
Error 1	(T*U)(R-1)	16	MS(E1)	MS(E1)/MS(E2)
S	(S-1)	1	MS(S)	MS(S)/MS(E2)
D	(D-1)	1	MS(D)	MS(D)/MS(E2)
S*D	(S-1)(D-1)	1	MS(SD)	MS(SD)/MS(E2)
T*S	(T-1)(S-1)	3	MS(TS)	MS(TS)/MS(E2)
U*S	(U-1)(S-1)	1	MS(US)	MS(US)/MS(E2)
T*U*S	(T-1)(U-1)(S-1)	3	MS(TUS)	MS(TUS)/MS(E2)
T*S*D	(T-1)(S-1)(D-1)	3	MS(TSD)	MS(TSD)/MS(E2)
T*D	(T-1)(D-1)	3	MS(TD)	MS(TD)/MS(E2)
U*D	(U-1)(D-1)	1	MS(UD)	MS(UD)/MS(E2)
T*U*D	(T-1)(U-1)(D-1)	3	MS(TUD)	MS(TUD)/MS(E2)
U*S*D	(U-1)(S-1)(D-1)	1	MS(USD)	MS(USD)/MS(E2)
T*U*S*D	(T-1)(U-1)(S-1)(D- 1)	3	MS(TUSD)	MS(TUSD)/MS(E2)
Error 2	(S*R)(T*U)+(D*R)(T*U)+ (S*D*R) (T*U)	48	MS(E2)	-
Y	(Y-1)	4	MS(Y)	MS(Y)/MS(E3)
T*Y	(T-1)(Y-1)	12	MS(TY)	MS(TY)/MS(E3)
U*Y	(U-1)(Y-1)	4	MS(UY)	MS(UY)/MS(E3)
S*Y	(S-1)(Y-1)	4	MS(SY)	MS(SY)/MS(E3)
D*Y	(D-1)(Y-1)	4	MS(DY)	MS(DY)/MS(E3)
T*U*Y	(T-1)(U-1)(Y-1)	12	MS(TUY)	MS(TUY)/MS(E3)
T*S*Y	(T-1)(S-1)(Y-1)	12	MS(TSY)	MS(TSY)/MS(E3)
T*D*Y	(T-1)(D-1)(Y-1)	12	MS(TDY)	MS(TDY)/MS(E3)
U*S*Y	(U-1)(S-1)(Y-1)	4	MS(USY)	MS(USY)/MS(E3)
U*D*Y	(U-1)(D-1)(Y-1)	4	MS(UDY)	MS(UDY)/MS(E3)
S*D*Y	(S-1)(D-1)(Y-1)	4	MS(SDY)	MS(SDY)/MS(E3)
T*U*S*Y	(T-1)(U-1)(S-1)(Y-1)	12	MS(TUSY)	MS(TUSY)/MS(E3)
T*U*D*Y	(T-1)(U-1)(D-1)(Y-1)	12	MS(TUDY)	MS(TUDY)/MS(E3)
U*S*D*Y	(U-1)(S-1)(D-1)(Y-1)	4	MS(USDY)	MS(USDY)/MS(E3)
T*U*S*D*Y	(T-1)(U-1)(S-1)(D-1)(Y-1)	12	MS(TUSDY)	MS(TUSDY)/MS(E3)
Error3	(Y*R)(T*U*S*D)	256	MS(E3)	
Total	(R*T*U*D*S*Y-1)	479	-	-

Note: T, Treatment; U, location of the plot; S, side of the stream; D, distance to the stream; Y, Year ;R, replication=3.

4.3 Results

4.3.1 Short-term successional trends

The effect of the buffer width treatments was different among years for all the variables tested (Table A3-1). In 1998, prior to harvesting, none of the treatments were significantly different one from the other for any of these variables. The total species richness was affected differentially by the treatment and by the year ($p < 0.0001$). According to the Bonferroni multiple comparison test using a split $\alpha = 0.0004$, the effect of the treatment on the species richness in the 0m buffer was first detected in 2000, in 2003 for the 10m buffer, and in 2005 for the 30m buffer. The years were not significantly different in the control (Fig 4.1). The 0m buffer and 10m buffer did not show significant differences when comparing individual years.

While shrub richness behaved similarly to overall species richness, temporal changes were highly variable among the other functional groups. Herb richness responded earlier to the effect of buffer width, while in the case of mosses, the response varied from year to year (Fig 4.3) (Fig. A3-1c). Deciduous and coniferous richness increased with time; however, the richness was lower than other functional groups. For example, after two years, 1.2 deciduous species on average were found in the 0m buffer, 0.5 in the 10m buffer, and none in the 30m buffer and control. In the fifth year, the 0m buffer reached 1.79 species on average and in the eighth year deciduous richness peaked with 2.45 species. Only a few deciduous species dominated the plant community in all treatments (Fig 4.2, Fig.A3-1d).

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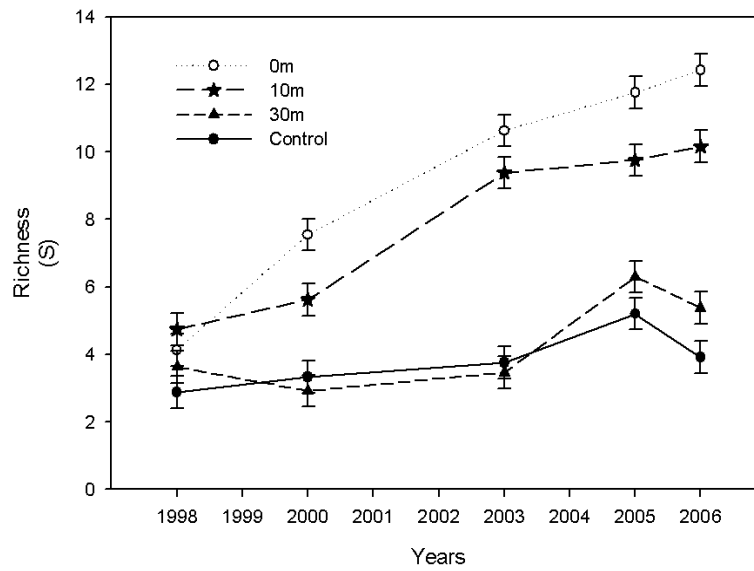
Figure 4.1. Total species richness over time by buffer treatment (mean ± SE).
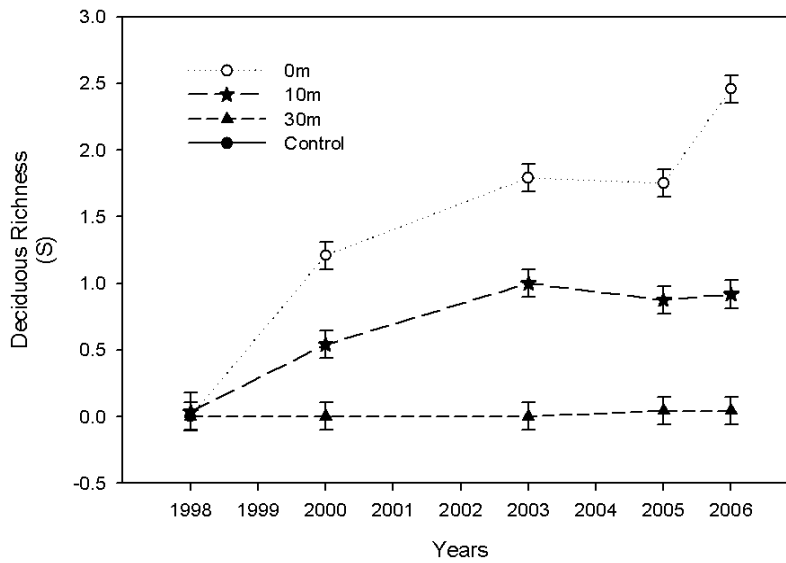
Figure 4.2. Total deciduous tree richness over time by buffer treatment (mean ± SE).
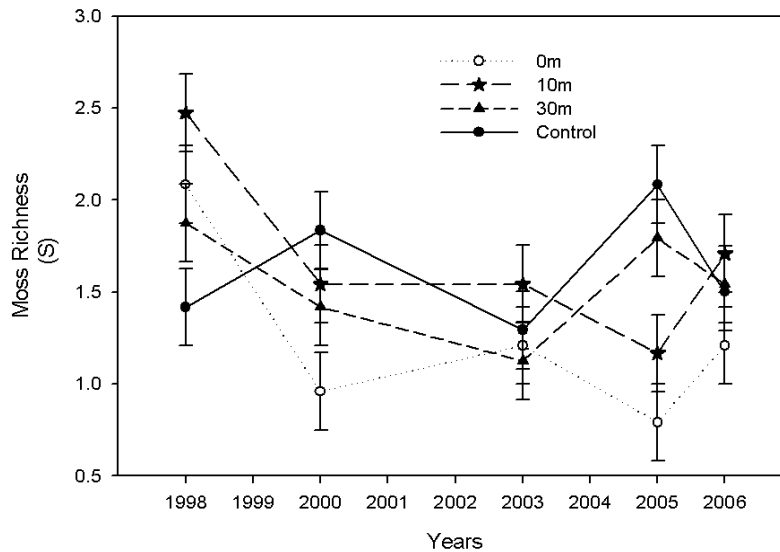
Figure 4.3. Total moss richness over time by buffer treatment (mean ± SE).

The total percent cover was also different among treatments and years (p< 0.0001). A pattern similar for the species richness variable was observed for the total percent cover. The total percent cover values varied by treatment and year. There was no change over time in the control. Not surprisingly, 2006 was the year with the highest values of percent cover for the 0m and 10m buffer (Fig.4.4). For the other treatments, the first year with a significant increase in percent cover values was 2000 in the 0m buffer, 2003 in the 10m buffer, and 2005 in the 30m buffer. Cover of understory deciduous and coniferous trees was initially zero in 1998 but increased sharply during the first three years after harvesting. By 2006, deciduous cover reached almost 70% compared to 32% of cover for the coniferous component. This pattern was also observed in the 10m buffer but with lower percent cover values (Fig 4.5, Fig. A3-2e).
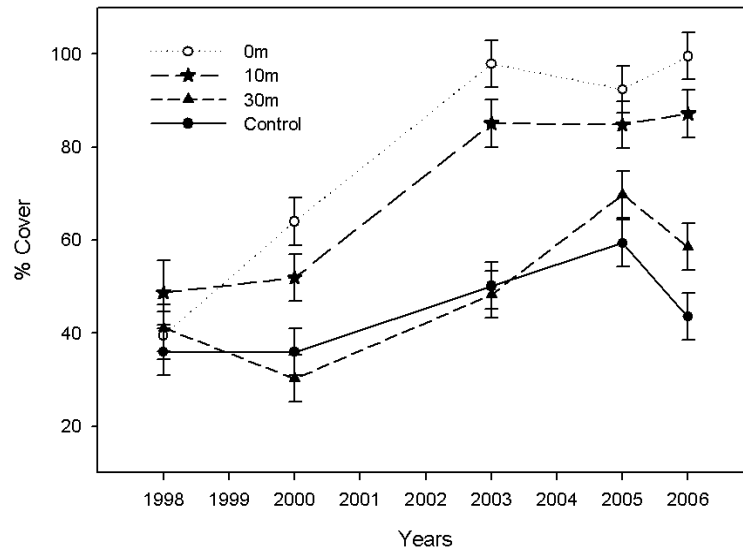
Figure 4.4. Total percent cover over time by buffer treatment (mean ± SE).

Species dominance represented by the Shannon-Wiener index and 1/D index, also changed significantly among treatments and years (Fig. 4.6, Fig. A3-3). The 0m and 10m buffers experienced major changes in dominance among years compared to the 30m buffer and control. According to a Bonferroni multiple comparison test using a split $\alpha=0.0004$, in 1998 the dominance in each treatment was significantly different from each other, however, by 2000, 2003, 2005 and 2006, the plant communities shared the same condition in terms of species abundance and dominance The 30m buffer and control behaved in a similar way in each year after harvesting and showed no changes until 2005, when significant changes were detected in both treatments (Table A3-1, Fig. 4.6, Fig. A3-3).
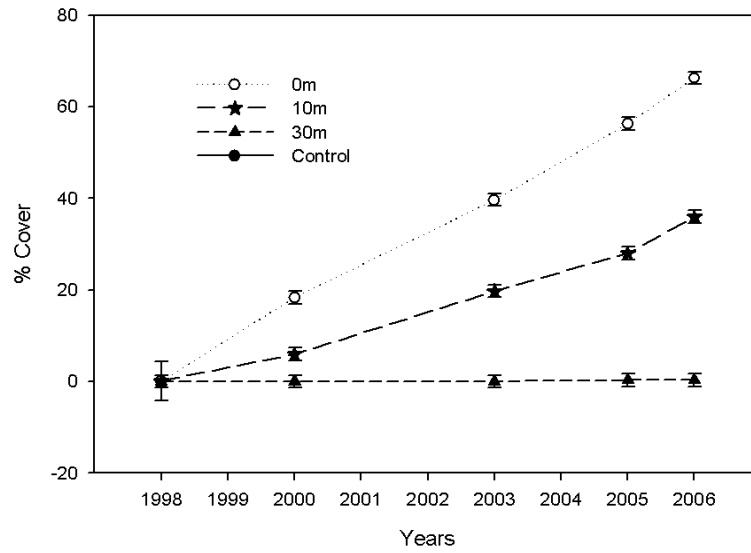
Figure 4.5. Deciduous tree percent cover over time by buffer treatment (mean ± SE).
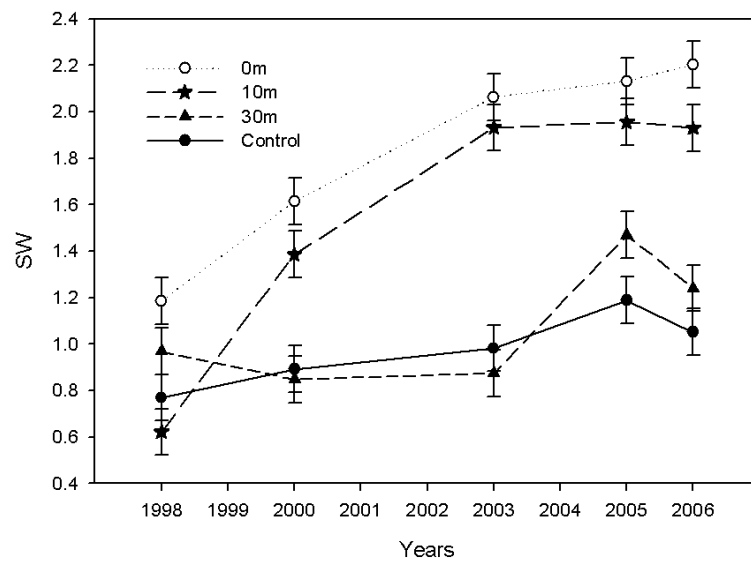
Figure 4.6. Shannon-Wiener diversity index over time by buffer treatment (mean ± SE).

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According to a Bonferroni multiple comparison test using a split α=0.0004, none of the treatment means for indicator species groups were different in the 1998 pre-treatment year. Treatment and year produced significant effects on the total richness of all the indicator groups, except again for mineral soil preferring mosses, wet mosses, dry shrubs and woody shrubs (Table A3-1). Temporal responses to the effect of buffer width during the course of initial succession varied among indicator groups. As expected, the mean percent cover of shade-intolerant shrub species increased dramatically in the 0m buffer during the first two years after harvesting and kept increasing until it reached its peak in 2003. The percent cover of shade-intolerant shrubs increased in the 0m buffer and 10m buffer treatments between 2000 and 2003. For the 30m buffer and control there was no significant change in cover (Fig. 4.7).
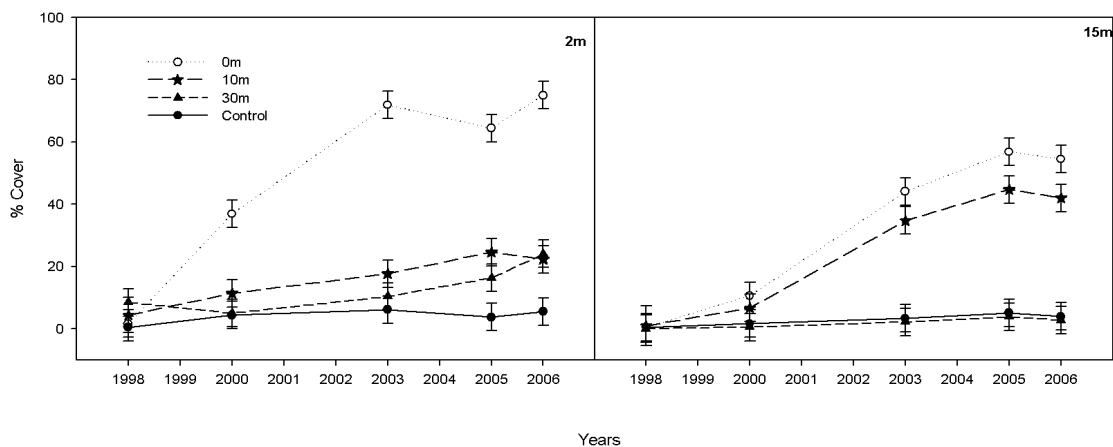
Figure 4.7. Percent cover of shade-intolerant shrubs (mean ± SE) over time by buffer treatment and distance from the stream.

There was no effect at all in the case of the percent cover of wet mosses (Table A3-1). The percent cover of woody shrubs displayed a delayed significant increase (2003-2005), whereas the wet shrubs and early-seral ferns responded much earlier (2000-2003) (Figs.

A3-6,8). The treatment and distance interaction had also a significant effect on total species richness, deciduous and shrub richness as well on the percent cover, shrub, coniferous and deciduous cover. The percent cover of some indicator groups such as wet shrubs, early ferns and shade-intolerant shrubs were also affected by the interaction between treatment and distance (Table A3-1, Fig. 4.7, Figs. A3-6, 7).
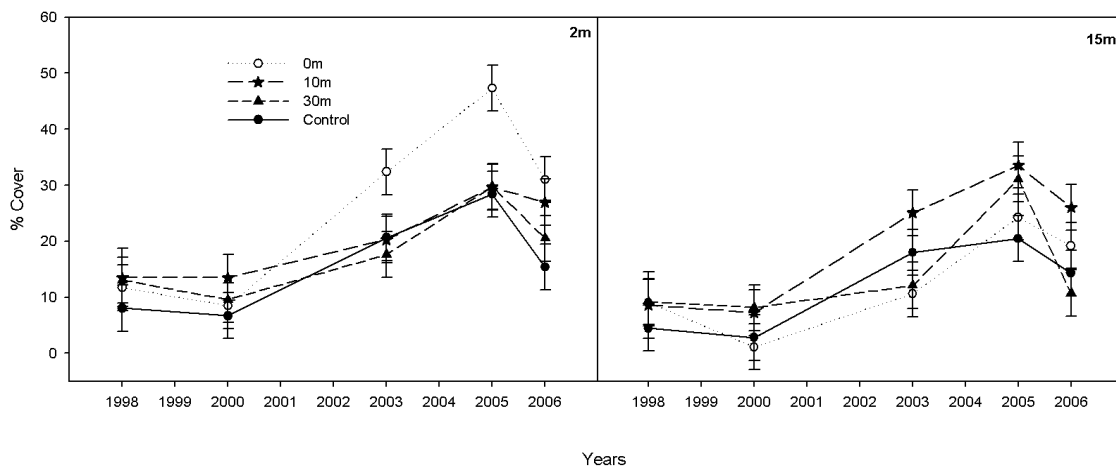
Figure 4.8. Percent cover of late ferns (mean ± SE) over time by buffer treatment and distance from the stream.
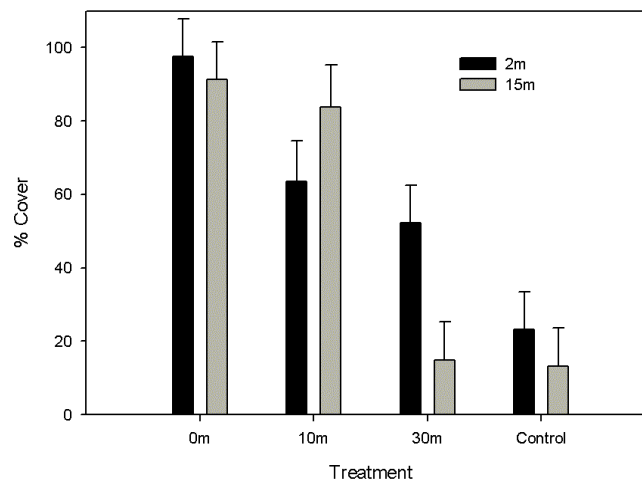
Figure 4.9. Percent cover of wet shrubs (mean ± SE) by buffer treatment and distance from the stream.

4.3.2 Chronosequence approach

As seen in Figure 4.10 to 4.12, the early growth forest showed higher percent cover of pioneer species, mainly shrubs (~ 80%) and deciduous trees (~ 60%). Dominant species such as salmonberry and bracken fern dominated the understory layer. In general, ferns, shrubs, herbs, mosses, deciduous and coniferous trees in the understory were more abundant in this seral stage than in the second-growth forest. The overstory was dominated by hardwood species such as red alder, bitter cherry and black cottonwood as well as young conifers, mainly western hemlock and redcedar. Salal, red huckleberry and hardhack had higher absolute abundance but represented a lower percentage of all species in the early growth seral stage (Fig 4.13).
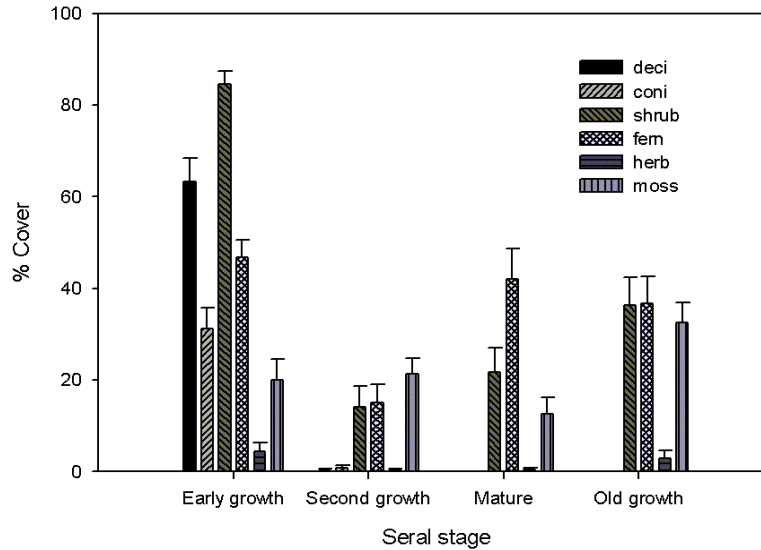
Figure 4.10. Percent cover % (mean ± SE) of functional groups at the Malcolm Knapp Research Forest. The early growth forest stage corresponds to the 0m buffer treatment in 2006, the second growth to the control in 2006, the mature to the 1868 stand and the old growth to itself.

The second-growth forest (70 year-old) at the Malcolm Knapp Research Forest had a

lower abundance of pioneer species, although they were still present. The deciduous

component no longer dominated the upper layer. This seral stage was characterized by

the presence of shrubs such as salal, red huckleberry and vine maple. However, the latter

species did not reach the same abundance as in the mature or old-growth forest

(Fig.4.13). Ferns were still an important component of the understory in terms of

abundance, but just one species (sword fern) dominated the ground (Fig 4.12).
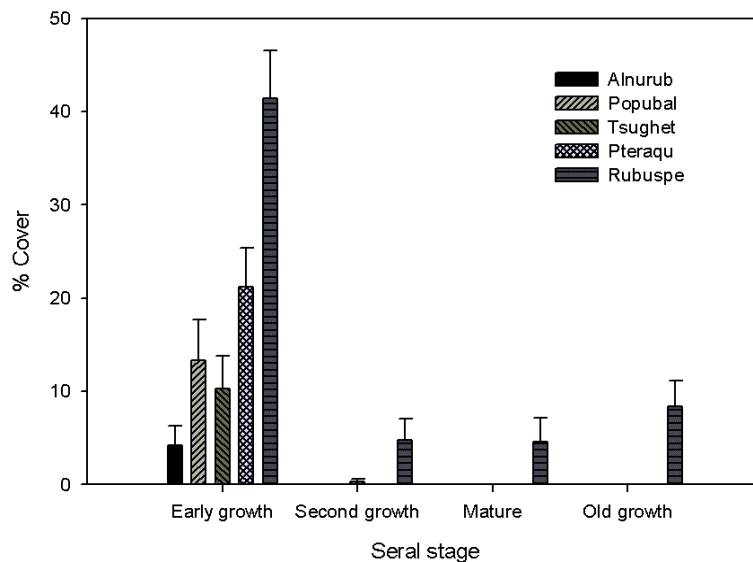
Figure 4.11. Percent cover % (mean $\pm$ SE) of selected species occurring at the Malcolm
Knapp Research Forest. The early growth forest stage corresponds to the 0m buffer
treatment in 2006, the second growth to the control in 2006, the mature to the 1868 stand
and the old growth to itself. The species code is as follows: red alder (Alnurub), black
cottonwood (Popubal), western hemlock (Tsughet), bracken fern (Pteraqu) and
salmonberry (Rubuspe).
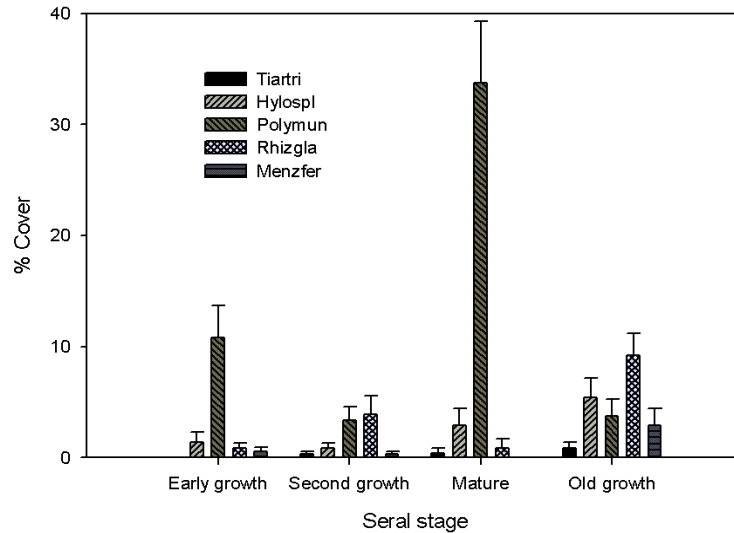
Figure 4.12. Percent cover % (mean ± SE) of selected species occurring at the Malcolm Knapp Research Forest. The early growth forest stage corresponds to the 0m buffer treatment in 2006, the second growth to the control in 2006, the mature to the 1868 stand and the old growth to itself. The species code is as follows: foamflower (Tiartri), step moss (Hylospl), sword fern (Polymun), fan moss (Rhizgla) and false azalea (Menzfer).

Mosses included oregon beaked moss and flat moss. Slower growing, shade-tolerant shrubs such as devil´s club and false azalea first appeared in this seral stage (Fig. 4.13). The overstory was dominated by medium-sized western hemlock, redcedar and Douglas-fir trees and as reported in Chapter 3, was still actively self-thinning.

The mature forest in the Malcolm Knapp Research Forest was characterized by a mostly closed conifer overstory and abundant cover of shade-tolerant sword fern while the pioneer species bracken fern was no longer present. Step moss (*Hylocomium splendens* (Hedw.) Schimp.) became more abundant (Fig 4.12).
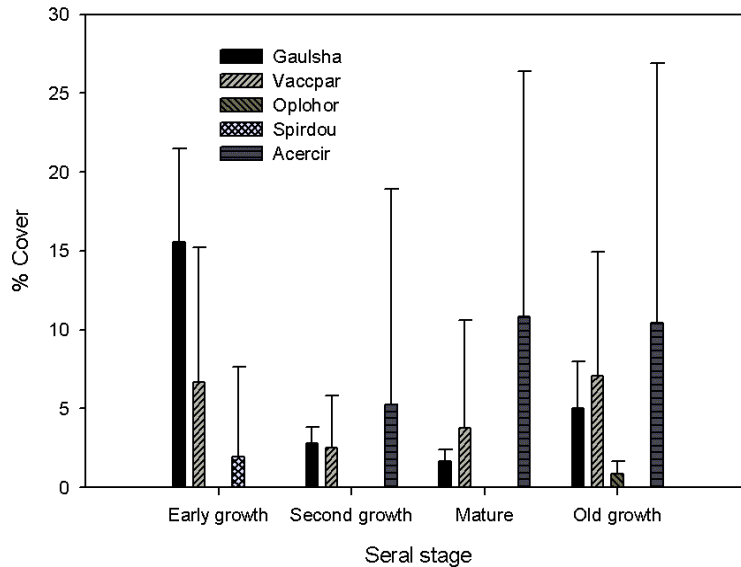
Figure 4.13 Percent cover % (mean $\pm$ SE) of selected species occurring at the Malcolm Knapp Research Forest. The early growth forest stage corresponds to the 0m buffer treatment in 2006, the second growth to the control in 2006, the mature to the 1868 stand and the old growth to itself. The species code is as follows: salal (Gaulsha), red huckleberry (Vaccpar), devil´s club (Oplohor), hardhack (Spirdou) and vine maple (Acercir).

Interestingly, the old-growth forest contained an array of species present at the pioneer stage including salmonberry and salal, along with sword fern, step moss and false azalea. Abundance of vine maple was also much higher than in other stages. Devil´s club was distributed only closer to the stream on humus. Deciduous trees were absent and mosses were abundant on decayed logs, where coniferous seedlings were also establishing in a clumpy fashion (although the latter were not detected in the point samples). In the upper forest layer, was a very tall, gappy overstory of large diameter, old redcedar and Douglas-fir trees with deep crowns. Clumps of hemlock of various ages, were also present and formed a closed sub-canopy in places.

4.4 Discussion

4.4.1 Short-term successional trends

The pre-harvest results indicate that the abundance and dominance of species among stands were similar and that the post-harvest changes are due to the effect of buffer width, stream proximity and time working together. Comparing the change in number of species with the change in percent cover in the early post-disturbance years provides useful insights into reproduction strategies and competition of the species and functional groups present in the ecosystem. The total richness increases faster than the percent cover during the first two years of succession in the 0m buffer. However, after this period there is a shift in this pattern and the percent cover increases abruptly until the rate of change reaches a stable point at the end of the fifth year (2003). This shift in the rate of change between richness and percent cover is partly due to the presence of an important shrub seed bank, herb bulbs and fern rhizomes that survive harvesting and rapidly respond to post-harvest conditions. In this sense, total richness will be affected by the pre-harvest species composition and by the main migration processes (Brunet and Von Oheimb 1998) and dispersal strategies (anemochorous and ectozoochorus modes) (Bonet and Pausas 2004). Species that quickly colonize a site may have a competitive advantage. For example, litter production by the diverse and vigorous shrub complex that established in the 0m buffer early after harvesting limited the establishment of seedlings and decreased water uptake. Furthermore, this dense understory canopy can suppress regeneration through resource competition (Royo and Carson 2006).

In the 10m buffer closer to the stream, the richness/cover change is more gradual. However, for the 15m transect the rate of change is similar to that in the 0m buffer. In this buffer treatment, richness increased in the first two years as in the 0m buffer, but percent cover began changing quickly after the second year reaching a peak in the fifth year when all the space was occupied and the resources became limited. The rate of change in the 30m buffer and control was neither as perceptible nor as directional as in the 0m and 10m buffer.

Several aspects of life-form seem to have an important bearing on the competitive abilities of plants (Daubenmire 1968). In general, shrubs, herbs, ferns and deciduous trees display quicker responses to the creation of gap openings where light is more available (Dyrness 1973; Schoonmaker and McKee 1988; Finegan 1996; Beach and Halpern 2001). The result of this is the formation of a dense understory layer that reduces the establishment of shade-intolerant tree species (Royo and Carson 2006). On the other hand, canopies of single aged secondary forests that are 5 to 18 years old are dominated by a small number of shade-intolerant pioneer species, and therefore low diversity values are found (Peña-Claros 2003).

The results show the coexistence of two or more functional groups during succession. Over time, the relative dominance of functional groups changes. As well, the functional groups and selected indicator groups show differential responses to buffer width and successional time. Other studies support this idea (Rankin and Tramer 2002; Peña-Claros 2003; Bonet and Pausas 2004). As expected, shrubs dominated the understory layer in all

treatments and contributed almost exclusively to the increase in the Shannon-Wiener and the inverse of Simpson indexes. Peña-Claros (2003) found a similar result in his study assessing changes in forest structure and composition during secondary succession. The percent cover of shrubs started increasing just after two years of harvesting, reaching almost 80% by 2003 in the 0m buffer. This means that shrubs are able to colonize successfully new sites due to their capacity of forming a persistent seed bank that responds immediately after disturbances (Decocq et al. 2004), their higher photosynthetic capacities, and compared to trees, their lower investment of resources in stems and branches (Finegan 1996). The species reaching peak cover early in succession are also present beneath the closed canopy (Rankin and Tramer 2002). This could explain in part why shrubs are the dominant functional group in all treatments.

The pattern of change for herbs was different from that for shrubs. Herbs dominated the 0m buffer immediately after harvesting, regenerating from buried seeds, bulbs or rhizomes (Van Cleve et al. 1996). They reached peak cover in the 0m buffer by 2000 and 2003. However, they decreased their cover substantially by 2005. In the 10m, 30m buffer and control, herbs are almost absent or scarce. Schoonmaker and McKee (1988) studying species composition and diversity during secondary succession of coniferous forests in Oregon also found a similar pattern in herb´s abundance along succession. Herbs are indicators of moist environments, therefore their greater abundance correlated negatively with tree density due to a response to lower light levels (Lindh 2005) and closer to the stream was expected (Pabst and Spies 1998). However, the perennial habit of shrubs

gives them an advantage over herbs of equal height in that the former have only to regenerate the leafy parts of their shoot systems each year (Daubenmire 1968).

Ferns and deciduous trees also experienced important changes in their cover along secondary succession. Ferns behaved in a similar way as shrubs suggesting similar responses and adaptive strategies for both functional groups. The deciduous cover increases faster than the richness suggesting the dominance of just a few species. Regeneration of deciduous trees is associated with the establishment of *Populus balsamifera*, *Betula papyrifera* and *Prunus emarginata* in the 0m and 10m buffers. The first two species have the capacity to sprout from buds near the root collar (Greene et al. 1999) and once established they can reproduce vegetatively at a great rate occupying the site, along with shrubs, herbs and ferns at different heights. Deciduous trees canopies allow more light to penetrate in early spring so understory growth is enhanced (Pabst and Spies 1998). However, it is interesting that once deciduous trees are well-established and the cover has reached around 40%, herb regeneration is suppressed, probably due to below- and above-ground competition.

After eight years of succession, the deciduous component is more important in terms of abundance than the coniferous one. By 2003, the deciduous component accounted for 40% compared to 11% for coniferous; by 2006, the difference in dominance was considerably larger (70% *versus* 32%). In this sense, it is expected that deciduous trees will dominate the overstory canopy for some years to come, but will eventually be replaced by the longer-lived conifers. For instance, cottonwood is associated with stands < 50 years old (Kobe and Coates 1997), paper birch with 30 or 50- year -old stands (Van

Cleve et al. 1996), and red alder tends to dominate mixed stands for the first 40 years (Schainsky and Radosevich 1992).

Although conifer regeneration began early in the 0m buffer and 10m buffer, it is much later in succession that shade-tolerant species such as western hemlock and red cedar dominate. By the time conifers establish, soils are rich enough to let conifers grow at rapid rates. Van Pelt et al. (2006) studied riparian forest stand development in Queets River on the western Olympic Peninsula in Washington State. They found that conifer seedlings are at a competitive disadvantage in the new conditions left by fluvial disturbances. However, their shade-tolerance allows them to persist in young, deciduous stands of *Salix sp.* and *Alnus rubra*. In the same context, Mallik and Prescott (2001) demonstrated in their study the effects of salal on western hemlock and red cedar, the negative influence of this shrub species on conifer growth through root competition and suggested a combination of fertilization and vegetation control to alleviate the harmful effects of this interaction.

The pattern of rapid change from herb to shrub-fern-deciduous dominance and finally conifer dominance after harvesting was expected. Schoonmaker and McKee (1988) found a similar trend of change reaching the conifer stage after 20-30 years. As far as the indicator groups are concerned, it is interesting that woody shrubs appeared later in succession. Bonet and Pausas (2004) attributed this to a higher competition of woody species seedlings in mesic habitats where the herbaceous layer is thicker than in drier habitats. Dry shrubs dominate the 0m buffer further from the stream whereas wet shrubs

dominate closer to the stream in the same treatment. Shade-intolerant shrubs (light shrubs) increase their cover faster in the open areas. It is important to recognize with this, the high variability of environments offered by the 0m buffer, particularly in mesic habitats where water is more or less available all the year. Other indicator groups such as feather mosses and wet mosses behave in a complex way, suggesting that the most important environmental influences on bryophyte community succession is the type and quality of the substrate and the microclimate (Rambo and Muir 1998; Hylander et al. 2005) and stand age (Boudreault et al. 2000).

Study results indicate that species composition is very dynamic during the first six years after harvesting. Given the full occupancy of the 0m treatment after eight years no further dramatic changes in the species composition are expected, in the absence of substantial disturbance events. This view, however, contrasts with the observation by Schoonmaker and McKee (1988) that species richness changed dramatically during the first 30 years of succession in a coniferous forest in the western Cascade Mountains of Oregon.

4.4.2 Chronosequence successional trends

I found that both pioneer and shade-tolerant species were present in the early-growth seral stage, suggesting that the initial floristics model of succession is more appropriate than the relay floristics model in this ecosystem (Egler 1954; Wilson et al. 1992; Vandermeer et al. 1995). The very low abundance of pioneer species in pre-harvest stands indicates that these species are either able to persist in the understory through potentially very long periods without stand-replacing disturbance (e.g. salmonberry), or rapidly colonize from external populations (e.g. red alder). Klinka et al. (1985) studied vegetation relationships among seral ecosystems in southwestern British Columbia. They concluded that after harvesting, there is an increase in heat and a decrease in soil acidity which promote rapid decomposition of surface organic materials and the release of nutrients, thus encouraging the development of plant communities characteristic of initial seral stages. Even if it is short-lived, this early seral community is important to long-term ecosystem health. For example, it has been shown that alder contributes major quantities of biomass and N during the 65-80 years of vegetation (O´Keefe and Naiman 2006). It has been demonstrated that litter quality changes across chronosequences (O´Keefe and Naiman 2006). Royo and Carson (2006) proposed a conceptual model through which alterations in the dynamics of the overstory, understory, or both generate increases in a select few understory plant species. With increasing age, thicker and more compacted acidic forest floors (humus) develop. These favor the establishment of *Menziesia ferruginea*, *Rhytidiadelphus loreus*, *Vaccinium parvifolium* and *Plagiothecium undulatum* (Klinka et al.1985). In contrast to this view however, there were several species that had a u-shaped trend in abundance over time. For example, red huckleberry (*Vaccinium*

parviflorum) is a slow growing species and is more associated with old-growth stands However, its density is greater in young stands (Kerns et al. 2004).

Dominance of the species differs between secondary-growth and old-growth forests. The 0m buffer, 10m buffer and old-growth stands possess high environmental heterogeneity as a result of overstory mortality which is translated into a higher diversity. It offers a great array of microhabitats: logs, boulders and gravel bars in which species with different requirements of light, moisture and nutrient can get established and spread successfully through time. Stream proximity also enhances the abundance of the species, in particular of those with special water requirements such as step moss.

The presence of an overstory, often with several layers of shade-tolerant tree species, also creates a buffered environment which experiences less variation in micrometeorological variables such as light level, temperature, and air moisture when compared with the extremes encountered in an open area (Swanson 2005).

4.5 Conclusions

In this study, species dominance increases with increasing light levels. The 0m buffer and 10m buffer at the 15m transect have a rapid species turnover during the first years of succession. Buffer width affects the richness and cover of functional groups over time, however the pattern of change is more evident for shrubs, ferns and deciduous trees. Narrower buffers tend to accelerate succession by increasing light and nutrient availability and promoting competition. In this study, stream proximity is a secondary factor in regulating the abundance and distribution of species, however, higher moisture levels are often related to higher diversity and greater structural complexity.

Different ecological processes such as competition, facilitation, inhibition take place in a different magnitude in each seral stage. These forces lead succession through a predictable series of seral stages which can be described both structurally and floristically. In this experiment, the sequence followed by the vegetal community after harvesting is as follows: early in succession shrubs, herbs and a few ferns regenerate rapidly and successfully. However, competition for available resources is intense and shrubs quickly dominate over herbs, displacing them by the fifth year. Deciduous trees become dominant in this same period and grow rapidly, expanding their canopies and suppressing but not inhibiting the growth of the understory. A few understory species can persist even under the canopy of deciduous trees. Conifer regeneration has already started and western hemlock and redcedar, due to their shade-tolerance can persist under the hardwood canopy for a long time, in spite of the strong competition imposed by them. This stage will persist for some decades until the deciduous component begins to get

weaker due to age or sickness. This fact will be followed by a rapid increment of conifer cover and high mortality rates due to thinning. It will take more than 200 years for the riparian forests to achieve old-growth characteristics but the increased windthrow mortality associated deposition of CWD and large gap creation in the 10m buffer appears to accelerate the development of old-growth like stand structure in a narrow belt along the stream.

5 SYNTHESIS, CONCLUSIONS AND RECOMMENDATIONS

This research investigates the effect of buffer width and stream proximity on the development of plant communities along small perennial streams in a cool temperate forest ecosystem. The design of the riparian buffers experiment enabled us to account for the spatial and temporal variability of the plant communities within riparian systems..

Important conclusions for forest management can be made as a result of this experiment. Firstly, buffer width appears to be the main factor affecting the composition and structure of both the understory and overstory. In this sense, the buffers enable timber production while maintaining overstory characteristics and the development of the understory, enhancing ecological processes such as nutrient cycling, photosynthesis and below- and above- ground competition, thus giving complexity to the vegetal community. In particular, the 10m buffer maintains high levels of diversity and a more structured forest composed of multiple layers, due to the edge effect created by clearcutting and the rapid development of 'gappyness' which results from windthrow mortality. Understanding the vegetation dynamics in this system will help other researchers within the integrated buffers experiment to interpret responses at various trophic levels. By placing the results from the buffers experiments in the context of longer term succession using a chronosequence approach, it has been possible to evaluate short- and long-term successional trajectories.

The response of the understory vegetation communities was primarily driven by changing light-levels associated with loss of overstory. Proximity to the stream had a very small

influence on species composition and successional trajectories. This is likely because the streams were narrow and primarily hillslope constrained, without significant areas of fluvial terraces. Furthermore, water availability is not the primary limiting resource in mesic habitats. However, some functional groups were more sensitive to stream proximity, particularly in the years immediately following disturbance. This included herbs and mosses, consistent with the ecophysiological properties of these species.

In the control and pre-harvest condition, the coniferous overstory was continuous across the riparian zone and above the streams. In comparing the trends in richness and percent cover over time, it is clear that plant diversity is constrained by competition for growing space on these sites, and species such as salmonberry and red alder are particularly effective at colonizing harvested sites. These two species also represent two different strategies of reproduction, the former expanding rapidly from persistent root and shoot bank along with buried seed, and the latter from seed dispersed from external sources. The sequence of vegetation communities that established in the 0m buffer treatments was consistent with the 'Initial Floristic Composition' model of succession, although shrubs were the dominant component even in the early post-harvest years. While their abundance varies through time, many species are shared by this early seral stage, young-mature (thrifty), mature and old-growth stands.

A central objective of the riparian buffers experiment was to evaluate the effectiveness of buffers at maintaining the functional integrity of small streams. Clearly the 0m buffer resulted in the complete loss of overstory attributes and major changes in understory. In

contrast, both the 30m buffer and 10m buffer maintained most overstory attributes present in the original 70 year-old stand, with moderated understory changes. In the 10m buffer, development of some 'old-growth' attributes, such as understory diversity, dominance, recruitment of coarse woody debris (CWD) and gap formation were accelerated by edge exposure and partial windthrow. Windthrow levels in the transects of the 10m buffer were higher than in the 30m buffer, but after eight years only 15% of stems were damaged. Direct windthrow impacts to the stream channels were not observed. However, in areas with greater windthrow hazard, wider buffers would be more appropriate.

As a consequence of the windthrow and the light coming from the edge, the 10m buffer, has stand structural components such as standing dead trees, coarse woody debris and understory characteristics most like the old-growth stand. However, the conifer overstory has not yet reached the condition of the 'old-growth' stand in terms of tree size, species importance values, density and 'gappyness'. In the long-run, the 30m buffer will also develop these attributes but because small streams are close together in this portion of the forest, there would be little area between buffers to sustain timber harvesting. The 10m buffer balances timber production and conservation of riparian ecological processes in this forest.

One of the most important conclusions of this study is that in order to maintain old-growth characteristics in managed stands, we need to be clear about what attributes are desirable to keep and how long it takes to reach them during the course of succession. In

this sense, conditions in the 30m buffer and control are revealing. At 70 years of age and after eight years of stand development and succession, these stands continue to display low values of diversity and structural complexity, and even the 1868 stand has only some of the properties of the old-growth stand. Increasing exposure, as in the case of the 10m buffer treatment, or opening up stands by thinning would accelerate the development of some aspects of old-growth structure. More importantly, large trees and CWD should be retained during harvest as legacies to carry forward into younger stands.

While the effect of stream proximity was limited to herbs and mosses, these are important components of overall biodiversity. For lower gradient streams with more extensive fluvial terraces, this component of the community would become even more significant. Forest managers should therefore take into account the differential response of functional groups to buffer width and proximity to the stream when it comes to timber planning and other prescriptions.

The limitations of this study, include the effects of year-by-year weather variability and its effect on percent cover, temporal variability inherent to the species, for instance, inter-annual variations in seed production, and slight variation in the timing of annual measurements and their effect on fullest development of percent cover. In addition, since the measurements were taken by different people each year, there may be some inconsistencies when it comes to species identification, height recording, the position of the pin on the ground and the criteria for discerning when a species is actually touching the pin or not. In terms of the design of the study, the nesting of sampling plots within

treatment replicates resulted in a loss of degrees of freedom; however, that is the nature of a large scale ecosystem study. More importantly, the fact that the 15m transect in the 10m buffer lies outside the buffer made it difficult to distinguish buffer and light effects from proximity to the stream effects for this particular treatment. However, by maintaining the same proximity distances in all treatments enabled direct comparisons of this effect amongst the other treatment levels.

This study provides ample scope for the development of new projects related to riparian areas along small streams and the formulation of new questions and hypothesis. One area that could be explored is the seedling-substrate preferences and seedling recruitment differences among different buffer widths and into the edge zone created by the treatments. It would be interesting to examine which dispersal and re-establishment mode is promoted by which buffer width and by proximity to the stream. It is also important to further investigate how these complexes of species interact (facilitation, inhibition, competition) and to explore possible mycorrhizal associations and below- and above-ground competition among different buffer widths.

Finally, long-term successional studies are required. This study demonstrates the value and importance of long-term monitoring, so continuing to monitor the plots is worthwhile. The integration of vegetation results from this project with the results from the other components of this integrated project is necessary for creating a more realistic picture of the effect of buffer width on overall riparian and stream processes.

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APPENDICES

Appendix 1. Measures of vegetation species diversity

Species richness (S)

This is simply the total number of species in a community (or sample) based on presence, rather than relative abundance.

Shannon-Wiener index (H´)

$$H' = -\sum_{i=1}^{S} pi \ln pi$$

where *pi* is the frequency of species in a community. H' is the average information per individual. For a given number of species, S, the index reaches its maximum value, ln S, when all species are equally frequent in the community.

Exp H' may be used as an alternative to H' and is equivalent to the number of equally common species required to produce the value of H' given by the sample.

Shannon Evenness

This is used to calculate

$$E = H'/H \max = H'/\ln S$$

E is constrained between 0 and 1 with 1 representing a situation in which all species are equally abundant or in other words, that it displays a low species dominance. The higher the value of E the greater the diversity of the community is.

Simpson's heterogeneity index

$$\lambda = \sum_{i=1}^{S} pi^{2}$$

where *pi* is the frequency of species in a community. λ is the probability that two randomly chosen individuals from a given community are the same species.

In this sense, 1-λ would be the probability that two randomly chosen individuals from a given community are different species.

Additionally, the reciprocal of Simpson´s index $1/\lambda$ is often employed to measure species diversity and for a given number of species, S, in a community it has a maximum value equal to S when all species are equally frequent.

Shannon´s index extended to diameter, height and species

$$H'_{dhs} = -\sum_{i=1}^{S} pi \ln pi$$

where pi is the proportion of basal area per hectare in each DBH-height-species combination.
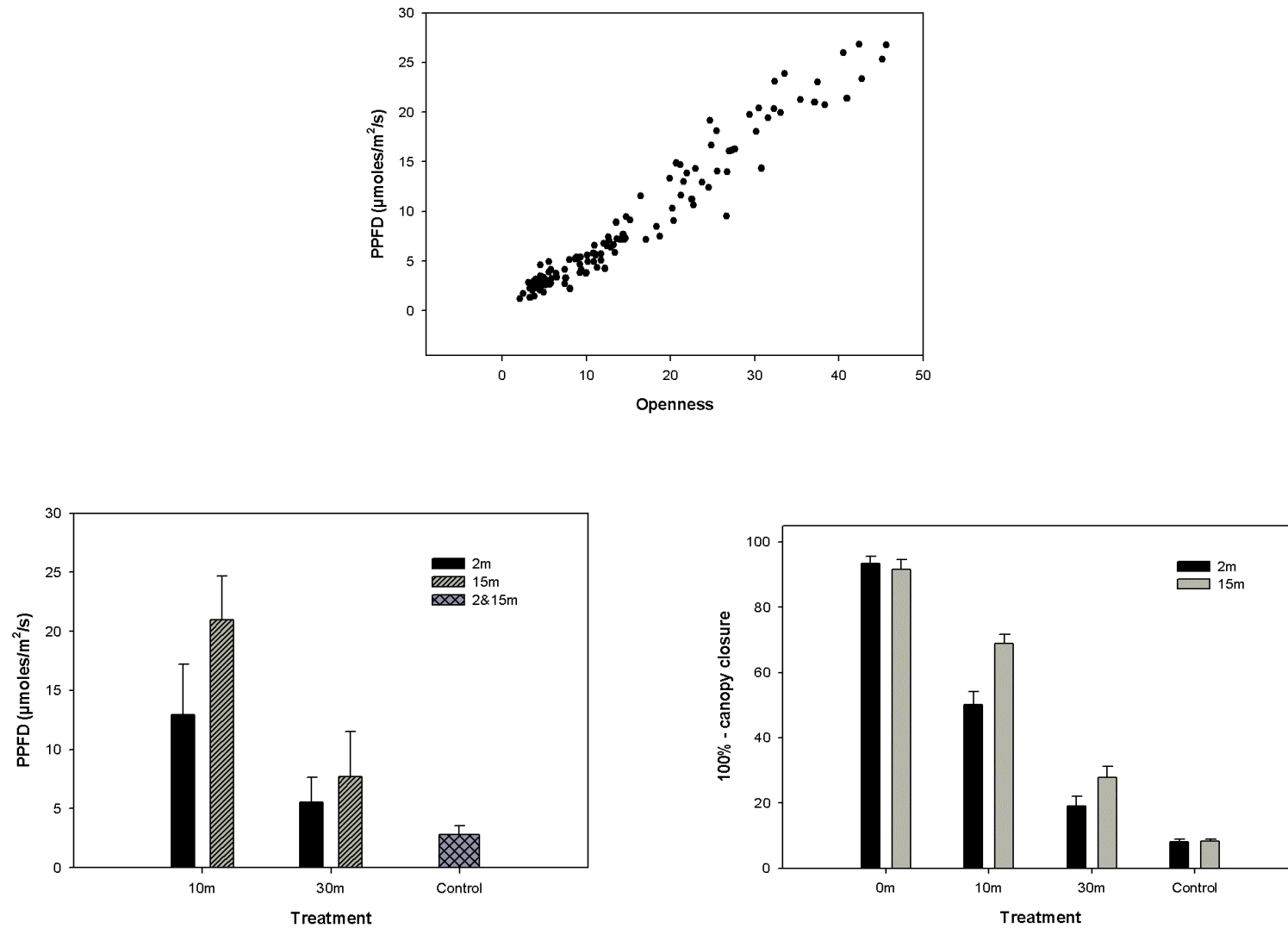
Appendix 2. Comparison of treatments eight years after harvesting

Figure A2-1. a) Relationship between photosynthetically active photon flux density (PPFD) and canopy openness, b) change in the (PPFD) (mean ± SD) and c) canopy openness (mean ± SE) by treatment and distance from the stream.
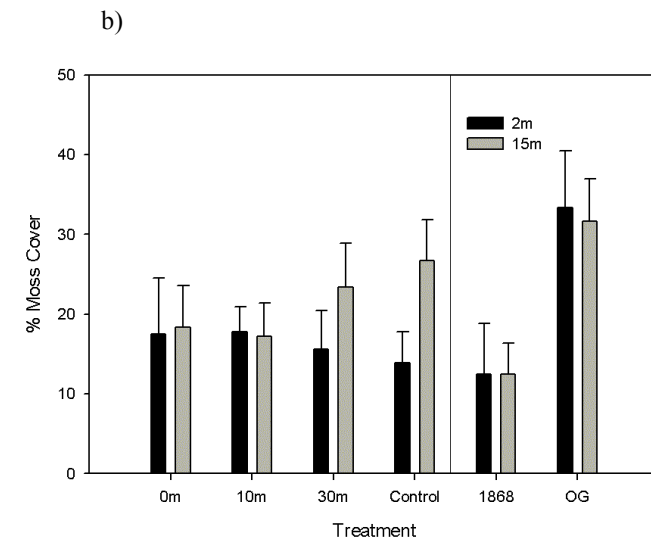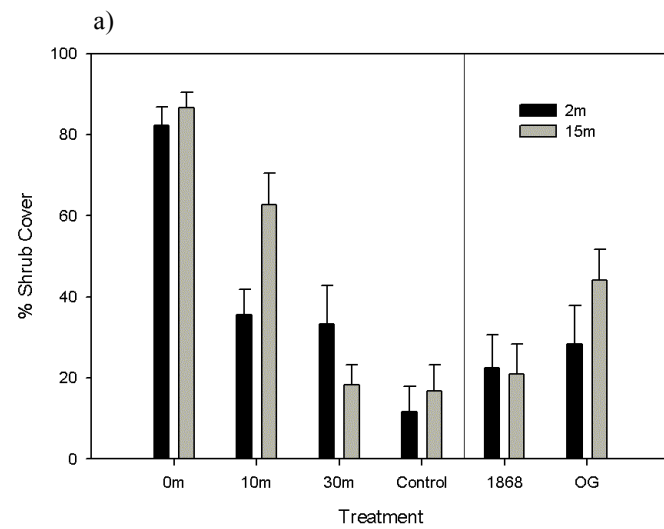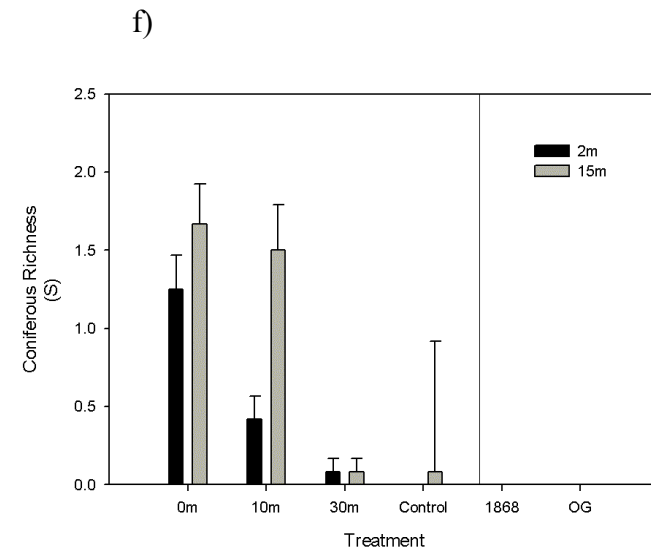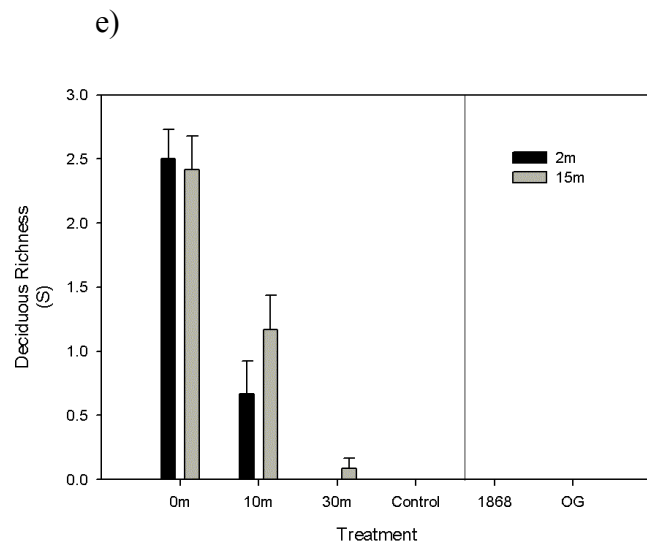
a)

b)

c)

d)
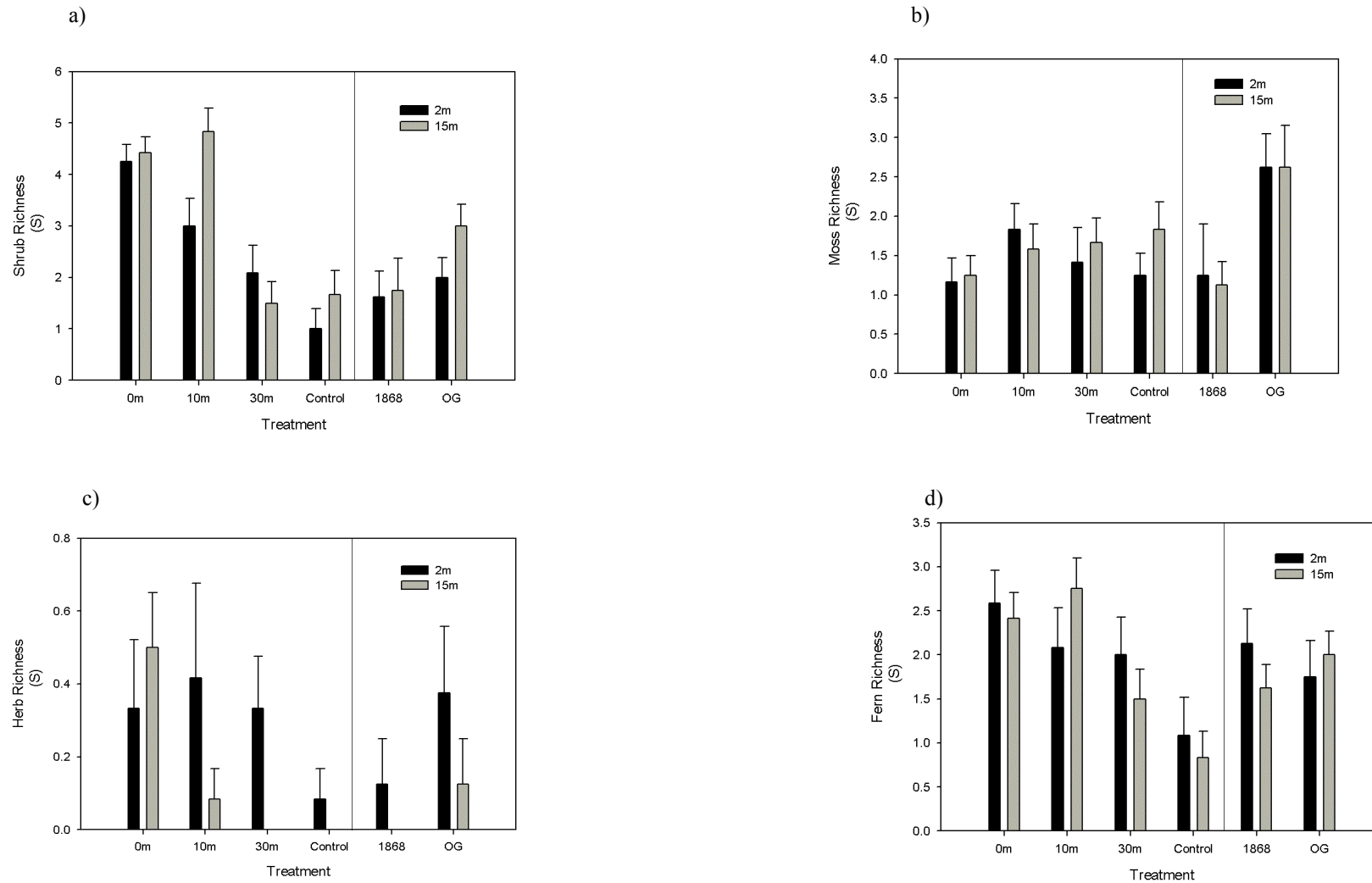
Figure A2-2. Effect of treatment levels and distance from the stream on the mean species number (mean ± SE) of a) shrubs, b) mosses, c) herbs, d) ferns, e) deciduous trees and f) coniferous trees eight years after harvesting. '1868'=Mature stand, 'OG'=old-growth stand.
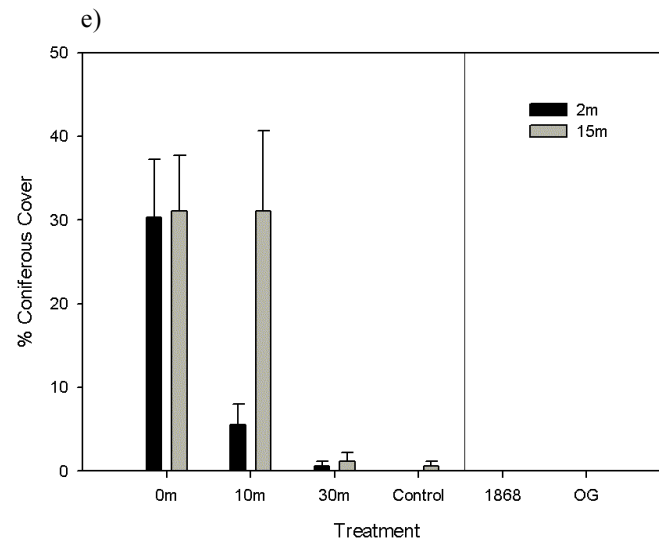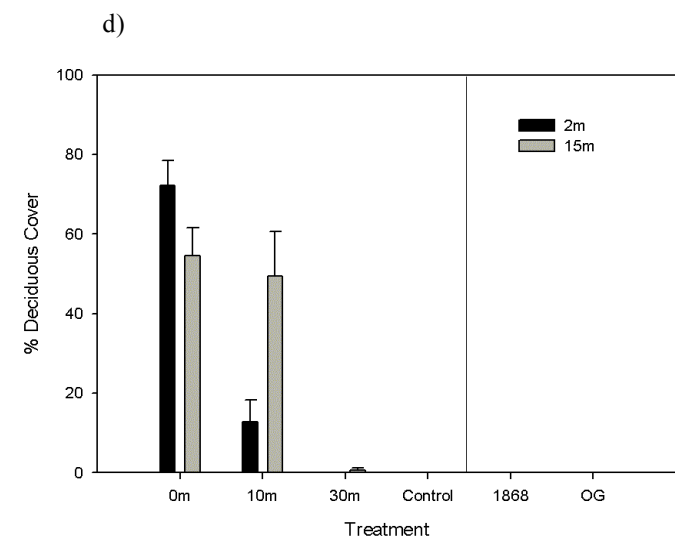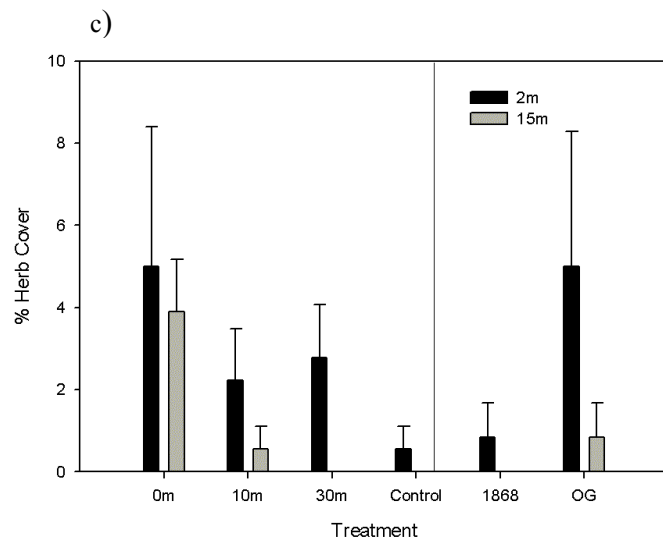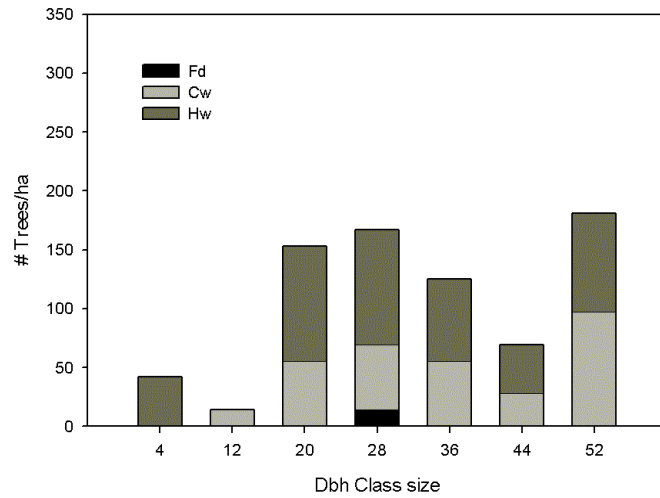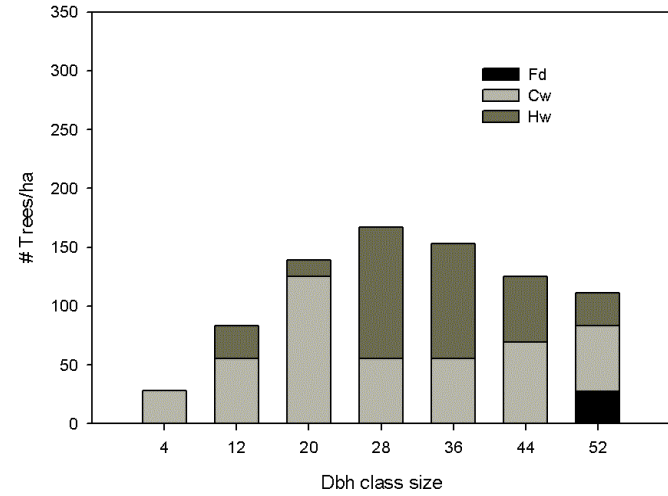
c)

d)

e)

Figure A2-3. Effect of treatment levels and distance to the stream on the mean % cover (mean ± SE) of a) shrubs, b) mosses, c) herbs, d) deciduous tree and e) coniferous trees species eight years after harvesting. '1868'=Mature stand, 'OG'=old-growth stand.

a)   10m buffer-2m

b) 30m buffer-2m

c) control-2m

d) control-15m

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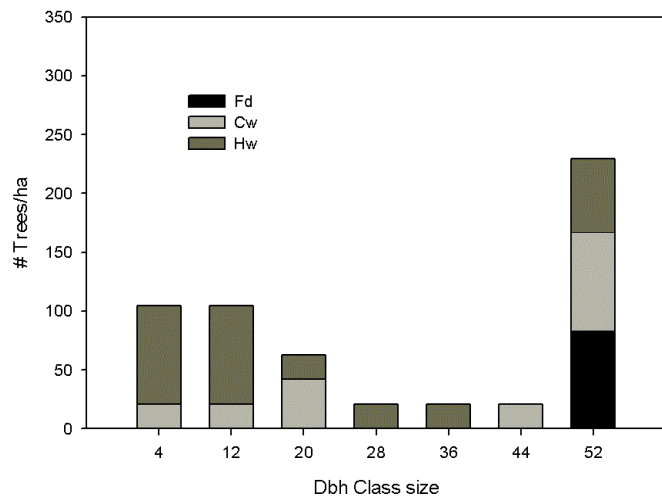
e) Mature-2m

f) Mature-15m
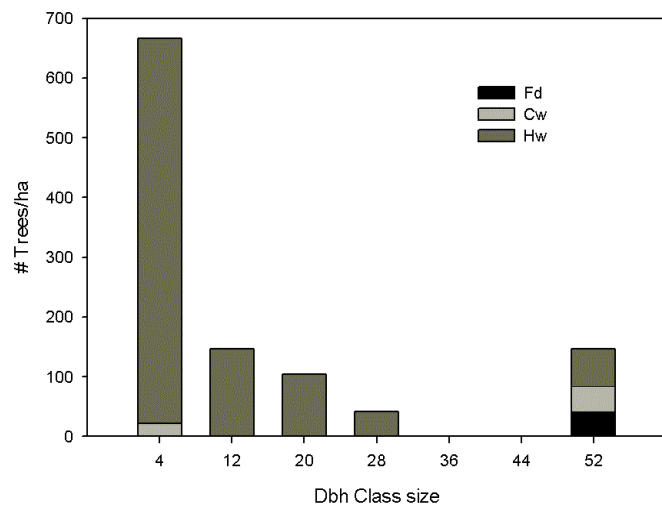
g) Old-growth-2m

h) Old-growth-15m

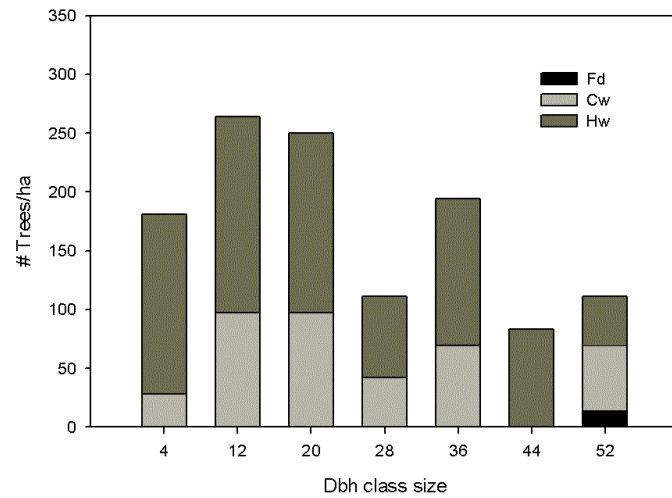Figure A2-4. Average number of live trees per hectare by DBH size class, species and distance to the stream in the a)10m buffer-2m, b)30m buffer-2m, c) control-2m, d) control-15m, e) Mature-2m, f) Mature-15m, g) Old-growth-2m and h) Old-growth-15m.

a) 10m buffer-2m

b) 30m buffer-2m

c) 30m buffer-15m

d) control-15m

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e) Mature-2m

f) Mature-15m

g) Old-growth-2m

h) Old-growth-15m

Figure A2-5. Average number of dead trees per hectare by DBH size class, species and distance to the stream in the a)10m buffer-2m, b) 30m buffer-2m, c) 30m buffer-15m, d) control-15m, e) Mature-2m, f) Mature-15m, g) Old-growth-2m and h) Old-growth-15m.
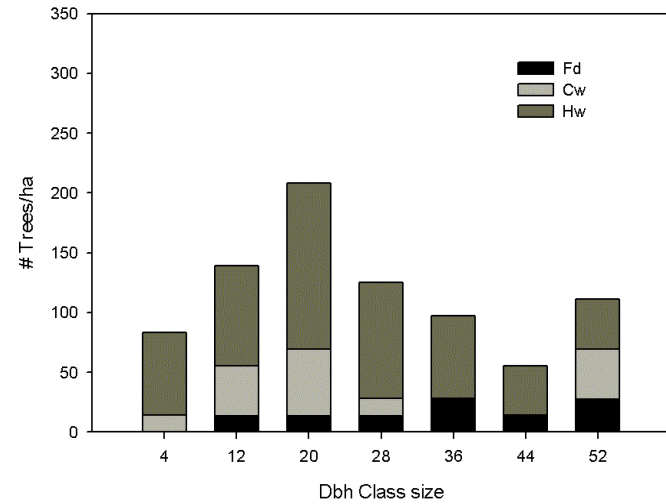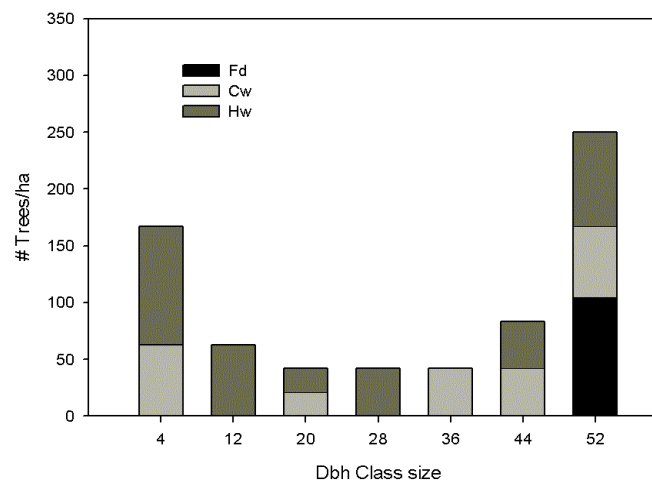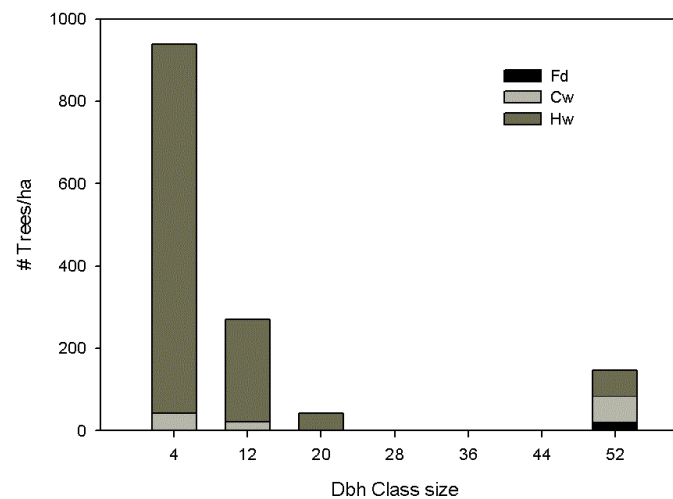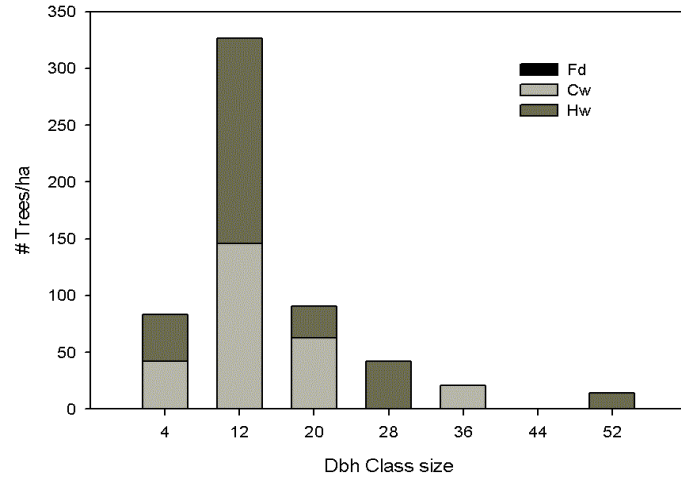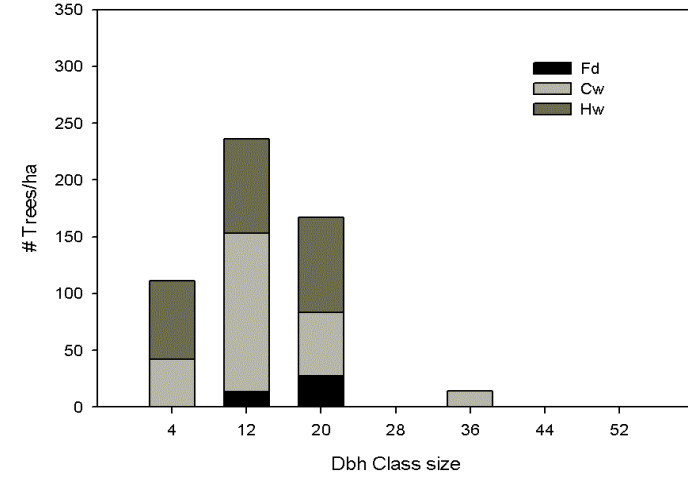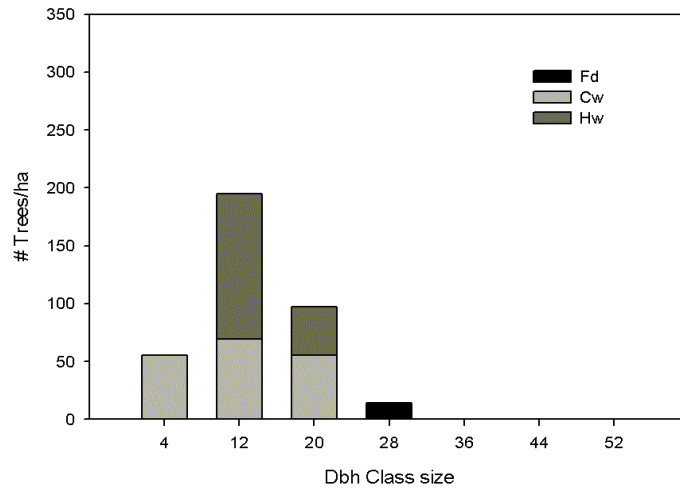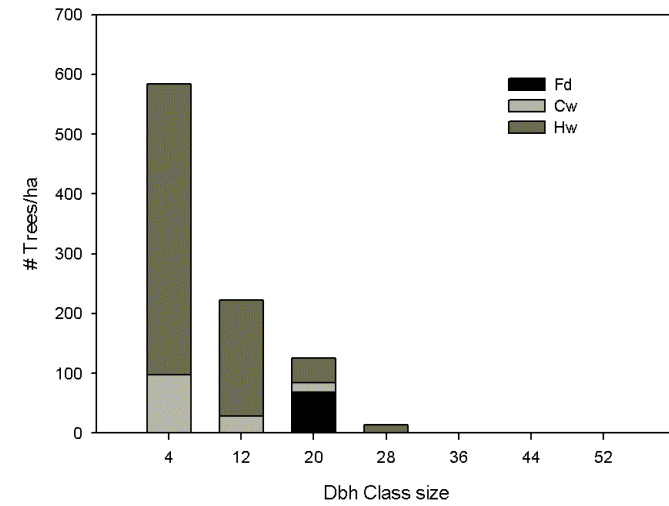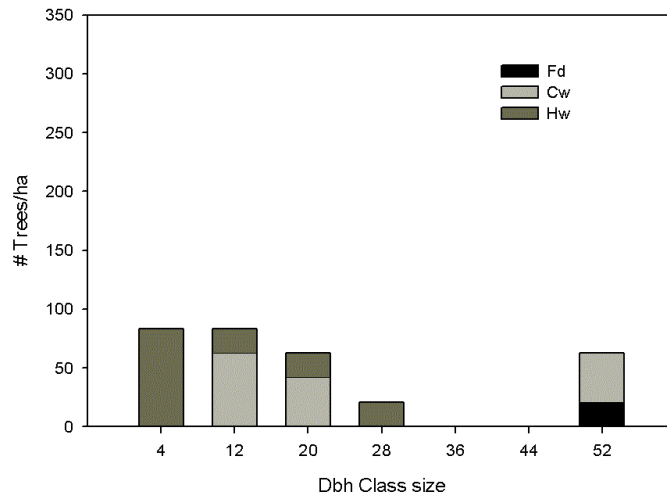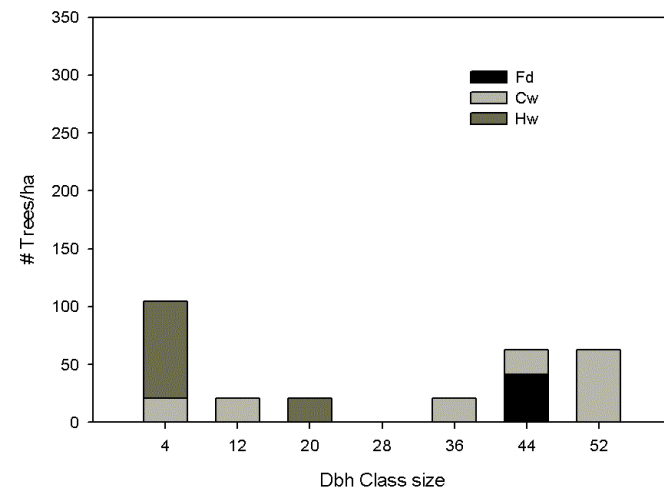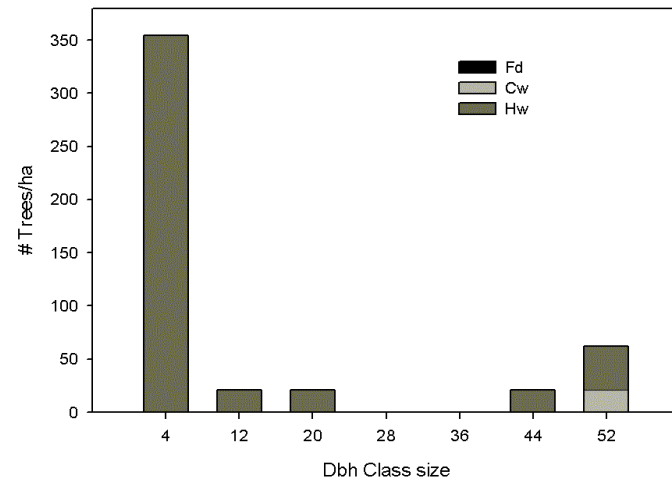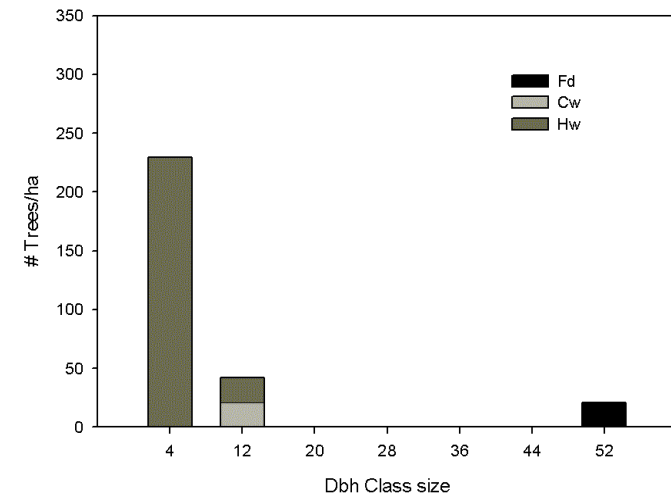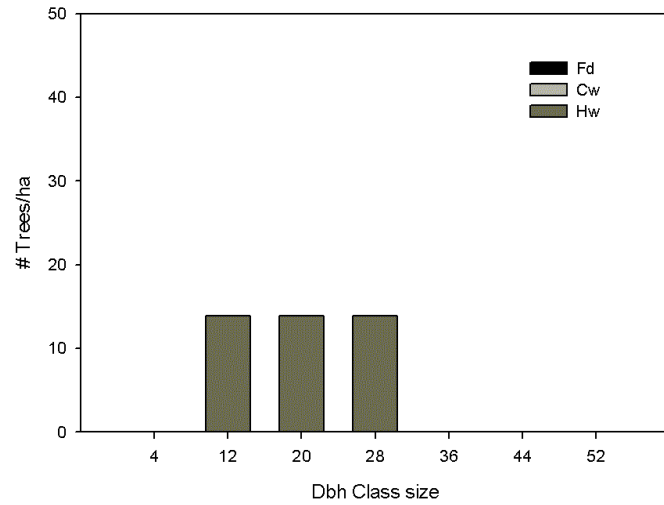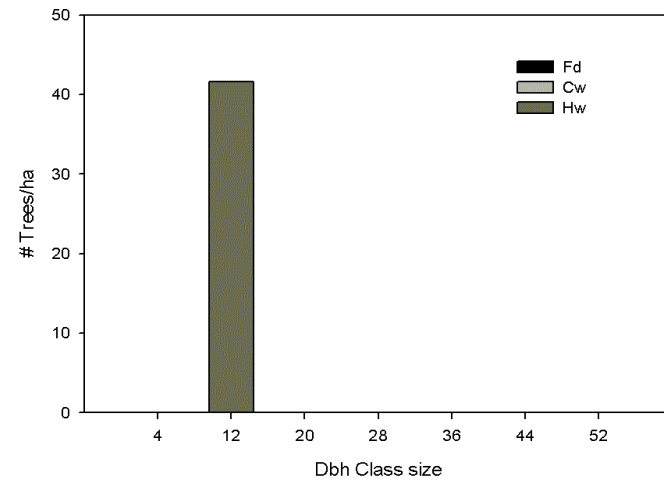
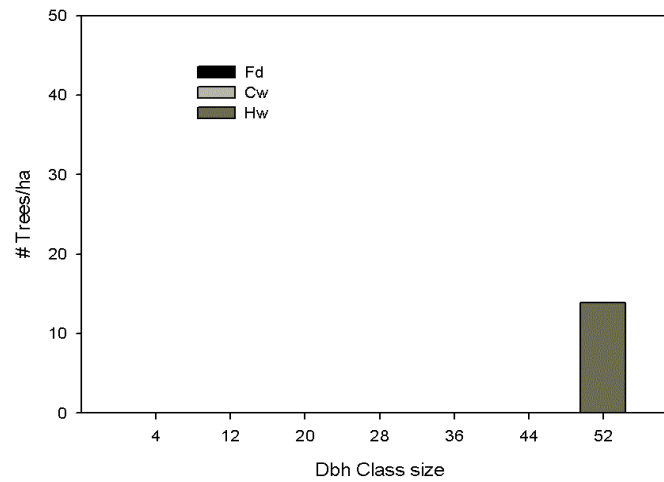a)30m buffer-15m

b) control-2m

c) control -15m

Figure A2-6. Average number of wind-blown trees per hectare by DBH size class, species and distance to the stream in the a) 30m buffer-15m, b) control-2m and c) control-15m.

Appendix 3. Successional trends

Table A3-1. Analysis of variance results (p values) for buffer width treatments (T), location of the plot (U), side of the stream (S), distance from the stream (D), year (Y) effects and interactions. Bold letters means significant results using an α =0.05. +Transformed prior to analysis using an arcsin function.

Variable	Sumspp	Sumshrub	Summoss	Sumfern	Sumherb	Sumconi	Sumdeci	Cover+	Covshrub+	Covmoss+	Covfern+	Covherb+	Covcon+	Covdec+	H´	1/D
T	**0.0004**	**0.0002**	0.6792	0.0755	**0.0004**	**<0.0001**	**<0.0001**	**0.0021**	**<0.0001**	0.5526	0.0846	**<0.0001**	**<0.0001**	**<0.0001**	**0.0072**	**0.0009**
U	0.4692	0.8579	0.0927	0.9542	0.1686	0.9682	0.7716	0.2772	0.8075	0.0847	0.9922	0.1318	0.9460	0.9460	0.5565	0.8059
T*U	0.7600	0.7064	0.6207	0.7968	0.4219	0.2923	0.8542	0.6950	0.7440	0.6090	0.6349	0.3769	0.9561	0.9561	0.8565	0.8854
S	**0.0366**	**0.0246**	0.6403	**0.0125**	0.6995	0.8803	0.1456	0.0568	**0.0054**	0.1720	**0.0335**	0.5584	0.3783	0.3783	0.8371	0.2679
D	0.3012	**0.0316**	0.2254	0.1290	0.1372	**0.0367**	0.1361	**0.0184**	0.1437	0.0513	0.4306	0.1607	**0.0209**	**0.0209**	0.4404	0.5082
S*D	0.8919	0.5764	0.8239	0.9291	0.1026	0.3376	0.9490	0.5193	0.3292	0.8405	0.5944	0.1952	0.3692	0.3692	0.8597	0.7844
T*S	0.2028	0.4112	0.1540	**0.0125**	0.2316	0.4033	0.1659	0.1222	0.2737	0.3542	**0.0033**	**0.0111**	0.1635	0.1635	0.2032	0.2723
U*S	0.2149	0.2298	0.1595	0.6790	0.6692	0.1892	0.7217	0.9824	0.9317	0.3644	0.5771	0.9115	0.3152	0.3152	0.3896	0.2614
T*U*S	0.5846	0.6461	0.7211	0.4429	0.7344	0.6026	0.8964	0.5958	0.3204	0.8954	0.3393	0.8457	0.8360	0.8360	0.1392	0.4561
T*S*D	0.7461	0.5404	0.1485	0.8463	0.4659	0.1325	0.9993	0.4184	0.9225	0.3337	0.5528	0.7881	0.2357	0.2357	0.6247	0.9102
T*D	**0.0135**	**0.0027**	0.3095	0.1786	0.9950	0.0707	**0.0120**	**0.0026**	**0.0027**	0.1024	0.0646	0.9120	**0.0420**	**0.0420**	0.0784	0.0822
T*U	0.0830	0.1190	**0.0244**	0.1917	0.2786	0.5248	0.4625	**0.0264**	0.1360	**0.0285**	0.0591	0.3326	0.9645	0.9645	0.1956	0.4457
T*U*D	0.4011	0.8637	0.1808	0.8488	0.2914	0.7213	0.1078	0.2949	0.9612	0.4151	0.3457	0.1809	0.9336	0.9336	0.1378	0.5569
U*S*D	0.7754	0.6598	0.7541	0.1689	0.9450	0.3845	0.7354	0.5772	0.9128	0.6065	0.6948	0.7128	0.5198	0.5198	0.4058	0.3912
T*U*S*D	0.3143	0.9995	0.2296	0.0530	0.7186	0.6954	0.8375	**0.0213**	0.7773	0.7150	**0.0013**	0.2915	0.7787	0.7787	0.4987	0.2459
Y	**<0.0001**	**<0.0001**	**0.0006**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	0.1023	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.000**
T*Y	**<0.0001**	**<0.0001**	**0.0005**	**0.0009**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**0.0014**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.000**
U*Y	0.4195	0.7387	0.0772	0.5339	0.3524	0.7840	0.3279	0.7253	0.3491	0.7713	0.2455	0.9594	0.7920	0.7920	0.3043	0.1890
S*Y	0.0574	0.1316	0.0699	0.3502	0.9655	0.4871	0.9156	0.3836	0.5304	**0.0491**	0.4717	0.6490	0.2694	0.2694	0.3189	0.3762
D*Y	0.0363	**0.0075**	0.0754	0.2316	0.6298	**0.0090**	0.2368	**0.0397**	**0.0007**	**0.0296**	0.7993	0.5651	**0.0097**	**0.0097**	0.2399	0.0920
T*U*Y	0.3971	0.6732	0.5746	0.4411	0.4873	0.9170	0.6189	0.6871	0.5492	0.7478	0.0730	0.8863	0.9982	0.9982	0.5562	0.1364
T*S*Y	0.1154	0.0861	0.4787	0.4004	0.8862	0.7437	0.2038	0.0774	0.9715	0.2272	0.4089	0.2569	**0.0462**	**0.0462**	0.4278	0.0924
T*D*Y	0.1563	0.0833	0.4812	0.7597	0.1438	0.1857	0.1270	**0.0007**	**<0.0001**	0.8616	0.0849	0.3706	**0.0102**	**0.0102**	0.7856	0.4871
U*S*Y	0.2308	0.0980	0.4965	0.1361	0.8154	0.0817	0.8369	0.9614	0.5280	0.6706	0.9702	0.7037	0.1237	0.1237	0.6322	0.2630
U*D*Y	0.3223	0.2124	0.3346	0.5467	0.6920	0.3130	0.9208	0.4526	**0.0443**	0.9299	0.5409	0.1325	0.7757	0.7757	0.1076	0.0972
S*D*Y	0.8592	0.5240	0.8849	0.7997	0.2669	0.9506	0.1594	0.9908	0.6382	0.3717	0.9054	0.4370	0.6702	0.6702	0.9818	0.7860
T*U*S*Y	0.4536	0.1658	0.9958	0.7737	0.9763	0.4361	0.9779	0.9265	0.8424	0.8323	0.9109	0.9714	0.9556	0.9556	0.8049	0.8780
T*U*D*Y	0.6412	0.7230	0.7144	0.4316	0.8505	0.2582	0.9906	0.3003	0.5137	0.6711	0.2998	0.1940	0.6553	0.6553	0.9235	0.5948
T*S*D*Y	0.8979	0.7328	0.9158	0.9825	0.5145	0.2509	0.9173	0.9401	0.8229	0.8151	0.9278	0.6348	0.6978	0.6978	0.9636	0.8591
U*S*D*Y	0.1384	0.3401	0.9249	0.7349	0.3439	0.4377	0.0858	0.9782	0.6724	0.9484	0.8023	0.6966	0.3441	0.3441	0.4594	0.1636
T*U*S*D*Y	0.3269	0.6567	0.5985	0.3945	0.8866	0.8228	0.2862	0.6513	0.5099	0.9962	0.3458	0.9575	0.8777	0.8777	0.2834	0.0741

Table A3-1 (*continued*)

Variable	Minemoss	Feathermoss	Wetmoss	Latefern	Earlyfern	Dryshrub	Woodyshrub	Lightshrub	Wetshrub	Covwetmoss+	Covminemoss+	Covfeathermoss+
T	0.2428	0.8764	0.1070	0.4205	**0.0030**	0.3150	0.8171	< **0.0001**	< **0.0001**	0.0847	0.2101	0.6980
U	0.5855	0.0828	0.4978	0.9200	0.2970	0.3416	0.5324	0.6822	0.7093	0.6015	0.5864	0.0590
T*U	0.7340	0.3547	0.8598	0.7672	0.7348	0.5122	0.4839	0.9212	0.9263	0.9349	0.8787	0.3615
S	**0.0227**	0.9727	**0.0320**	0.0166	0.8868	0.2800	0.7219	**0.0159**	**0.0186**	**0.0097**	**0.0257**	0.9785
D	0.0524	0.0021	0.2325	**0.0450**	**0.0019**	0.3977	0.2076	0.2100	0.1922	0.5607	0.1359	**0.0009**
S*D	0.4543	0.5761	0.9305	0.9817	0.7464	0.7813	0.7436	0.6372	0.6780	0.5628	0.6445	0.9927
T*S	**0.0204**	0.5931	**0.0471**	**0.0160**	0.6640	0.5184	0.3790	0.0451	**0.0408**	0.1594	0.0592	0.2094
U*S	0.4820	0.0419	0.7145	0.9452	0.4019	0.9178	0.9463	0.2523	0.2317	0.9637	0.3626	0.1623
T*U*S	0.3163	0.7321	0.5713	0.3196	0.7521	0.9827	0.8911	0.4294	0.4722	0.8623	0.4419	0.9657
T*S*D	0.4232	0.1522	0.2101	0.9494	0.9745	0.4325	0.8444	0.7763	0.7702	0.0985	0.4232	0.4832
T*D	0.5197	0.7149	0.1920	0.4466	**0.0076**	0.6144	0.8397	**0.0182**	**0.0177**	0.1711	0.6386	0.8652
T*U	0.3124	**0.0109**	0.1668	0.0835	0.1790	0.3291	**0.0407**	0.7184	0.7288	0.5152	0.6862	**0.0147**
T*U*D	0.3186	0.0229	0.2296	0.8644	0.2532	0.2374	0.4725	0.6911	0.6930	0.5843	0.8682	0.0611
U*S*D	0.5703	0.5684	0.5775	0.2019	0.9484	0.7813	1.0000	0.4221	0.4558	0.5821	0.9663	0.8565
T*U*S*D	0.7329	0.1803	0.1006	0.1696	0.2338	0.4696	0.8217	0.5626	0.4715	0.9417	0.9891	0.8187
Y	0.0103	< **0.0001**	0.0003	< **0.0001**	< **0.0001**	< **0.0001**	< **0.0001**	< **0.0001**	< **0.0001**	0.0569	**0.0108**	0.0217
T*Y	0.0036	**0.0474**	0.2732	**0.0207**	< **0.0001**	0.5461	0.1225	< **0.0001**	< **0.0001**	0.0787	**0.0002**	**0.0019**
U*Y	0.4550	0.3098	0.6432	0.7085	0.8257	0.4330	0.4611	0.4070	0.4931	0.9820	0.7318	0.5180
S*Y	0.4467	0.1864	0.1753	0.8004	0.7247	0.1784	0.1071	0.7236	0.7795	0.2437	0.2939	0.5211
D*Y	0.8802	0.6364	0.0815	0.5894	**0.0456**	0.0839	0.7200	0.1180	0.1166	0.0963	0.8790	0.7837
T*U*Y	0.3077	0.6810	0.4349	0.1549	0.1988	0.4414	0.7903	0.0676	0.0531	0.7584	0.5962	0.6133
T*S*Y	0.7152	0.1201	0.5333	0.4016	0.8090	0.5963	0.4268	0.1600	0.1281	0.0639	0.7517	0.4985
T*D*Y	0.9183	0.3301	0.8279	0.7872	0.0547	0.4763	0.5338	0.0782	0.0666	0.8196	0.9890	0.0928
U*S*Y	0.8777	0.3031	0.5971	0.6778	0.4201	0.6675	0.7918	0.1262	0.0943	0.6531	0.6151	0.6533
U*D*Y	0.9374	0.8682	0.7018	0.1775	0.2275	0.7227	0.3209	0.6808	0.7362	0.6351	0.8920	0.9957
S*D*Y	0.5439	0.8912	0.9436	0.9252	0.6108	0.7820	0.7011	0.7484	0.8303	0.6511	0.5948	0.4566
T*U*S*Y	0.1745	0.9969	0.4307	0.9806	0.9658	0.8319	0.5546	0.2602	0.1873	0.9670	0.7059	0.7080
T*U*D*Y	0.8957	0.6040	0.7954	0.5810	0.1346	0.1998	0.2461	0.5875	0.5103	0.9704	0.2391	0.8333
T*S*D*Y	0.8535	0.8839	0.4934	0.7675	0.9906	0.9777	0.9860	0.7820	0.7598	0.1435	0.7160	0.7489
U*S*D*Y	0.8122	0.2504	0.2961	0.7434	0.7128	0.7820	0.1070	0.3690	0.4418	0.1689	0.9741	0.2101
T*U*S*D*Y	0.7026	0.9909	0.3945	0.2649	0.9587	0.4748	0.3338	0.6943	0.5924	0.9914	0.7766	0.9800

Table A3-1 (*concluded*)

| Variable	Covearlyfern+	Covlatefern+	Covwoodyshrub+	Covdryshrub+	Covlightshrub+	Covwetshrub+
T	**0.0039**	0.7610	0.2524	**0.0405**	**0.0003**	**0.0003**
U	0.6279	0.9402	0.7253	0.5928	0.6107	0.6186
T*U	0.8707	0.7440	0.6449	0.7464	0.8041	0.8126
S	0.3690	**0.0085**	0.7301	0.5490	**0.0045**	**0.0048**
D	**0.0047**	**0.0258**	**0.0379**	0.0754	**0.0394**	**0.0380**
S*D	0.5066	0.7225	0.6043	0.9352	0.8149	0.8004
T*S	0.7252	**0.0054**	0.5958	0.9451	**0.0368**	**0.0365**
U*S	0.9028	0.4693	0.6664	0.5532	0.7393	0.7253
T*U*S	0.6365	0.4344	0.9814	0.8981	0.2392	0.2494
T*S*D	0.8937	0.9703	0.9488	0.9966	0.9866	0.9840
T*D	**0.0089**	0.2244	0.6725	0.1187	**0.0018**	**0.0017**
T*U	0.4927	0.1702	0.3012	0.6853	0.2175	0.2292
T*U*D	0.4250	0.3079	0.7437	0.8718	0.9628	0.9644
U*S*D	0.2645	0.9315	0.2335	0.4019	0.2733	0.2823
T*U*S*D	0.1311	0.0052	0.2312	0.6039	0.9694	0.9689
Y	< **0.0001**	< **0.0001**	< **0.0001**	< **0.0001**	< **0.0001**	< **0.0001**
T*Y	< **0.0001**	0.1794	**0.0107**	0.0910	< **0.0001**	< **0.0001**
U*Y	0.6686	0.6552	0.8445	0.4735	0.3117	0.3262
S*Y	0.8813	0.7040	0.2161	0.2368	0.3585	0.3674
D*Y	0.0842	0.9227	**0.0150**	**0.0100**	0.2132	0.2367
T*U*Y	0.3049	**0.0106**	0.5545	0.4768	0.4545	0.4725
T*S*Y	0.5475	0.4067	**0.0258**	**0.0027**	0.9506	0.9368
T*D*Y	0.1211	0.2430	0.7039	0.2406	**0.0015**	**0.0016**
U*S*Y	0.5856	0.8267	0.8681	0.9335	0.5368	0.5263
U*D*Y	0.9796	0.3652	0.5549	0.3603	0.1046	0.1124
S*D*Y	0.9465	0.8764	0.4692	0.8105	0.5118	0.4731
T*U*S*Y	0.9883	0.8253	0.8587	0.9507	0.8211	0.8350
T*U*D*Y	0.7833	0.7703	0.2136	0.1392	0.4596	0.4850
T*S*D*Y	0.8874	0.7936	0.8135	0.5861	0.2065	0.1698
U*S*D*Y	0.9015	0.4803	0.8447	0.9404	0.7079	0.7150
T*U*S*D*Y	0.2329	0.6116	0.9416	0.9866	0.1884	0.1682
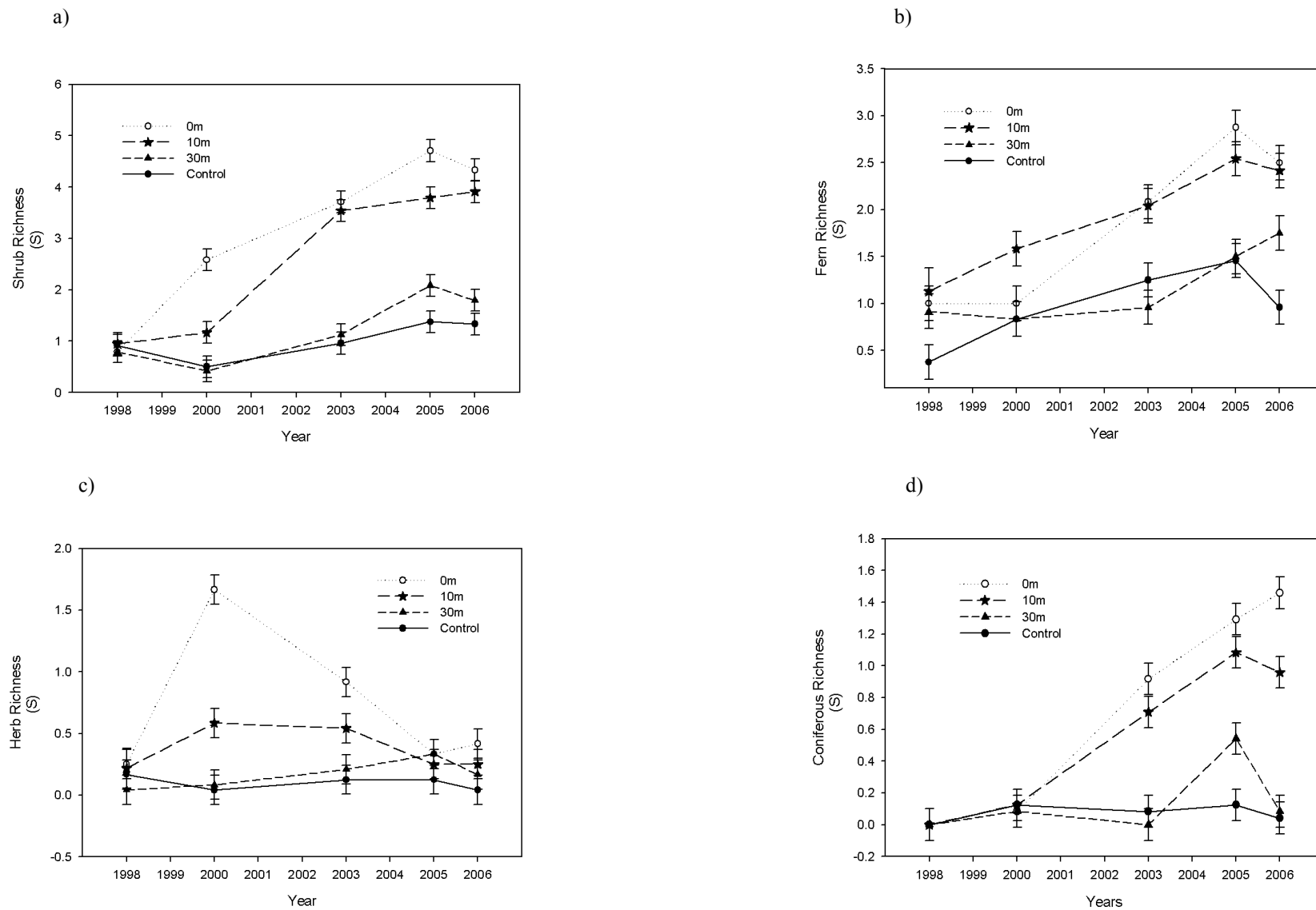
Figure A3-1. Total species richness (mean ± SE) over time by buffer width of a) shrubs, b) ferns, c) herbs and d) coniferous trees.
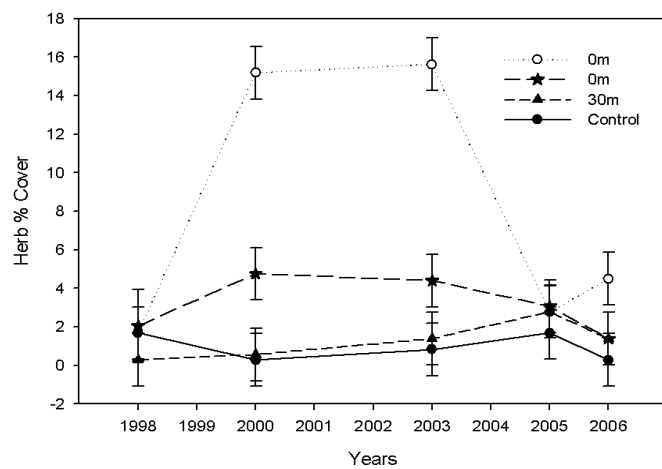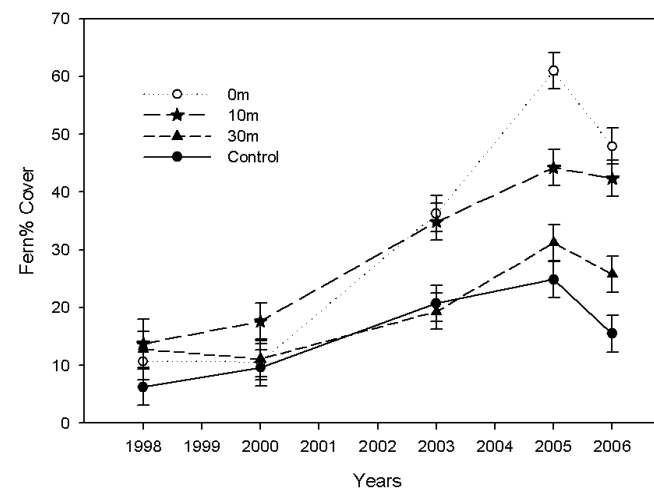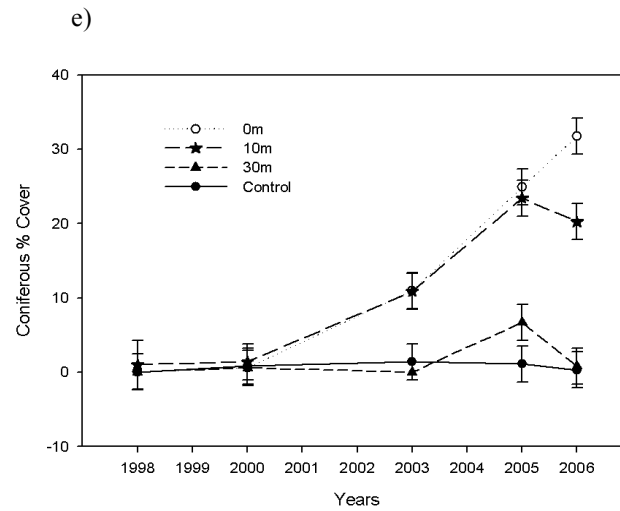
a)

b)

c)

d)

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e)
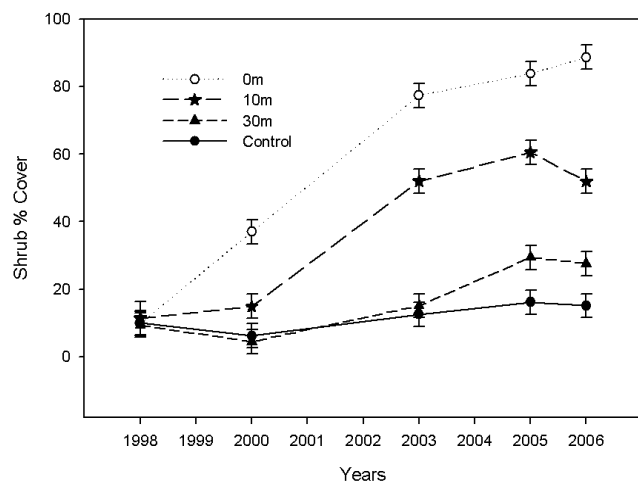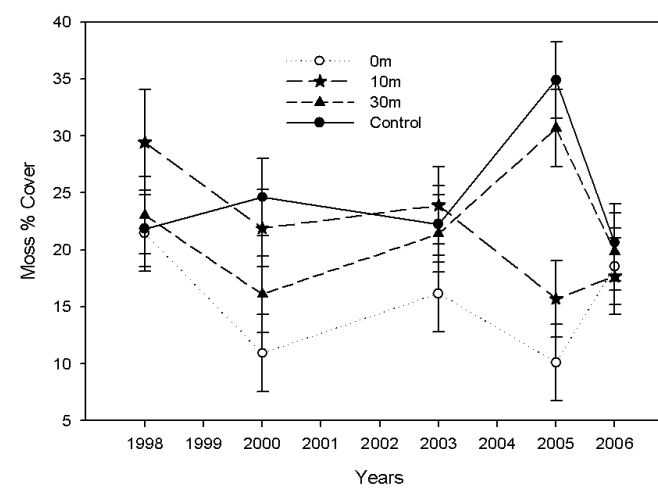
Figure A3-2. Percent cover (mean ± SE) over time by buffer width of a) shrubs, b) mosses, c) herbs, d)ferns and e) coniferous trees.
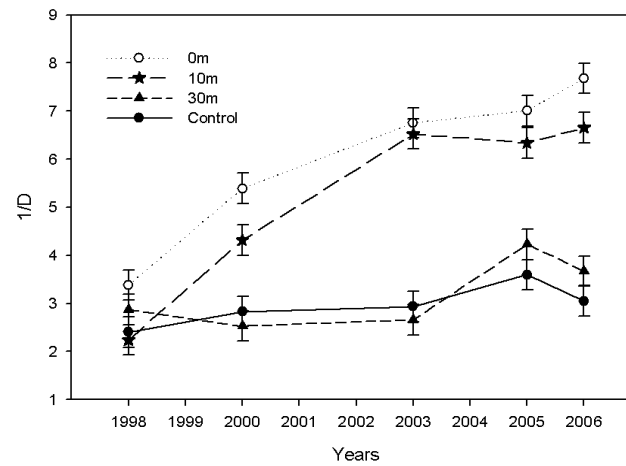

Figure A3-3. Reciprocal of Simpson index (1/D) (mean ± SE) over time by buffer treatment.
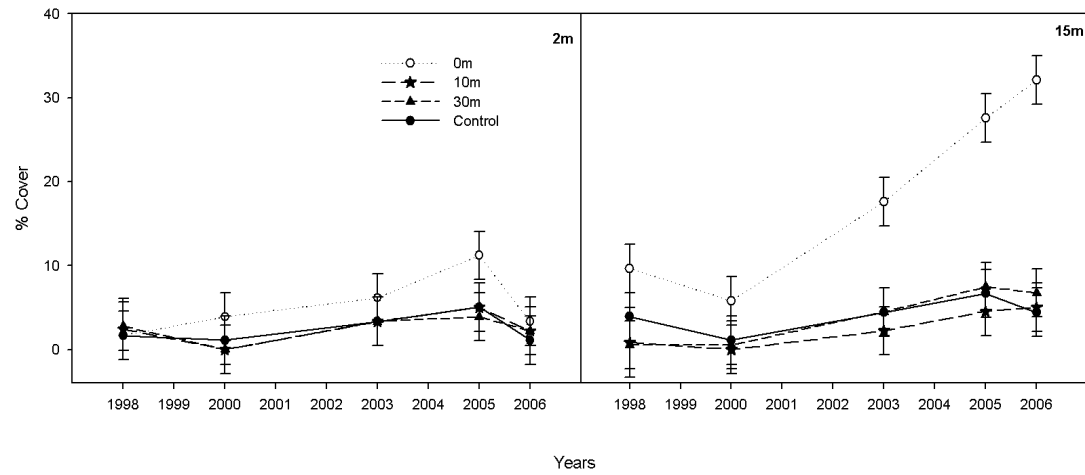
Figure A3-4. Percent cover of dry shrubs (mean ± SE) over time by buffer treatment and distance from the stream.
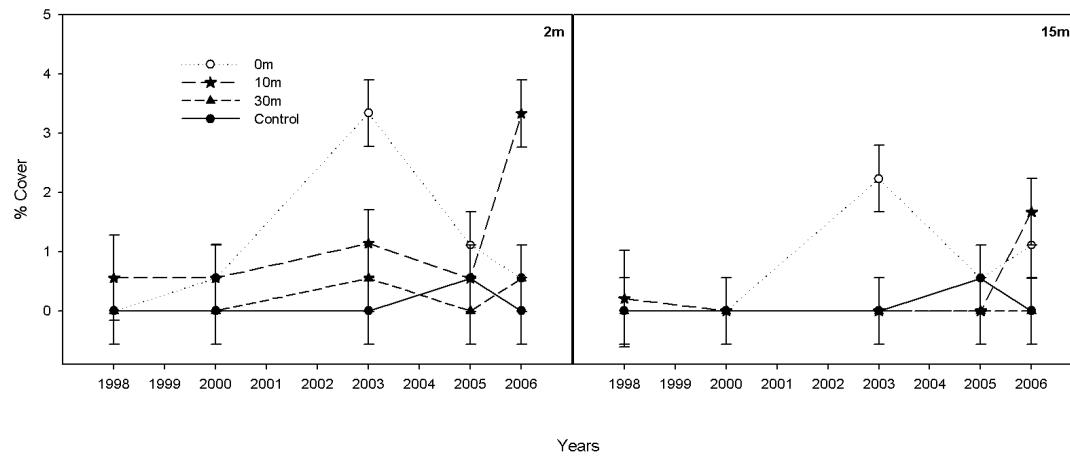

Figure A3-5. Percent cover of mineral mosses (mean ± SE) over time by buffer treatment and distance from the stream.

Figure A3-6. Percent cover of early ferns (mean ± SE) over time by buffer treatment and distance from the stream.

Figure A3-7. Percent cover of wet shrubs (mean ± SE) over time by buffer treatment and distance from the stream.

Figure A3-8. Percent cover of woody shrubs (mean ± SE) over time by buffer treatment and distance from the stream.

Figure A3-9. Percent cover of wet mosses (mean ± SE) over time by buffer treatment and distance from the stream.

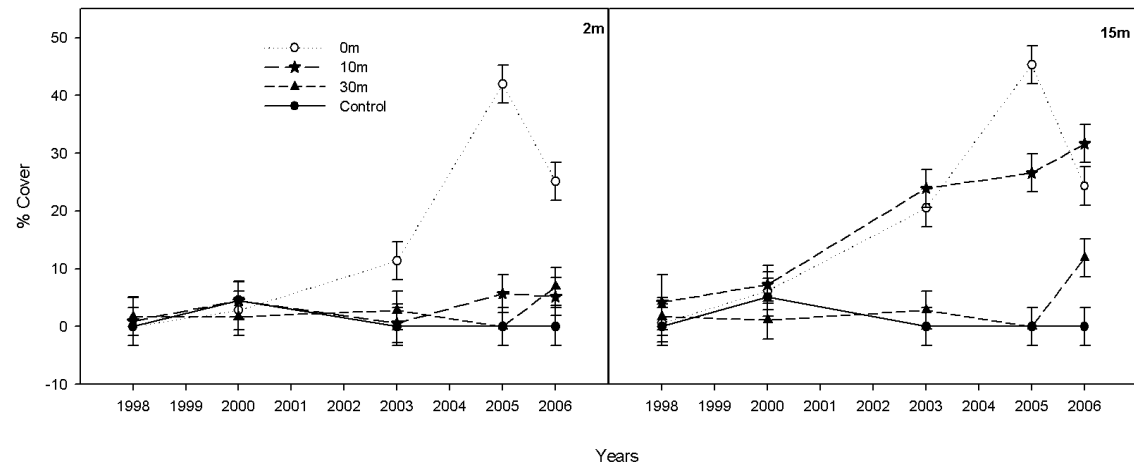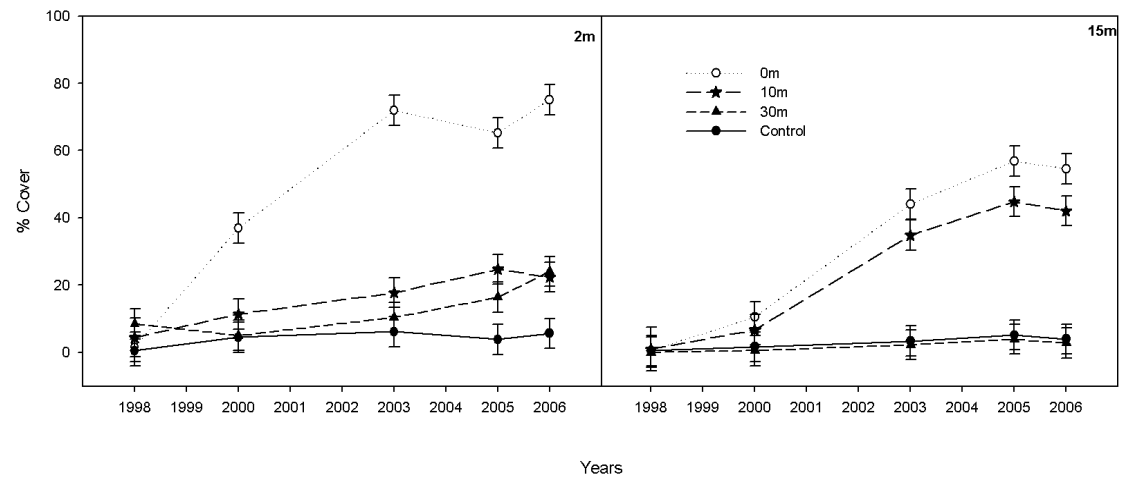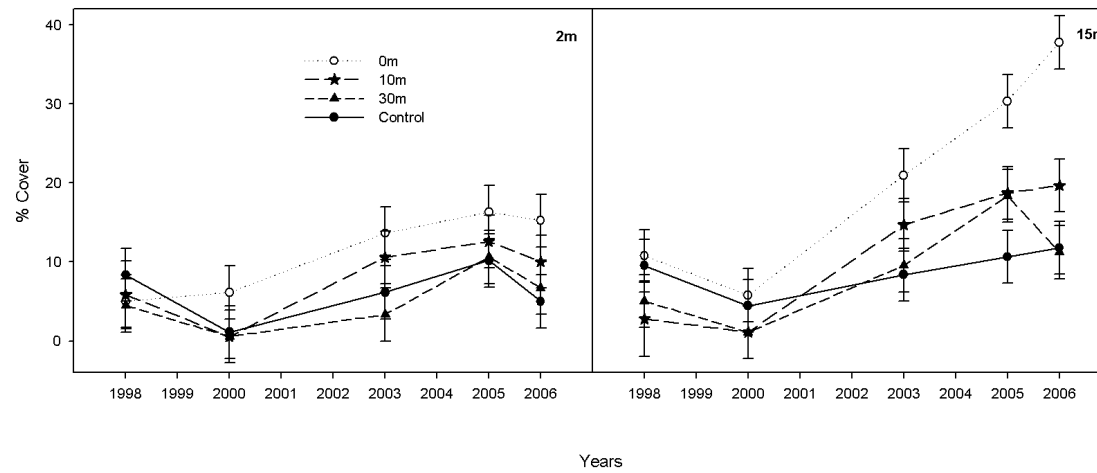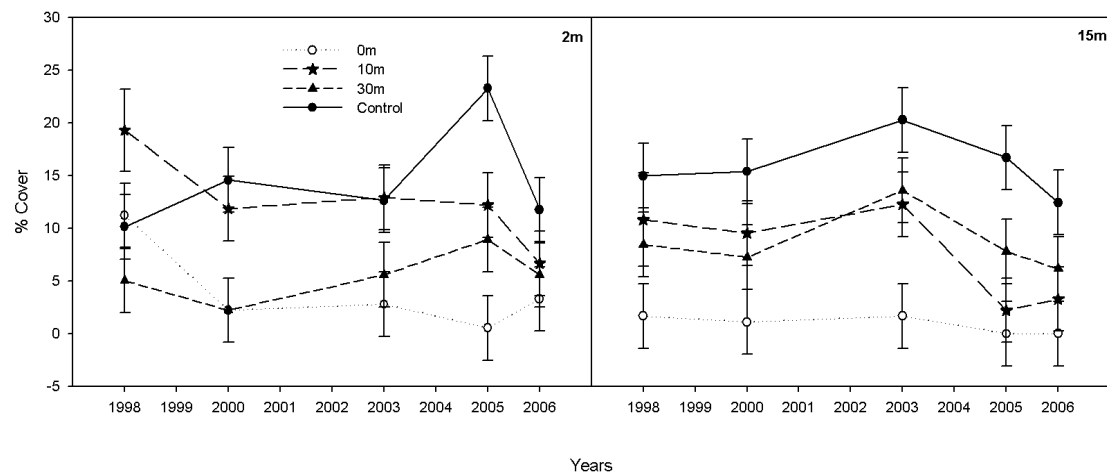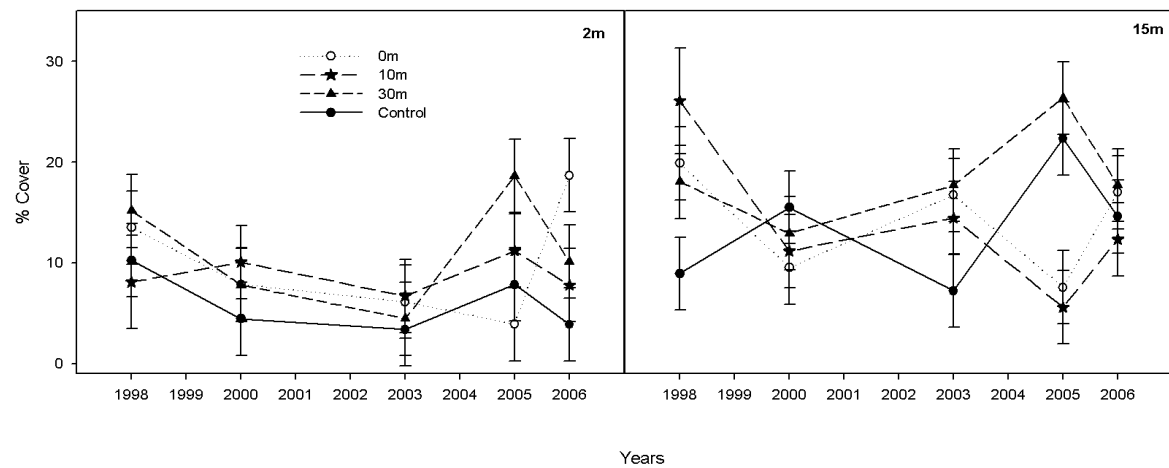Figure A3-10. Percent cover of feather mosses (mean ± SE) over time by buffer treatment and distance from the stream.

Appendix 4. Vegetation attributes

Table A4-1. Ecological attributes of plant species occurring at the Malcolm Knapp Research Forest from 1998 to 2006.

Scientific name	Common name	Family	Functional Group	Seral stage	Habitat
Alnus rubra	Red alder	Betulaceae	Deciduous	Early	Moist woods
Acer circinatum	Vine maple	Aceraceae	Tall shrub	Early	Moist to wet sites
Acer macrophyllum	Big-leaf maple	Aceraceae	Deciduous	Early-mid-late	Dry to moist
Amphidium lapponicum	Bottle moss	Orthotrichaceae	Moss		
Anaphalis margaritaceae	Pearly everlasting	Asteraceae	Herb	Early-mid-late	Dry woods
Arctostaphylos uva-ursi	Kinnikinnick	Ericaceae	Shrub	Early-mid	Dry forests
Aster spp.	Aster	Asteraceae	Herb		Wet bogs
Aster conspicuus	Showy aster	Asteraceae	Herb	Early	
Athyrium filix-femina	Lady fern	Dryopteridaceae	Fern	Mid-late	Moist to wet forests
Betula papyrifera	Paper birch	Betulaceae	Deciduous	Early	Moist woods. Bogs
Blechnum spicant	Deer fern	Blechnaceae	Fern	Early-mid-late	Moist to wet forests
Bryum miniatum	Red bryum	Bryaceae	Moss	Mid-late	Moist rock surface
Campylopus atrovirens	Black fish hook moss	Dicranaceae	Moss		
Carex anthoxanthea	Sedge	Cyperaceae	Sedges-Herb	Early	
Carex aquatilis	Water sedge	Cyperaceae	Sedges-Herb	Early	
Carex deweyana	Dewey sedge	Cyperaceae	Sedges-Herb	Early	
Carex vaginata	Yellow-flowered sedge	Cyperaceae	Sedges -Herb	Early	
Cirsium arvense	Bull thistle	Asteraceae	Herb	Early*	Disturbed sites
Claopodium crispifolium	Rough moss	Leskeaceae	Moss	Early-mid	Light-gap sites
Climacium dendroides	Tree moss	Climaciaceae	Moss		
Cornus canadensis	Bunchberry	Cornaceae	Herb	Mid-late	Boreal forest
Corylus cornuta	Beaked hazelnut	Betulaceae	Tall shrub	Early	
Dicranum fuscescens	Dusky fork moss	Dicranaceae	Moss		
Dryopteris expansa	Spiny woody fern	Dryopteridaceae	Fern	Early	Moist openings
Epilobium angustifolium	Fireweed	Onagraceae	Herb	Late	
Epilobium ciliatum	Purple-leaved willowherb	Onagraceae	Herb	Early	Wet
Equisetum arvense	Common horsetail	Equisetaceae	Horsetail-Fern	Early-mid-late	Moist to wet forests
Equisetum telmatiea	Giant horsetail	Equisetaceae	Horsetail-Fern	Early-mid-late	Streambanks
Galium trifidum	Small bedstraw	Rubiaceae	Herb	Early-mid-late	Moist
Gaultheria shallon	Salal	Ericaceae	Shrub	Early-mid	Coniferous forests
Gymnocarpium dryopteris	Oak fern	Dryopteridaceae	Fern	Early-mid	Moist openings

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Heterocladium procurrens	Tangle moss	Pterigynandraceae	Moss		
Hookeria lucens	Clear moss	Hookeriaceae	Moss	Late	Moist humus
Hylocomium splendens	Step moss	Hylocomiaceae	Moss	Late	
Ilex aquifolium	Holly tree	Aquifoliaceae	Shrub		
Isothecium myosuroides	Cat-tail moss	Brachytheciaceae	Moss		
Juncus effusus	Common rush	Juncaceae	Rushes-Herb	Early-mid	
Juncus tenuis	Slender rush	Juncaceae	Rushes-Herb	Early-mid	
Kinbergia oregana	Oregon beaked moss	Brachytheciaceae	Moss		
Kindbergia praelongum	Slender beaked moss	Brachytheciaceae	Moss		
Lactuca muralis	Wall lettuce	Asteraceae	Herb		
Leucolepis acanthoneuron	Menzies' tree moss	Mniaceae	Moss	Late	Logs, organic soil
Linnaea borealis	Twinflower	Caprifoliaceae	Shrub	Mid-late	Dry to moist
Lysichiton americanus	Skunk cabbage	Araceae	Herb	Mid-late	
Mahonia nervosa	Dull oregon-grape	Berberidaceae	Shrub	Mid-late	Dry to moist sites
Menziesia ferruginea	False azalea	Ericaceae	Shrub	Mid-late	Streambanks
Oligotrichum parallelum	Large hair moss	Polytrichaceae	Moss		Acidic soils
Oplopanax horridus	Devil's club	Araliaceae	Shrub	Late	Moist woods
Plagiomnium insigne	Coastal leafy moss	Mniaceae	Moss	Late	On humus
Plagiothecium undulatum	Flat moss	Plagiotheciaceae	Moss	Late	
Pleurozium schreberi	Red-stemmed feathermoss	Hylocomiaceae	Moss		
Polytrichum commune	Common haircap moss	Polytrichaceae	Moss	Mid-late	Moist forests
Polytrichum juniperinum	Juniper haircap moss	Polytrichaceae	Moss	Early-mid	Disturbed soils
Polystichum munitum	Sword fern	Dryopteridaceae	Fern	Early-mid-late	Moist forests
Populus balsamifera	Cottonwood	Salicaceae	Deciduous	Early-mid	Moist to wet sites
Prunus emarginata	Bitter cherry	Rosaceae	Deciduous	Early	Moist forests
Pseudotsuga menziensii	Douglas fir	Pinaceae	Conifer	Early-mid-late	Very dry to moist
Pteridium aquilinum	Bracken fern	Dennstaedtiaceae	Fern	Early-mid-late	Dry to wet sites
Racomitrium lanuginosum	Hoary rock moss	Grimmiaceae	Moss	Late	
Rhamnus purshiana	Cascara	Rhamnaceae	Shrub	Early-mid-late	Dry to wet sites
Rhizomnium glabrescens	Fan moss	Mniaceae	Moss	Late	Rotten logs, humus
Rhytidiadelphus loreus	Lanky moss	Hylocomiaceae	Moss		
Rhytidiadelphus triquetrus	Electrified cat' tail moss	Hylocomiaceae	Moss	Late	
Ribes bracteosum	Stink currant	Grossulariaceae	Shrub	Early-mid	Moist to wet sites
Rubus discolor	Himalayan blackberry	Rosaceae	Shrub	Early*	Streambanks
Rubus laciniatus	Evergreen blackberry	Rosaceae	Shrub	Early	
Rubus leucodermis	Black raspberry	Rosaceae	Shrub	Early	Disturbed sites

Rubus parviflorus	Thimbleberry	Rosaceae	Shrub	Early	Moderate moisture
Rubus pedatus	Five-leaved bramble	Rosaceae	Shrub	Late	Streambanks
Rubus spectabilis	Salmonberry	Rosaceae	Shrub	Early	Moist to wet
Rubus ursinus	Trailing blackberry	Rosaceae	Shrub	Early	Dry open sites
Salix sitchensis	Stika willow	Salicaceae	Tall shrub	Early	Wet openings
Salix commutata	Variable willow	Salicaceae	Tall shrub	Early	Wetland
Sambucus racemosa	Red elderberry	Caprifoliaceae	Tall shrub	Mid-late	Streambanks
Senecio sylvaticus	Wood groundsel	Asteraceae	Herb	Early*	Disturbed sites
Smilacina racemosa	False Solomon's seal	Liliaceae	Herb	Mid-late	
Solanum dulcamara	Bittersweet	Solanaceae	Herb		
Sonchus asper	Prickly sow-thistle	Asteraceae	Herb	Early	Disturbed sites
Sorbus sitchensis	Stika mountain-ash	Rosaceae	Shrub	Early	Streambanks
Sphagnum squarrosum	Shaggy sphagnum	Sphagnaceae	Moss		
Spiraea douglasii	Hardhack	Rosaceae	Shrub	Early-mid	Streambanks
Taraxacum officinale	Common dandelion	Asteraceae	Herb	Early	Disturbed sites
Thuja plicata	Western red cedar	Cupressaceae	Conifer	Mid-late	Moist to wet
Tiarella trifoliata	Foamflower	Saxifragaceae	Herb	Mid-late	
Timmia austriaca	False polytrichum	Timmiaceae	Moss	Early-mid	Calcium rich soils
Trientalis latifolia	Starflower	Primulaceae	Herb	Early-mid-late	Moist, bogs
Tsuga heterophylla	Western hemlock	Pinaceae	Conifer	Mid-late	Dry to wet
Vaccinium alaskaense	Alaskan blueberry	Ericaceae	Shrub	Mid-late	Moist forests
Vaccinium membranaceum	Black huckleberry	Ericaceae	Shrub	Early-mid-late	Dry to moist sites
Vaccinium ovalifolium	Oval-leaved blueberry	Ericaceae	Shrub	Early-mid-late	Bogs. Moist forests
Vaccinium parviflorum	Red huckleberry	Ericaceae	Shrub	Mid-late	Coniferous forests

Sources : Haeussler and Coates (1986); Klinka et al. (1989); Pojar and MacKinnon (1994); Plant Database: www.plants.usda.gov