THE EFFECTS OF NATURAL AND ANTHROPOGENIC DISTURBANCES ON THE STRUCTURE AND COMPOSITION OF EARLY-SUCCESSIONAL PLANT COMMUNITIES IN THE INTERIOR CEDAR-HEMLOCK (ICH) ZONE OF SOUTHERN BRITISH COLUMBIA

by

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Abstract

Wildfire is the primary natural disturbance in Interior Cedar-Hemlock (ICH) forests, and since the mid-20th century, forest harvesting (clearcutting, in this case) has become the primary anthropogenic disturbance type. Forest management in British Columbia is currently governed by a paradigm that maintains that biological diversity can be preserved by utilizing forest harvesting regimes that closely mimic "natural" disturbance regimes, but a question remains as to how closely these regimes mimic wildfire disturbances. More specifically, how do clearcutting and wildfires compare in their effects on the structure and composition of early-successional ICH plant communities? This study compares vegetation structure, composition, relative abundance and diversity among 39 sites that experienced either a stand-replacing fire or a clearcut within the last 40 years. Sites of different ages and disturbance types were located within the wet cool ICHwk1 and very-wet cool ICHvk1 biogeoclimatic variants near Revelstoke, B.C. For each site, overstory structural characteristics (tree and snag diameters, basal area and density), overstory composition, and surface fuels (volume of coarse woody debris (CWD)) were assessed. Understory vegetation percent cover, species richness, composition and diversity were also determined. Linear regression analysis was used to examine differences in each of these variables between disturbance types, over time. The trends in structural legacies (especially snag and CWD dynamics) varied greatly between wildfire and clearcut sites. Compared to burned sites, clearcut sites exhibited patterns of accelerated succession in several characteristics (overstory tree regeneration, vegetation cover and understory species richness) due to planting treatments and pre-disturbance relicts. Understory species composition also varied between disturbances, with clearcut sites containing more shade-tolerant survivors initially. Both disturbance types had similar levels of floristic diversity during early succession. These results suggest that clearcut harvesting may not emulate stand-replacing fires in terms of impact on early ICH plant succession in any aspect but diversity. However, it is unclear if these early-successional differences will continue through time. There is a need for further research in this ecosystem, as well as any other ecosystems where emulation silviculture is applied, in order to confirm that silvicultural effects mimic those of natural disturbance regimes.

Table of contents

List of Tables

List of Figures

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Dedication

For Trevor,
for his unfailing enthusiasm, support, understanding and confidence in my abilities
while I endeavoured to successfully complete it.

Co-Authorship Statement

A version of this thesis will be submitted for publication: Corriveau B.M. and M.C. Feller. 2008. The effects of natural and anthropogenic disturbances on the structure and composition of early-successional plant communities in the Interior Cedar-Hemlock (ICH) Zone of southern British Columbia.

This project was initiated by discussions between Dr. Michael Feller and B.M. Corriveau. The research program was developed by Dr. Feller and B.M. Corriveau, as an addendum to a research project that had already been initiated by Parks Canada. The Parks Canada research dealt with determining fire hazard in various ages of Interior Cedar-Hemlock forests in and around Revelstoke, B.C. B.M. Corriveau and Dr. Feller proposed to examine various successional forest characteristics following different disturbance types in the same forests. The design of the research program was based on the fire hazard measurements developed by Dr. Feller that were being used in the Parks Canada study; and by methods previously used by B.M. Corriveau in other successional studies. The literature research was performed by B.M. Corriveau, as well as all of the field research (with the help of a field crew). All data analyses were performed by B.M. Corriveau. The manuscript was completely written and prepared by B.M. Corriveau, with extensive input and feedback from Dr. Feller.

Britt M. Corriveau

Chapter I: Introduction

1.1 Natural and Anthropogenic Disturbances

Fire is a natural part of ecosystem function in most North American forest types. Suppression activities in the last century have resulted in a widespread build-up of fuels across many forest types (e.g. Albrecht and McCarthy, 2006; Steele et al., 2006; Collins et al., 2007). It is believed that this build-up has led to larger, more frequent, and more destructive fires than ecosystems have encountered to date, making suppression activities more difficult and costly (e.g. Collins et al, 2007). Moreover, fires that are more severe and of higher frequency can be very detrimental to species which have adapted to traditional fire regimes, and ecosystem function may be compromised (Shiplett and Neuenschwander, 1994). Concurrent with the suggested increase in the frequency and severity of fires in North American forests over the last century, there has been an increase in logging operations (Steele et al., 2006) which is often the most important anthropogenic disturbance in forests. The importance of understanding the impacts of these changing, and often more severe, disturbance regimes on forest succession can not be understated if appropriate forest management strategies are to be undertaken.

1.2 Factors Influencing Post-Disturbance Succession

Forest succession has been defined by Lyon and Stickney (1974) as the sequential development of dominance during which the forest community reverts to its pre-disturbance structure, with some random variations in composition and duration of seral stages. More to the point, it is a temporal change of forest stand composition and vegetation physiognomy from disturbance to an eventual stable climax community (Yang et al., 2005), which may be interrupted and reset by subsequent disturbance events. Succession is commonly described using revegetation rates, species composition, diversity, richness and structural characteristics, such as stand initiation and canopy closure.

Several contradictory theories have been put forth to describe the progression of succession in ecosystems with regards to species composition, diversity and richness. The intermediate disturbance hypothesis (IDH) put forth by Connell (1978) predicts that species richness will be highest in communities with moderate levels of disturbance. It assumes a trade-off exists between a species competitive ability and its tolerance to disturbances, rendering good competitors vulnerable to disturbance (Collins et al., 1995). At very high or low frequencies of disturbances, richness declines; at very long or short intervals of time since disturbance, richness also declines (Collins et al., 1995). A study by Collins et al. (1995) on prairie tall grass ecosystems only partially supported this theory, while many of the remaining results could have been explained instead by the initial floristic composition model (IFCM). This model was first suggested by Egler (1954), and refers to a system where all species are established immediately after the disturbance, followed by a progressive development of these species. It predicts that richness and diversity peak early in the seres (Hibbs, 1983), since all species are present at the beginning, and some will eventually outcompete others causing some species to become locally extinct (Collins et al., 1995).

These theories are based on relatively simple assumptions, yet they are limited as they only take into account survivorship and competition. The vital attribute theory (VAT) includes characteristics such as persistence, dispersal, establishment and life history to explain the progression of succession (Cattelino et al., 1979; Noble and Slatyer, 1980). This theory also includes the idea of multiple pathways of succession (Cattelino et al., 1979), rather than one simple pathway, which is fixed and highly predictable. The VAT may be the most useful theory of succession when addressing disturbances like wildfire in forested ecosystems. Cattelino et al. (1979) pointed out that the multiple pathway succession model can offer both descriptive and predictive capabilities when applied to natural communities exposed to various fire frequencies. More recently, Noble has continued upon this line of reasoning when he used the VAT to develop functional classifications of species following fires (Noble and Gitay, 1996). The VAT helps to explain more concrete observations of succession (like rates of recovery) and renders successional theory more generally applicable to a variety of ecosystems and disturbances by including more specific information about many of the factors that may affect succession following disturbances.

Rates of recovery of forest ecosystems following disturbances can vary widely since they are influenced by many factors. First, and perhaps most importantly, the type of the disturbance - its severity and its extent - will determine to which successional stage the community returns following the disturbance (Shiplett and Neuenschwander, 1994; Zach and Morgan, 1994; Yang et al., 2005). Disturbance type will also determine how much of the forest floor is lost or damaged (Feller, 1998), which will influence revegetation rates. The rate at which succession proceeds depends on the history of the site and the conditions following the disturbance, both biotic and abiotic (Zach and Morgan, 1994). The pre-disturbance successional stage, vegetation composition (Lyon and Stickney, 1974), climate and traditional disturbance regime will all influence the rate of recovery (Shiplett and Neuenschwander, 1994). The post-disturbance surviving vegetation, intact seed bank, neighbouring seed sources, seed dispersal and the competitive abilities and life histories of each species will not only affect the rate of recovery, but will also influence the successional trajectory of the ecosystem and the type of community that results (Lyon and Stickney, 1974; Noble and Slatyer, 1980; Shiplett and Neuenschwander, 1994; Coates, 2002). Likewise, the moisture regimes, nutrient availability (Kranabetter and Coates, 2004), light availability (Simard and Vyse, 2006) and soil stability following a disturbance can drastically affect the rate and trajectory of the forest's recovery.

With all of these complicated factors interacting, understanding succession in forests, particularly in more floristically diverse ones, such as the Interior-Cedar-Hemlock (ICH) forests (Ketcheson et al., 1991) of British Columbia, can be difficult. Prior to settlement by Europeans, secondary forest succession in the ICH zone was initiated primarily by wildfire of varying intensities and frequencies (Stickney, 1986; Anon., 1995). Though the community types in the mature ICH forests of B.C. have been described in impressive detail (Lloyd et al., 1990; Ketcheson et al., 1991), plant succession following natural disturbance is still not fully understood. There is some agreement regarding the general trend that natural post-disturbance succession follows. Initially, nearly all species, representing all seral and climax stages, are present, although herbs and shrubs are dominant. Dominance later shifts to shade-intolerant tree species, and their presence reduces light availability (canopy closure), thus eventually causing their own exclusion. The slower-growing shade-tolerant conifers then gain dominance and form the final climax association (Lyon and Stickney, 1974; Shiplett and Neuenschwander, 1994). What is not yet understood is the exact longevity of each successional stage, and how the successional trajectory will vary when disturbance type and other determining factors vary (Shiplett and Neuenschwander, 1994). This thesis will explore the dominant natural (wildfire) and anthropogenic (forest harvesting) disturbance regimes, currently present in the ICH zone of southern B.C., and the effects these disturbances have on plant succession.

1.3 Natural Disturbance: Fire in the Interior Cedar-Hemlock (ICH) Zone

The Interior Cedar-Hemlock (ICH) biogeoclimatic zone extends from west central British Columbia south to Idaho and Montana (Figure 1.1). It is a high-diversity, inland rainforest whose climax communities are dominated by western red cedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*) (Ketcheson et al., 1991). The natural disturbance regime of ICH forests involves relatively infrequent disturbances, with wildfire as the main disturbance type followed by insects, pathogens and windthrow (Lewis and Lindgren, 2000; DeLong et al., 2005). In the drier areas of the ICH zone, fire plays an important role and ensures that climax stands are interspersed with successional stands (Ketcheson et al., 1991). Prior to European settlement (c. 1760's), the fire disturbance frequency varied widely in this biogeoclimatic zone, with average fire return interval (FRI) estimates ranging between 150-500 years (Parminter, 1992; Shiplett and Neuenschwander, 1994; Van Wagner et al., 2006) to 64-603 years (Sanborn et al., 2006) depending on the subzone. These natural wildfires, ignited primarily by lightning strikes, were typically between 150-1400ha in size (Parminter, 1992; Rogeau, 2000) and usually burned in the late-summer dry season (Lyon and Stickney, 1974). This varied burn frequency ensured that seral community types in all stages of succession were well represented across the landscape (Shiplett and Neuenschwander, 1994). Between the 1760's and the 1940's, there was a sharp drop in burning rates, possibly due to the cooler, wetter conditions experienced at that time (Van Wagner et al., 2006). After 1940, fire suppression efforts increased and a continued drop in fire frequency was observed (Van Wagner et al., 2006). This drop may have been counteracted slightly by the increase in ignition frequency (introduction of human-caused fires) and the increasing fuel loading resulting from suppression. However, despite this research, detailed fire history studies of the ICH are few (Arno, 2000) and there are still uncertainties regarding the effects of fire on the ecosystem (Shiplett and Neuenschwander, 1994).

Figure 1.1 has been removed due to copyright restrictions. The information removed is a map of the Interior Cedar-Hemlock (ICH) zone throughout British Columbia. It was obtained from: Ketcheson M.V., T.F. Braumandl, D.Meidinger, G. Utzig, D.A. Demarchi and B.M. Wikeem. 1991. Chapter 11: Interior Cedar-Hemlock Zone. In: Ecosystems of British Columbia. Eds. D.V. Meidinger and J. Pojar. Research Branch. B.C. Ministry of Forests. SRS06. pp 167-181.

Figure 1.1. The distribution of the Interior Cedar-Hemlock Zone in British Columbia (from Ketcheson et al., 1991).

Many studies have described the effects of forest fires on succession in a variety of North American forest ecosystems, and for a variety of different fire severities (e.g. Agee, 1993; Turner et al., 1997; Doyle et al., 1998; Albrecht and McCarthy, 2006; Franklin et al., 2006). A common finding is that succession following fires often returns the area to its pre-fire community composition and structure, due to extensive biotic residuals (rhizomes and roots at moderate fire severities, seeds at higher severities) persisting in the burn area (Turner et al., 1997; Doyle et al., 1998). Fires are natural disturbances and species have had time to evolve adaptations to survive them. These adaptations permit certain species to persist and dictate the composition of future communities. This, of course, is not the case for all species. In the mixed-conifer forests of southern California, a large fire drastically reduced conifers, but promoted oaks (*Quercus* sp.) instead, which is an alternate stable state of this ecosystem (Franklin et al., 2006). The conifer seedlings had difficulty establishing, while the oak trees re-sprouted (Franklin et al., 2006). In some forest ecosystems, periodic fires can also control the encroachment of opportunistic species permitting economically valuable species to persist (Albrecht and McCarthy, 2006). This has been one of the reasons for the prescribed burning of forests.

Within ICH forests, few attempts have been made to describe the variable effects of fire on plant succession, and the majority of that research was performed in the cedar-hemlock forests of Montana and Idaho (e.g. Habeck, 1968; Lyon and Stickney, 1974; Shiplett and Neuenschwander, 1994; Brown and Smith, 2000). Lyon and Stickney (1974) characterized plant succession for 10 years following three large, intense, wildfires in different forest types within the cedar-hemlock zone of the US. They found that pre-disturbance vegetation played a very important role in determining post-fire species composition (Lyon and Stickney, 1974). Also, as in other forest ecosystems, most plant species on-site at the time of the fire survived (as mature individuals, viable seeds or rhizomes) and re-established, while a smaller proportion of the species assemblage originated from colonization by nearby species that were good dispersers (Lyon and Stickney, 1974). All dominants of early succession became established in the initial post-fire growing season (Lyon and Stickney, 1974). Knowing the initial post-fire species composition has allowed predictions of early-successional vegetation composition to be made. Shiplett and Neuenschwander (1994) have described five different successional chronologies following fire in the ICH forests of northern Idaho, which result in different early-successional pathways. The chronologies varied with pre-disturbance community types, fire frequency, intensity and severity. During the first 60-80 years, successional trajectories appeared quite different. The different fire severities/intensities and pre-burn communities seemed to have important effects on early succession in ICH forests, but the communities all seemed to tend towards a common cedar-hemlock dominated climax community when fire is the disturbance type (Shiplett and Neuenschwander, 1994). This finding was corroborated by Lyon and Stickney (1974) who noted that despite different initial successional trajectories, the communities ultimately had similar assemblages of plant life. However, it should be noted that the chronologies reported by Shiplett and Neuenschwander (1994) were idealized situations and, even without the interactions of anthropogenic factors, may vary substantially with fire severity, climate and ecosystem.

The adaptations of many North American forest species to wildfire allow succession to begin immediately following the fire, and although factors like fire severity may cause successional trajectories to vary initially, the trend has been towards a final assemblage that was similar to the pre-fire community.

1.4 Anthropogenic Disturbance: Logging in the Interior Cedar-Hemlock (ICH) Zone

Over the last century, the dominant forms of forest disturbance in the ICH zone have been fire and timber harvesting (DeLong et al., 2005). In some ICH forests, as in northern Idaho, logging has become a more important disturbance factor than fire, in terms of area affected

(Shiplett and Neuenschwander, 1994). Also, disease and insects still play important roles. Thus, there are a variety of disturbance types which result in very diverse disturbance patterns across the landscape (DeLong et al., 2005).

Clearcut logging in the ICH zone of southern British Columbia began in the 1930's (B.C. Ministry of Forests silviculture database, accessed January 2007). There are 14 commercially valuable tree species in the ICH zone (DeLong et al., 2005). Until recently, most timber harvesting operations in the area were exclusively clearcutting (B.C. Ministry of Forests forest cover maps, accessed January 2007). More recently, some partial retention harvests have been implemented, when a change in public perception prompted forestry practitioners to address values beyond timber production (DeLong et al., 2005). However, in general, harvesting in the ICH forests of southern B.C. consists of clearcutting, followed by planting of valuable conifer species, such as *Pinus* or *Picea* species. Further site preparation, in some capacity, usually occurs in the form of slash burning, mounding and/or subsequent brushing in order to remove broadleaf competitors (Simard and Vyse, 2006). These harvesting methods can result in drastically different species assemblages than those there previously. For example, often the tree species planted following harvesting are not the same as those that previously dominated the overstory (McRae et al., 2001).

This leads one to ask how altering disturbance frequency and type might affect plant successional trajectories in the ICH forests. Do these harvesting regimes cause succession to proceed differently than natural fire regimes do? When compared with research on the effects of fire, there has been less research, in general, regarding the long-term effects of harvesting on ecosystem structure and function. This information gap is surprising given the indications from other studies that post-disturbance conditions following clearcutting can differ drastically from most natural disturbances in everything from community types to structural legacies (Nuguyen-Xuan et al., 2000; Franklin et al., 2002). Clearcuts can be extremely variable in size, severity and in effects on ecosystems (McRae et al., 2001). This variability reinforces the need for more research in this area.

Some experimental work has been performed to determine the effects of forest harvesting on the structure, composition and diversity of the vegetation in various forest ecosystems. In the Appalachians, Elliot et al. (1997) performed a twenty-year study that looked at changes in species composition and diversity following clearcutting. In the mixed-wood boreal forests of Alberta, MacDonald and Fenniak (2007) studied the richness, diversity and composition of understory vascular plant communities before and up to 2 years following clearcut and variable retention harvesting. In general, these studies found that clearcutting was the most extreme harvesting regime, causing the greatest alterations in subsequent species assemblage primarily by removing potential relict seed sources, promoting certain opportunistic species and by causing the most damage to the forest floor (highest severity).

Within the last 10 years, several studies have taken a modelling approach to quantify the effects of harvesting on forest succession. These models are useful as they are often versatile and transferable to different ecosystems. One such study, by Yang et al. (2005), used a combination of modelling and aerial photographs of clearcut areas in Oregon to determine the early-successional pathways of the forests there. The general trend found was a rapid occupation of herbaceous life forms followed by a gradual return to closed-canopy recovery (predominantly conifer) for most of the stands (Yang et al., 2005). Similar to findings in cedar-hemlock forests after fire (Lyon and Stickney, 1974; Shiplett and Neuenschwander, 1994), Yang et al. (2005) found that the process of returning to conifer-tree-domination was not the same for all stands, with many successional trajectories being manifested. Roberts (2007) developed a conceptual model for the early-successional boreal forest to characterize disturbance severity with varying forest harvesting regimes by concentrating primarily on its effects on the herbaceous layer (a good indicator of severity), while still considering shrubs and trees. As previously mentioned, the severity of the disturbance is one of the factors that determine the successional trajectory following the disturbance. Roberts (2007) found that within the first year, total species richness decreased after all harvesting treatments, and that clearcutting with site preparation was the treatment that caused the most species loss and disturbance in general, thereby agreeing with Elliot et al. (1997) and MacDonald and Fenniak (2007). Importantly, Robert's (2007) model provides a basis for comparing forest harvesting treatments to natural disturbances, in their effects on ground vegetation.

With regards to harvesting effects on succession in the ICH zone in B.C., there has been even less reported research. Coates et al. (1997) described the Date Creek study which involved the assessment of the effects of forest harvesting on ICH vegetation succession and stand dynamics, but results of this aspect of the study have apparently not been reported. Coates (2002) examined tree recruitment in clearcuts vs. smaller canopy gaps in the ICH zone and found that recruitment was poorest on large clearcuts due to a combination of unfavourable micro-climate and lack of seed source. Kranabetter and Coates (2004) compared the effects of silvicultural systems 10 years post-harvest on conifer nutrition and the availability of soil resources in a northern ICH subzone. In general, they found that clearcutting had the most influence on forest floor depth, pH and moisture and also net N loss, and was therefore the most severe harvesting treatment when compared to partial-cut and unharvested treatments (Kranabetter and Coates, 2004). Despite clearcutting resulting in much greater height increments for regeneration, Kranabetter and Coates (2004) predicted that other destructive effects (especially N loss) would ultimately negatively impact tree growth more than in the other harvesting treatments.

Forest harvesting is a common anthropogenic forest disturbance in North America. As such, further research is needed, both experimental and modeling, to ensure that forest managers are well informed on the effects such practices have on ecosystem structure and function.

1.5 Natural vs. Anthropogenic Disturbance: Management Implications & Current Research

Management of the ICH forests of B.C. depends on an understanding of forest processes. Given the current ICH disturbance regimes, managers need to know how successional plant communities change over time and how the existing vegetation will respond to different types of disturbance (Zach and Morgan, 1994). Research indicates that most of the important processes that will determine the future form and function of a forest community, including tree seedling recruitment (Coates, 2002), occur in the earlier stages of succession (Lyon and Stickney, 1974; Shiplett and Neuenschwander, 1994). Early succession is therefore of interest if the manager wishes to predict which community will likely result from a disturbance.

This raises the question: How do fire and logging disturbances affect the early-successional trajectory of ICH forests? Fire and clearcutting are, in some ways, comparable (McRae et al., 2001). Both disturbances will return a seral or climax community to a much earlier stage of succession. Also, both disturbances often increase species diversity in the short term (McRae et al., 2001). However, fire and clearcutting can vary greatly in their effects on an ecosystem (McRae et al., 2001; Uotila and Kouki, 2005; Collins et al., 2007). For example, clearcutting sometimes initially results in uneven-aged stands due to the presence of advanced and post-disturbance regeneration, while severe wildfires usually result in even-aged regeneration (McRae et al., 2001). Harvesting often favours angiosperms (McRae et al., 2001) and therefore, resulting stands sometimes have less conifer dominance than do post-fire stands. The differences in successional trajectories that may exist between disturbance types have not been explored in the ICH forests of B.C.

This study compares early plant succession in stands in the ICH forests near Revelstoke B.C., that have been burned or clearcut from 0 to 40 years prior to field sampling. The specific objectives of this study were to test whether:

a) disturbance type influences overstory tree structure and composition, as well as surface fuel dynamics of early-successional ICH forests (Chapter II);

b) disturbance type influences understory plant structure, composition, richness and diversity of early-successional ICH forests (Chapter III);

c) rates of revegetation and early plant successional patterns will differ with disturbance type (Chapter III).

Plants are excellent indicators of disturbance severity and post-disturbance nutrient and moisture regimes, and the order in which certain indicator species appear in the community helps to define seral stages (Lloyd et al., 1990; Ketcheson et al., 1991).

Managers need a comprehensive understanding of natural stand development processes when designing silvicultural systems that integrate ecological and economic objectives, including a better appreciation of disturbance regimes (Franklin et al., 2002). Forest management in B.C is currently governed by a paradigm that maintains that biological diversity can be preserved by utilizing forest harvesting regimes that closely mimic "natural" disturbance regimes (Anon., 1995). By understanding vegetation patterns in the early-successional stages following natural and anthropogenic disturbances, better informed management decisions may be made to reach these specified goals.

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Chapter II: The effects of wildfire and forest harvesting on early-successional overstory structure and composition, and on surface coarse woody debris in the Interior Cedar-Hemlock zone of British Columbia[1]

2.1 Introduction

In most North American forest ecosystems, wildfire is the most important natural disturbance type (McRae et al., 2001). Fire is an integral part of ecosystem function, maintaining biodiversity (Rogeau, 2000) and creating a patchy mosaic of stands of different ages, structure and compositions across the landscape (Shiplett and Neuenschwander, 1994; McRae et al., 2001). Suppression activities in the last century have resulted in a widespread build-up of fuels across many forest types (e.g. Albrecht and McCarthy, 2006; Steele et al., 2006; Collins et al., 2007). It is believed that this build-up has often led to a greater frequency and severity of wildfires than ecosystems have encountered to date (Swetnam et al., 1999). There has also been a significant increase in forest harvesting in North American forests (Steele et al., 2006), which today can be the most important anthropogenic disturbance type. The frequency of forest harvesting (dictated by rotation age or socio-economic factors) is also generally very different from typical fire return intervals (which can vary widely) (McRae et al., 2001). Forested ecosystems are therefore exposed not only to an overall increased frequency of disturbance, but also to a completely different, and hitherto un-encountered disturbance type in the form of harvesting. Changes in disturbance regimes can affect forest structure and composition, such as: altering coarse woody debris patterns, shifting forest age structure, thereby

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increasing the proportion of young stands, and changing species composition (Kurz et al., 1995). It is imperative that the effects of these changing disturbance regimes are understood by managers in order to conserve biodiversity and to meet other ecological and economic goals (Franklin et al., 2002).

There are several similarities in the effects of wildfire and forest harvesting disturbances on forest species composition and abundance. On a larger scale, both create large gaps in the canopy in a mosaic over the landscape. These gaps are at an earlier stage of succession, creating habitat for ungulates and other species (Ketcheson et al., 1991). At a stand scale, both modify overstory structure significantly by removing overstory trees, thus reducing basal area and canopy closure, and ultimately increasing the potential growing space in the understory (Collins et al., 2007). This encourages resprouting and the establishment of regenerating seedlings. Both disturbance types also generate an increase in coarse woody debris (CWD) on the forest floor, the presence of which is critical for the conservation of biodiversity (McRae et al., 2001).

Despite these similarities, fire and forest harvesting are fundamentally different in their nature (e.g. chemical versus mechanical). They can also vary in intensity, size, frequency, and homogeneity resulting in widely contrasting starting points for stand development (Franklin et al., 2002). At the stand level, wildfires and harvesting differ in their patterns of structural legacies (Franklin et al., 2002). For example, wildfires leave large numbers of snags and abundant coarse woody debris, while some types of harvesting typically leave few standing trees and not much large debris (McRae et al., 2001). In general, severe wildfires often create even-aged stands while harvesting may create uneven-aged stands due to advanced regeneration followed by post-disturbance seedlings (McRae et al., 2001). Or conversely, wildfires can create a multi-aged stand which is a mixture of fire-damaged living and dead trees, while harvesting can simplify stand structure by creating a single cohort of regenerating trees (Lindenmayer and McCarthy, 2002). Logging is also very specific as to the age and composition of stands selected for harvesting in each forest type, where fires are somewhat less selective in the age and composition of vegetation they consume. At the landscape level, forest harvesting frequencies and the size of the cutblocks differ from those of natural fire patterns, so harvesting does not maintain natural stand-age distributions (McRae et al., 2001). McRae et al. (2001) considered that in certain forests, harvesting tends to favour angiosperm trees and can result in less dominance by conifers, although this may not be the case for B.C. The fundamental differences between each disturbance type can create very different initial stand species composition, ages and other characteristics.

Because of these differences, emulation silviculture is gaining popularity. Emulation silviculture is the use of silvicultural techniques that try to imitate natural disturbances such as wildfire (McRae et al., 2001). It offers a guiding principle to forest managers, along with an appealing tool set for dealing with ecological issues important to the domestic and international public (McRae et al., 2001). Forest management in B.C. is currently governed by a paradigm that maintains that biological diversity can be preserved by utilizing forest harvesting regimes that closely mimic "natural" disturbance regimes (Anon., 1995). This concept has become controversial. In some cases, silvicultural methods can emulate the effects of natural disturbances quite successfully, as with some fuel reduction treatments (Collins et al., 2007). However, in others, such as Australian montane ash forests, Lindenmayer and McCarthy (2002) found that current harvesting regimes were inconsistent with the effects of the natural wildfire disturbance regime. However, aside from the boreal and sub-boreal forests, there appears to be a lack of research to verify that current practices do indeed 'mimic' natural disturbances in

Canadian forest ecosystems. For example, do current harvesting regimes and wildfires have similar effects on forest structure and composition through time?

The Interior Cedar-Hemlock (ICH) zone of southern interior B.C. is one of these forest ecosystems where emulation silviculture is presumed, but whose successional patterns following natural and anthropogenic disturbances are not fully understood. The natural disturbance regime of ICH forests involves relatively infrequent wildfire as the main disturbance type, as well as gap phase disturbances due to insects, pathogens and windthrow (Shiplett and Neuenschwander, 1994; Lewis and Lindgren, 2000; DeLong et al., 2005). Forest harvesting, the vast majority of which is clearcutting, began in the 1930's and since 1990, more than 184 000 ha of forest has been cut in the ICHmw, ICHvk and ICHwk biogeoclimatic subzones[2] (B.C. Ministry of Forests and Range silviculture database, accessed January 2007). Though the community types in the ICH forests of B.C. have been described in impressive detail (Lloyd et al., 1990; Ketcheson et al., 1991), plant succession is still not fully understood. There is some agreement regarding the general trend that natural post-disturbance succession follows in the U.S.A. (Lyon and Stickney, 1974; Shiplett and Neuenschwander, 1994). What is not yet understood is the longevity of each successional stage, and how the successional trajectory will vary when disturbance type and other determining factors vary (Shiplett and Neuenschwander, 1994).

Given the context of emulation silviculture, in this chapter I will compare the effects of wildfire and forest harvesting on early-successional forest stand structure and composition in the ICH zone of southern B.C. More specifically, this study aims to test whether disturbance type influences forest structural characteristics in early-successional ICH forests, to predict the structure and composition of the forest that will result after 40 years of succession depending on

[2] These are the ICH moist-warm, very wet-cool and wet-cool subzones, respectively. These subzones are described in more detail in Appendix I.

disturbance type, and to provide a better understanding for forest management purposes of early-successional patterns in the ICH following wildfire and harvesting.

The type of fire and harvesting activities that are compared are stand-replacing fires and clearcuts specifically. High-severity, stand-replacing fires were chosen since a) severity is the property of fire that most influences forest vegetation and propagules (Stickney and Campbell, 2000) and b) fires in the ICH have generally resulted in stand replacement (Shiplett and Neuenschwander, 1994; Anon., 1995; McRae et al., 2001). Low severity fires were excluded as they cause very little regression in the dominant overstory (Shiplett and Neuenschwander, 1994), and both large wildfires and intense logging activities result in stand replacement (Nuguyen-Xuan et al., 2000). Clearcutting is the most common type of forest harvesting practiced in Canada, representing approximately 90% of all annual harvesting operations (Stocks and Simard, 1993). Also, clearcutting is, and has historically been, the most common forest harvesting method used in the ICH (Vyse and DeLong, 1994). Clearcutting has been considered most similar to fire of all types of logging in its effects on living standing trees and on surface fuels (Shiplett and Neuenschwander, 1994). Partial cutting yields many vegetation complexes (Delong and Butts, 1994) rendering it less comparable to wildfires than clearcutting. Fires in cedar-hemlock forests are generally intense crown fires which can kill the existing overstory, thus renewing the successional pathway (Shiplett and Neuenschwander, 1994). Therefore, there is merit in comparing successional pathways of clearcuttting and stand-replacing fires in the ICH zone, given their assumed similar influences on ecosystems (McRae et al., 2001).

I hypothesize that disturbance type is an important determinant of post-disturbance stand structure and specifically that clearcutting will result in a different stand structure (tree species composition, size density) and surface coarse woody debris volume than will severe wildfires, during the first 40 years following disturbance.

2.2 Methods

Study Area

The study area was restricted to the Interior Cedar-Hemlock (ICH) zone surrounding Revelstoke, B.C. The ICH zone (Figure 1.1), an inland rainforest that stretches from west central B.C. south to Idaho and Montana, is found at low to mid elevations (400-1500m) (Ketcheson et al., 1991). In southeastern B.C., it occupies the lower slopes of the Columbia Mountains and the western side of the continental divide along the Rocky Mountains (Ketcheson et al., 1991). This zone's climate is characterized by cool wet winters and warm dry summers. Mean annual precipitation is 500-1200mm, 25% to 50% of which falls as snow (Ketcheson et al., 1991). Average annual temperatures in the ICH zone range from 2 to 8.7 ^{o}C, which reflects its latitudinal range (Ketcheson et al., 1991). Soils in zonal ecosystems are primarily Humo-Ferric Podzols, or Brunisolic or Orthic Gray Luvisols with finer textured parent materials (Ketcheson et al., 1991).

The ICH zone has the highest diversity of tree species of any biogeoclimatic zone in the province (Ketcheson et al., 1991). On a single site in the ICH zone, up to ten tree species can co-exist (Simard and Vyse, 2006). Mature ICH climax forests are generally dominated by western hemlock (*Tsuga heterophylla*) and western red cedar (*Thuja plicata*). Common seral species include western larch (*Larix occidentalis*), Douglas-fir (*Pseudotsuga menziesii* var. *glauca*), western white pine (*Pinus monticola*), ponderosa pine (*Pinus ponderosa*), interior spruce (*Picea engelmannii x glauca*), white spruce (*Picea glauca*), subalpine fir (*Abies lasiocarpa*), lodgepole pine (*Pinus contorta* var. *latifolia*), trembling aspen (*Populus tremuloides*), black cottonwood (*Populus trichocarpa*) and paper birch (*Betula papyrifera)* (Lloyd et al., 1990; Ketcheson et al., 1991).

The ICHwk1 and ICHvk1 biogeoclimatic variants were chosen for study because they contain ample potential clearcut sites and the majority of recent ICH wildfires. These variants are characterized by wet-cool and very-wet-cool climates, respectively, which sets them apart from the other drier ICH variants. They occur at mid- to high-elevations (650-1300m), below the Engelmann spruce – subalpine fir (ESSF) zone and above the moist warm ICHmw subzone, throughout the wet Columbia and Selkirk mountain ranges (Lloyd et al., 1990). The ICHvk1 occurs upslope of the ICHwk1, and is wetter and cooler (Lloyd et al., 1990). The climax tree species of both variants are western red cedar and western hemlock, and seral overstory species (western white pine, Douglas-fir and interior spruce) appear on drier site series. Appendix I includes further information on ICH subzones and site series.

Disturbance Regimes

In ICH forests, many wildfires tend to have high intensities and severities and are therefore stand-replacing (Shiplett and Neuenschwander, 1994; McRae et al., 2001). The Natural Disturbance Type (NDT) of the ICHvk and ICHwk subzones is described as NDT1, which are ecosystems with rare stand-initiating events (Anon., 1995). The mean return interval for these disturbances is generally 250 years (Anon., 1995). Fires in the Revelstoke area are typically caused by lightning strikes, usually on steep slopes in mid to high elevations (Glen Burgess, Fire Protection Officer, Revelstoke, B.C., Personal Communication).

Typical clearcut logging methods in the area are determined by slope and road access. When road access is unavailable, helicopter logging is utilized. Cable logging occurs on steep slopes (approximately 30%-40%) with road access. Trees are hand felled and skidded to a landing using the cable to avoid machine damage to the slope. At the landing, the trees are bucked to length and limbed, and the waste is either piled below the landing or burned in piles on the landing. When slopes are gentle (<30%), ground skidding and machine felling is used in the winter to minimize soil damage. The trees are bucked and de-limbed at the landing, as in cable logging. Planting often occurs without any site preparation. Historically, broadcast burning was performed to reduce slash to facilitate planting. However, more recently, the size and shape of the cutblocks has prevented burning, and so planters must plant through the slash. The proportion of cable logging to helicopter logging to ground skidding used by the Revelstoke Community Forest Corporation (RCFC) is 70%, 10% and 20% respectively. (Del Williams, RPF Operations Forester, RCFC, personal communication).

Study Site Selection

Study sites (Figure 2.1) were selected according to criteria to minimize the confounding effects of factors such as varying fire severities and ecosystem types. These criteria were:

A) Disturbance type: In general, efforts were made to standardize each disturbance type to facilitate comparisons. Each disturbance type was also defined based on what is typical of the area, to increase the study's relevance and applicability. Since wildfires tend to be stand-replacing in the ICH, all of the sites in this study were selected with a minimum of 95% mortality of overstory trees. The studied fires were lightning-caused wildfires or escapes from prescribed-burning operations. Fire sites had an average slope of 69% and an average elevation of 850m. No sampling was performed in areas where the fires had been partially salvage logged.

Figure 2.1 has been removed due to copyright restrictions. The information removed is a geographical map of British Columbia centered on Revelstoke, with this study's site locations indicated. It was obtained from: The Atlas of Canada, Natural Resources Canada.
Available online at: http://atlas.nrcan.gc.ca/site/english/index.html

Figure 2.1: Map of study area, with approximate study site locations indicated for fires (yellow) and clearcuts (red). Note that more than one study site may be located in each indicated location.

The clearcut study sites had an average slope of 35% and an average elevation of 712m. These sites were typical of the actual clearcutting practices in the area. This required considering the prevalence of each clearcutting method. Due to site slopes, approximately 70% of the sites were clearcut using cable logging, none of the sites were logged via helicopter, and approximately 30% were logged using ground skidding in the winter. Consequently, the study sites are a good representation of the actual proportional prevalence of these logging methods in the area. Clearcuts with broadcast burning were avoided. All areas disturbed by post-harvesting site preparation (e.g. by herbicides or by mounding) were avoided. Some clearcut sites (29%) had been planted. Planted species were typically interior hybrid spruce and interior Douglas-fir. The lower-than-average proportion of planting represented in the study sites is explained by timing. Planting generally occurs within 2-3 years of logging, and many of the most recent clearcuts had not yet been planted at the time of sampling (Table 2.1).

B) Ecosystem and topography: all sites occurred in the ICHwk1 and ICHvk1, on similar site series that were as close to zonal as possible (Appendix I). Site series and topography were necessarily as uniform as possible within the site.

C) Access: road access to sites was required to facilitate field sampling. All sites were within 1000m of an active road.

D) Distance from Revelstoke: All sites were within a 1.5 hour drive from the base of operations in Revelstoke B.C. to maximize the time spent sampling in the field.

E) Size: sites were large enough to accommodate three $100m^2$ overstory plots, while maintaining a buffer of a minimum of 10m to the edge of the disturbed area. All fire sites were > 0.25 ha and all clearcut sites were > 1.5 ha.

F) Pre-disturbance community: given its great importance in determining the composition and abundance of the post-disturbance community, efforts were made to standardize the type of pre-disturbance community on a site. Each disturbed site studied was preceded by a mature to old ICH forest, at least 100 years old (verified by stumps and forest cover maps).

Table 2.1: Complete list of study sites, including ecosystem, site treatment and location information.

site id	disturbance	years since disturbance	planting/site preparation	subzone/ variant	site series	location name	elevation (m)	UTM coordinates
111	fire	1	salvage logging avoided	wk1	03	Transcan West, Bell Pole	525	0410224; 5649391
112	fire	1	salvage logging avoided	wk1	03	Transcan West, Bell Pole	525	0410224; 5649391
113	fire	1	none apparent	wk1	03	French Creek	924	0409311; 5718807
114	fire	1	none apparent	wk1	03	French Creek	930	0409299; 5718848
115	fire	1	salvage logging avoided	wk1	03	behind Bell Pole logging	525	0410224; 5649391
121	fire	4	salvage logging avoided	vk1	02	Downie, Oak Street	1145	0428564, 5692038
122	fire	9	none apparent	wk1	03	Goldstream, Blackfoot Trail	1008	0416942; 5718521
123	fire	9	none apparent	wk1	03	Goldstream, Blackfoot Trail	1025	0416921; 5718455
124	fire	4	none apparent	wk1	03	Carnes	805	0418413; 5682951
125	fire	4	none apparent	wk1	03	Carnes	805	0418413; 5682951
131	fire	16	none apparent	wk1	03	Downie, Sorcerer	927	0417793; 5705183
132	fire	16	none apparent	wk1	03	Downie, Sorcerer	956	0417762; 5705221
211	clearcut	2	none apparent	vk1	05	Downie	716	0409456; 5708825
212	clearcut	1	none apparent	vk1	04	Downie	771	0409020; 5708939
213	clearcut	1	planting (Douglas-fir)	vk1	05	Carnes	807	0419138; 5682342
214	clearcut	1	planting (Douglas-fir)	vk1	05	Carnes	807	0419138; 5682342
215	clearcut	0	none apparent	vk1	04	Downie, Sorcerer	807	0417208, 5704305
216	clearcut	0	none apparent	wk1	03	3 Valley Gap	607	0397125; 5642435
217	clearcut	1	planting (Interior spruce)	wk1	03	3 Valley Gap	730	0400603; 5644060
221	clearcut	10	none apparent	wk1	04	Downie	776	0419977, 5701576
222	clearcut	10	none apparent	wk1	04	Downie	776	0419977, 5701576
223	clearcut	9	none apparent	wk1	04	Laforme	1070	0418193, 5674535
224	clearcut	9	none apparent	wk1	04	Laforme	1070	0418193, 5674535
225	clearcut	7	none apparent	wk1	04	Goldstream, Blackfoot Trail	863	0417004; 5718865
226	clearcut	9	none apparent	wk1	04	Downie, Hemlock	696	0408273; 5707857
227	clearcut	9	none apparent	wk1	05	Downie, Hemlock	649	0407417; 5707599
231	clearcut	12	planting (Western red cedar)	wk1	03	Hwy 23 North	597	0414768; 5677154
232	clearcut	15	planting (Douglas-fir)	wk1	03	Hwy 23 North	605	0414860, 5677116
233	clearcut	11	none apparent	wk1	05	Downie	776	0417841, 5704765
234	clearcut	11	none apparent	wk1	05	Downie	776	0417841, 5704765
235	clearcut	11	none apparent	wk1	05	Downie	610	0404663, 5706183
236	clearcut	12	planting (Douglas-fir)	wk1	01	Transcan East, Greely	537	0423245, 5651877

Table 2.1 continued:

site id	disturbance	years since disturbance	planting/site preparation	subzone/ variant	site series	location name	elevation (m)	UTM coordinates
237	clearcut	12	planting (Douglas-fir)	wk1	01	Transcan East, Greely	537	0423245, 5651877
238	clearcut	14	none apparent	wk1	03	3 Valley Gap	719	0397172; 5641304
241	clearcut	29	none apparent	wk1	03	Westside Road	603	0415390; 5656978
242	clearcut	29	none apparent	wk1	03	Westside Road	620	0416348; 5657862
243	clearcut	33	none apparent	wk1	03	Hwy 23 North	587	0414301; 5678109
244	clearcut	18	planting (Interior spruce)	wk1	05	Downie, Sorcerer	490	0417650, 5704944
245	clearcut	33	none apparent	wk1	03	Hwy 23 North	620	0415225; 5676267

G) Age: Though wildfires have been historically ubiquitous, logging operations in the ICH forests near Revelstoke have only occurred over the last 80 years. Substantial logging in the ICHwk1 and ICHvk1 variants did not start until 1961 and 1970, respectively, according to the silvicultural database of the B.C. Ministry of Forests and Agriculture (M. Feller, UBC Forest Sciences Department, personal communication). To date, the areas logged in the ICHwk1 and ICHvk1 variants exceed 61 000 ha and 26 000 ha, respectively. This study was therefore restricted to an early-successional timescale which, in the ICH zone, is described as taking place in the first 40 years following disturbance (Zach and Morgan, 1994).

The design involved sampling two disturbance types over time. Time was measured in "years since disturbance" in this case. Sampling was to occur in forests where clearcutting or a stand-replacing fire had occurred within the last 40 years (1967 to 2007). For sampling purposes, sites were selected within pre-determined age classes. The age classes were defined respectively as: 0-2, 3-10, 11-17, and 18-40 years since disturbance. These age classes were designed to provide appropriate resolution for periods of succession when rapid changes are predicted to occur (Dr. Suzanne Simard, UBC Forest Sciences Department, personal communication).

Sites were initially located using GIS forest cover maps (Integrated Land Management Bureau, Government of B.C., updated January 2006), B.C. Ministry of Forests and Range forest cover maps (accessed January 2007) and fire location maps for the area around Revelstoke. These methods were supplemented by extensive in-situ ground-based scouting. Study site suitability, age and disturbance type were then assessed from the ground. When an acceptable site was located, elevation and UTM coordinates were noted using a GPS unit (Garmin GPS12). Slope and aspect were also noted.

Finalization of study site selection depended on all of the above characteristics, and also on how reliable the available information was with regards to these characteristics. For example, certain areas, like Downie Creek (Figure 2.1), contained more sites than other areas due partially to its high level of logging activity and also due to the excellent quality of logging information and up-to-date maps that were available.

Field Methods

Three 10 x 10m square, non-overlapping, overstory plots were randomly placed in each study site (Figure 2.2). The north-west corner of each overstory plot was randomly located within the acceptable area of the site. If a random location was selected for a plot and was deemed unsuitable because it occurred in a seepage area for example, the plot location was randomly selected again. These plots were buffered by a minimum of 10m from the edges of the cut block or fire to avoid edge effects. The slope and aspect of each overstory plot were noted.

These 10 x 10m overstory vegetation plots were used to determine structural characteristics and various measurements of the live trees and snags present. Using methods from Feller and Pollock (2006), one of the largest early-successional live trees inside the plot was cored for age verification. A core was extracted from those trees using an increment borer and the rings were subsequently counted. The diameters at breast height (DBH) of all trees higher than 1.3m were measured and the species were noted. Furthermore, the DBH was measured for each snag. Snag species was also noted where identification was possible.

Coarse woody debris (CWD) was measured using a line transect method described by Feller and Pollock (2006). Starting in the northwest corner of each overstory plot, triangular CWD plots were systematically placed. These plots were equilateral triangles with 20m sides (60m of total line).

Diameters of all CWD pieces were measured at their point of intersection with the transect line. CWD pieces were all approximately level with the horizontal ground surface, with very few exceptions. Species (or decay class) of CWD was also recorded.

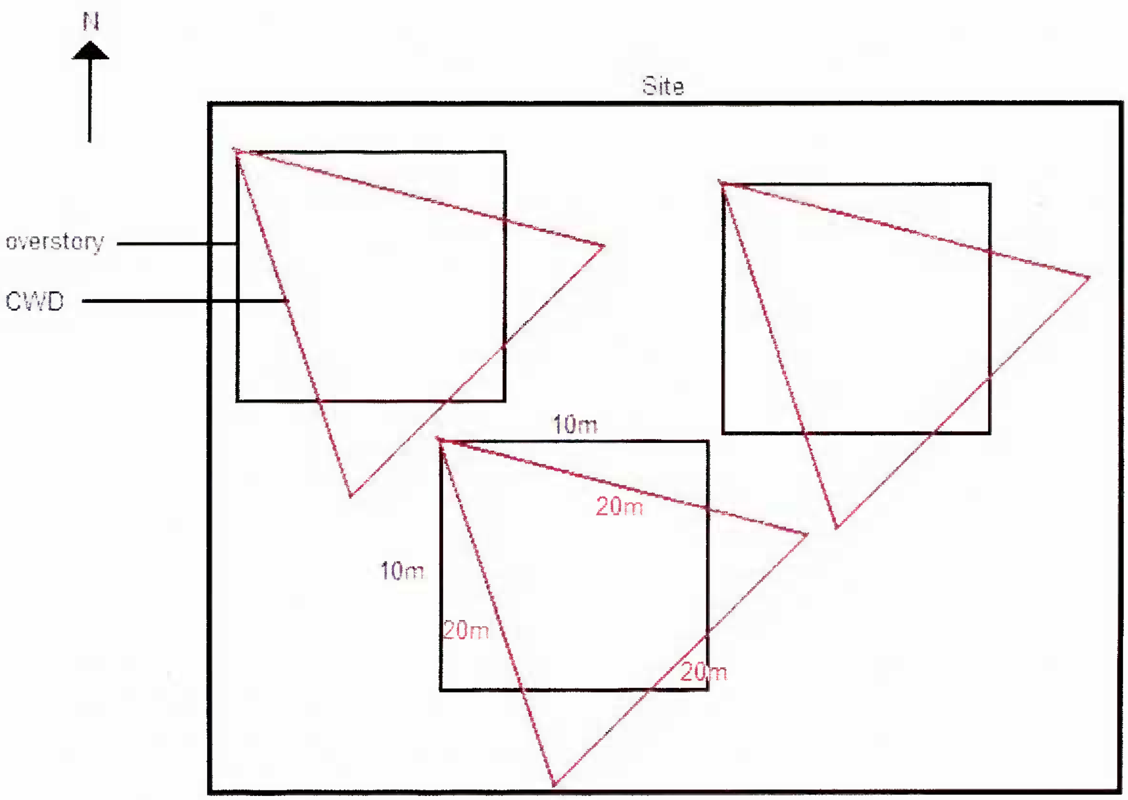


Figure 2.2: Representation of an idealized field site. A buffer of at least 10m would exist around the plots, within the site.

Data Analysis

The analysis tested for differences in all measured characteristics between disturbance types over time (at the site level) to assess whether the resulting early-successional plant communities varied with disturbance type and years since disturbance in stand structure and composition. All statistics were performed using SAS 9.1.3 Service Pack 4 (SAS Institute, Inc, 2002-2003).

A chronosequence of structural and compositional characteristics was constructed from similar sites of different ages, rather than the same sites monitored over time. The living tree data include only overstory trees, greater than 1.3m in height, originating post-disturbance (regeneration). The structural components examined included the living tree data (stems per hectare (SPH), diameter at breast height (DBH), basal area per hectare (BAHA)), the snag data (DBH, BAHA, snag density) and the volume of CWD per hectare. CWD volume was calculated from the following formula:

$$V = [(1.234)/L] \times \Sigma D^2$$

Where V = CWD volume (m^3/ha), L = line length (m), & ΣD^2 = piece diameter (cm) squared, summed by plot.

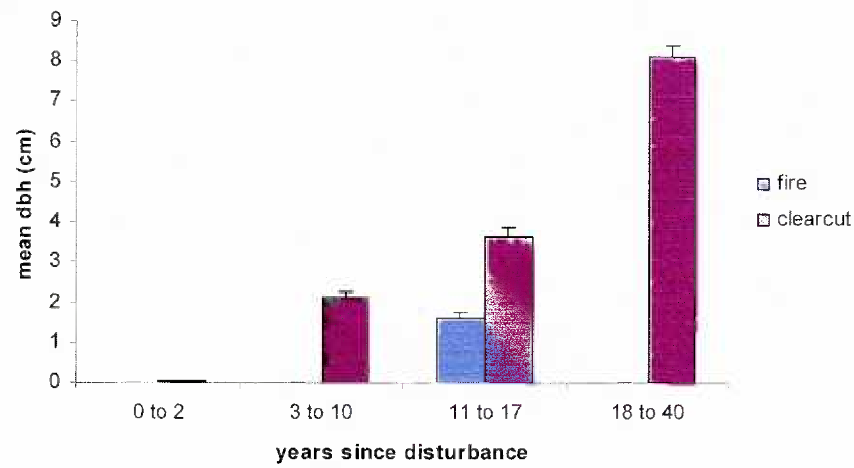
A General Linear Model (GLM), more specifically linear regression analysis with a class variable (ANCOVA with non-homogenous slopes), was used to identify differences in each of these variables, as well as the number of trees and species richness characteristics, between disturbance types, over time. The significance level used throughout was $\alpha=0.05$. Where the assumptions of linear regression (equal variance, linearity, normality) were not met, simple mathematical transformations, such as natural logarithm or square root, were applied to the variables. It should be noted that time in the linear regression analysis was continuous (years since disturbance) rather than discrete (age classes used for even field sampling purposes). However, for presentation purposes and to facilitate comparisons, for certain untransformed variables, time is also presented as discrete age classes.

2.3 Results

The complete detailed results of each linear regression (including regression equations and general linear model details) are included in Appendix II.

A square root transformation of mean diameters (mean dbh) was used to meet the assumptions of linear regression. Mean dbh and the linear regression results for the square root of mean dbh for each disturbance type was plotted over time (Figure 2.3). The square root of mean dbh increased significantly over time (ie. had a positive slope) ($p<0.0001$) and was significantly greater on clearcut than on burned sites ($p=0.006$).

a)



b)

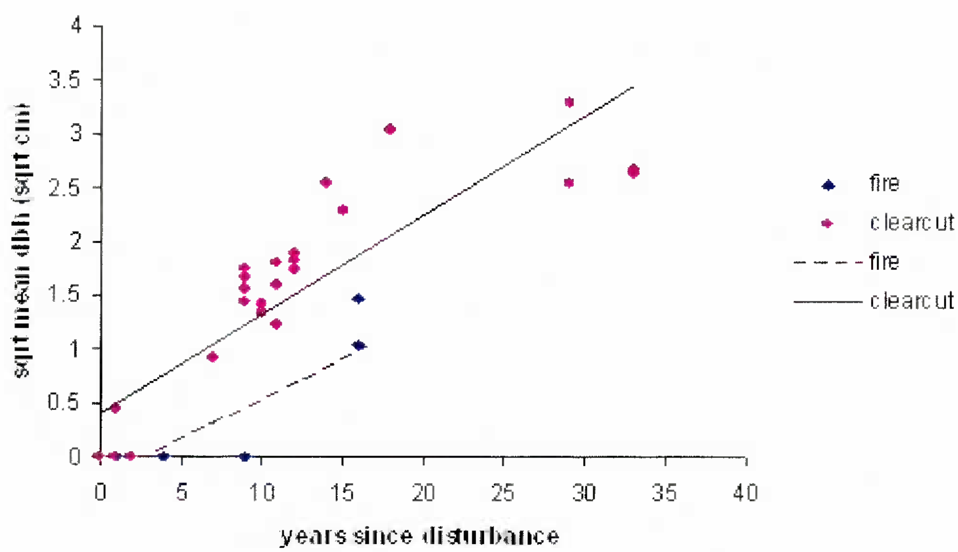
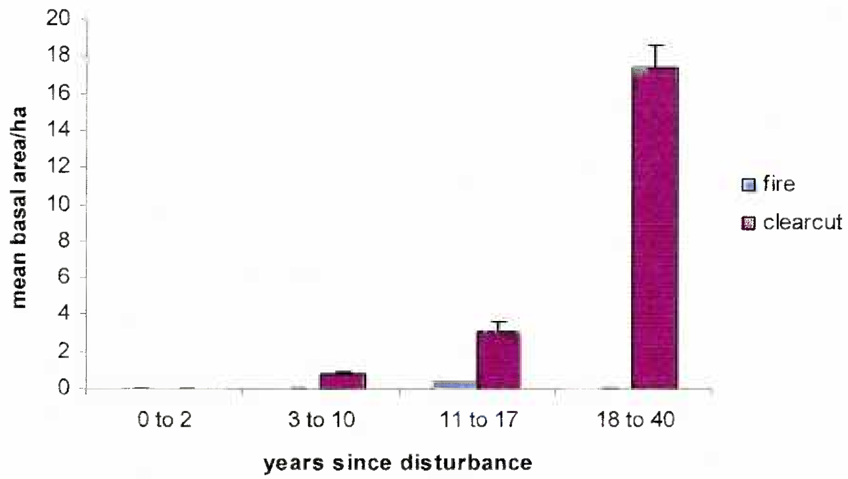


Figure 2.3: a) The mean dbh (cm) of all live trees for fire and clearcut sites, by age class. Standard error bars are included. No information was available for sites 18 to 40 years post-fire. b) The square root of the mean dbh (sqrt cm) of all live trees in all fire and clearcut sites, by years since disturbance, with linear regression lines indicated (n=39). Several data points are superimposed at sqrt dbh = 0.

A square root transformation of mean basal area (per hectare) was used to meet the assumptions of linear regression. The square root of mean basal area by age class and linear regression results for the square root of mean basal area for each disturbance type were plotted over time (Figure 2.4). The regression results indicated an interaction between time and disturbance type, represented as dummy variables (p<0.0001), indicating that the trends of basal area over time differed between the two disturbance types. Basal area was zero following disturbance (no trees), and then trees greater than 1.3m in height appeared about 4 years after clearcutting and about 16 years following fire. Also, the basal area of trees was higher on clearcut sites than on fire sites.

a)



b)

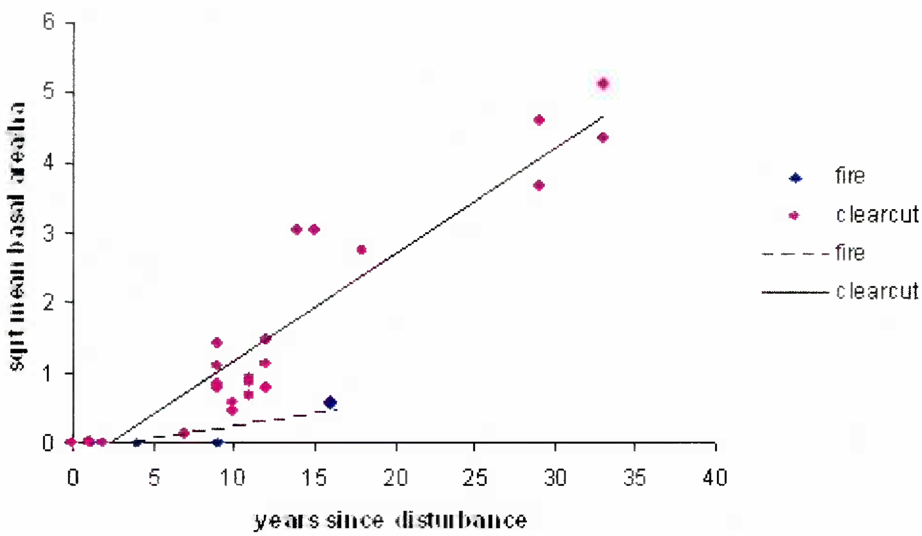
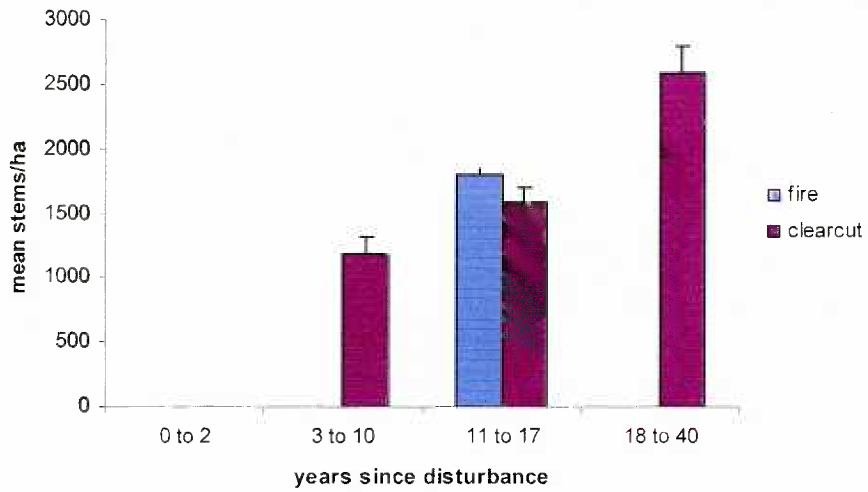


Figure 2.4: a) The mean basal area/ha of all live trees for fire and clearcut sites, by age class. Standard error bars are included. No information was available for sites 18 to 40 years post-fire. b) The square root of the mean basal area/ha of live trees in all fire and clearcut sites, by years since disturbance, with linear regression lines indicated (n=39). Several data points are superimposed at sqrt baha=0.

Mean number of stems per hectare (sph) and the linear regression results for mean stems per hectare for each disturbance type were plotted over time (Figure 2.5). Mean stems per hectare increased over time ($p<0.0001$), but this trend did not differ significantly between disturbance types.

a)



b)

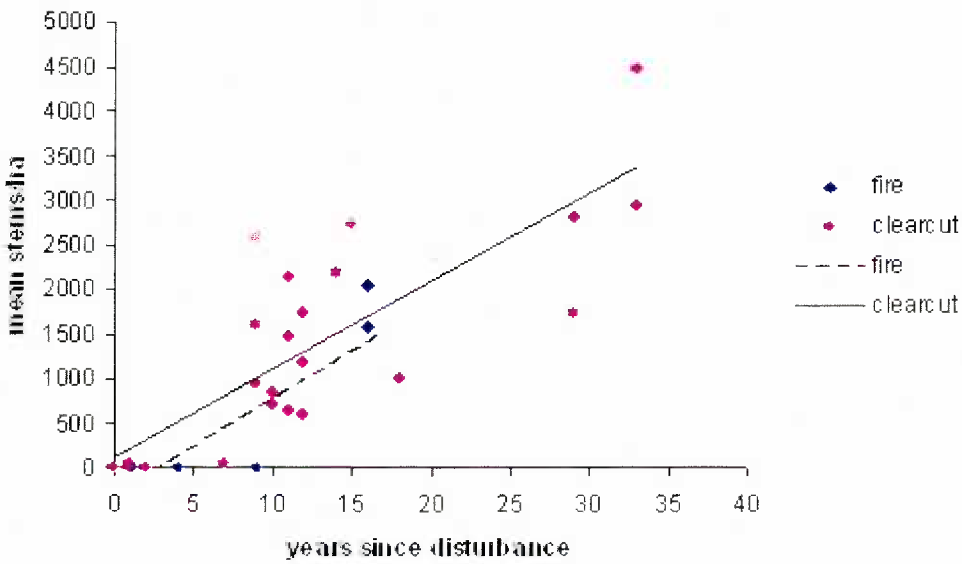
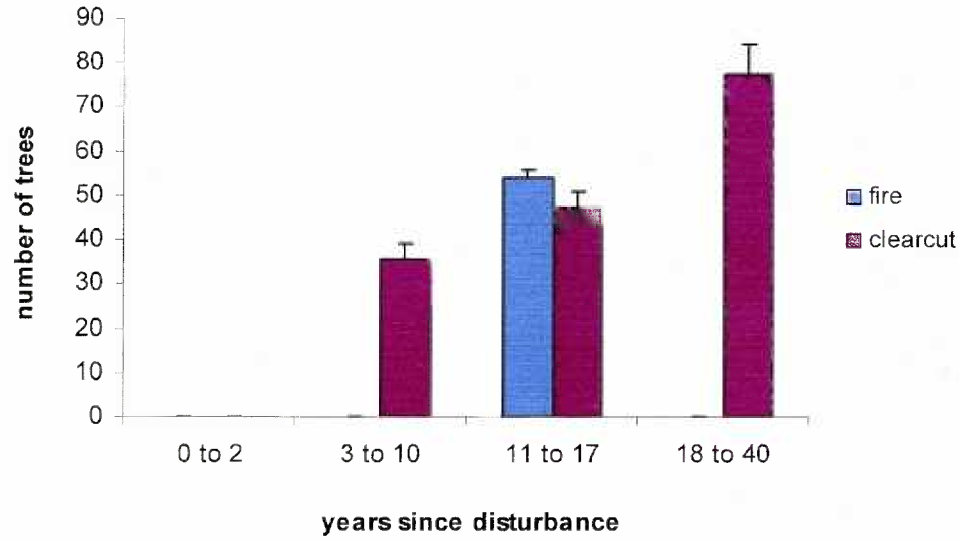


Figure 2.5: a) The mean stems/ha of all live trees for fire and clearcut sites, by age class. Standard error bars are included. Note that no information was available for sites 18 to 40 years post-fire. b) The mean stems/ha of live trees in all fire and clearcut sites, by years since disturbance, with linear regression lines indicated (n=39). Note that several data points are superimposed at sph=0.

Neither disturbance type had any regenerating tree seedlings (greater than 1.3m in height) within the first two years post-disturbance (Figure 2.6a). The number of trees per site (per $300m^2$) increased with time over the last three age classes for clearcut sites. The number of trees did not increase for fire sites until the 3rd age class. No information was available for the 4th age class for fire sites and therefore no trends can be implied. It is however interesting to note that in the 3rd age class, fire sites had more regenerating trees than clearcut sites, which may be evidence for an exponential-like increase in seedlings or high variation among sites. The number of trees increased significantly over time ($p<0.001$) (Figure 2.6b). The regression line for the clearcut sites appeared to suggest greater numbers of tree at any given time than the wildfire regression line, but this difference was not significant. Between-site variability appears to be substantial.

a)



b)

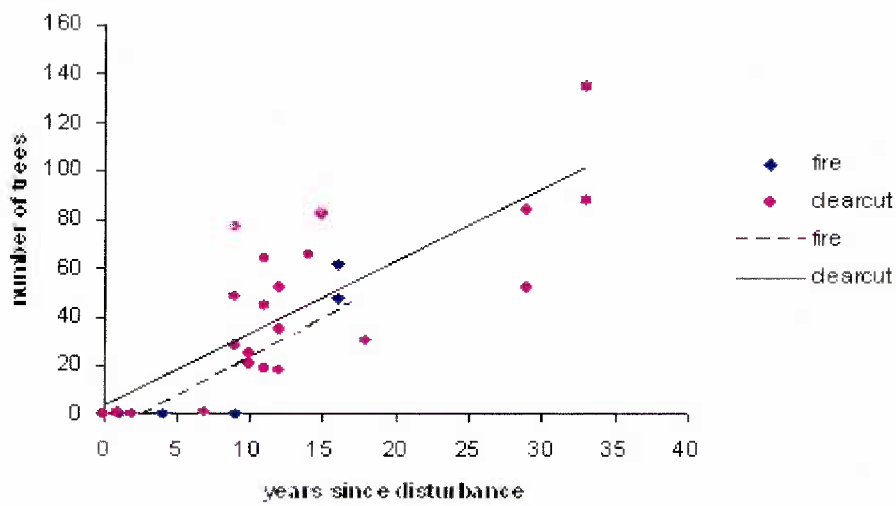
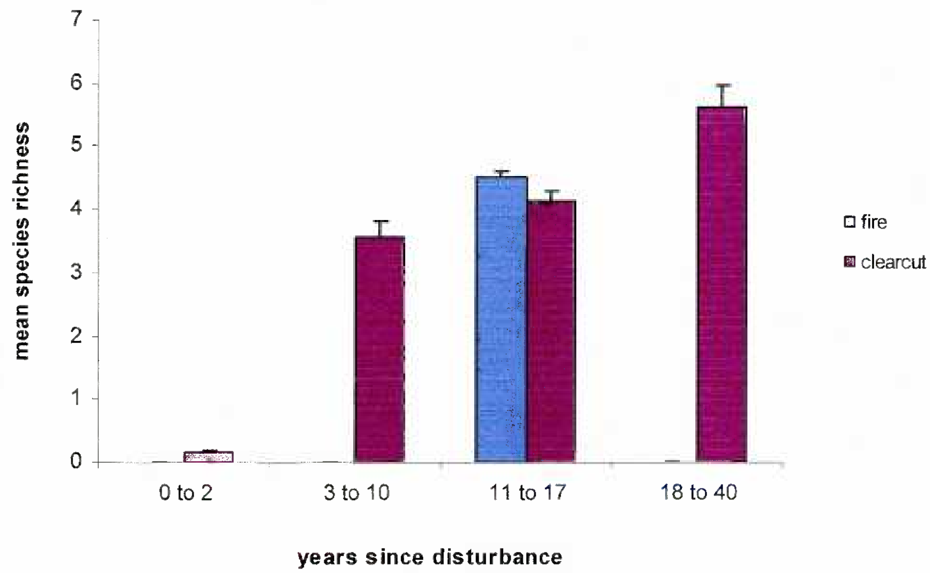


Figure 2.6: a) Number of overstory trees per site ($300m^2$) for fire and clearcut sites, by age class. Standard error bars are included. Note that no information was available for sites 18 to 40 years post-fire. b) Number of live overstory trees per site ($300m^2$) for fire and clearcut sites, by years since disturbance, with linear regression lines indicated (n=39). Note that several data points are superimposed at number of trees = 0.

Species richness of live overstory trees (Figure 2.7a) showed the same trends as number of overstory trees (Figure 2.7a); that is an increase in species richness beginning in the second age class for clearcut sites, and in the 3rd age class for fire sites. The linear regression analysis found that species richness increased over time ($p<0.001$). Species richness also differed with disturbance type ($p=0.013$).

a)



b)

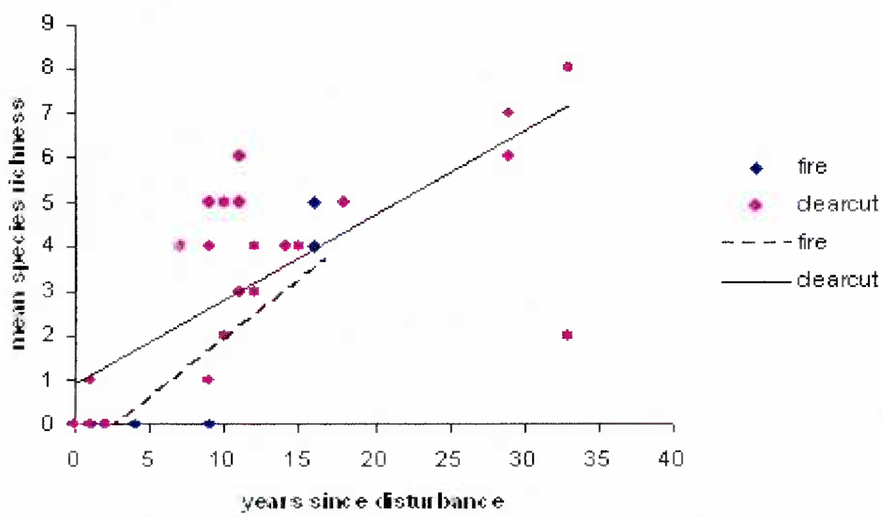
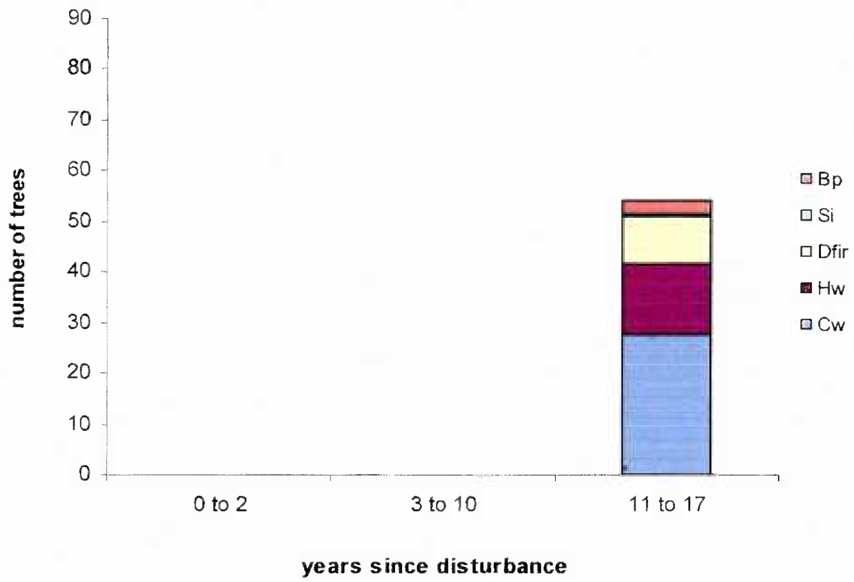


Figure 2.7: a) Mean tree species richness in fire and clearcut sites, by age class, including standard error bars. Note that no information was available for sites 18 to 40 years post-fire. b) Mean tree species richness in all fire and clearcut sites, by years since disturbance, with linear regression lines indicated (n=39). Note that several data points are superimposed at richness = 0.

In clearcut sites, the numbers of western hemlock and western red cedar trees increased over time (Figure 2.8). When comparing the 3rd age class of fire and clearcut sites, fire sites had fewer species yet slightly higher total numbers of trees.

a)



b)

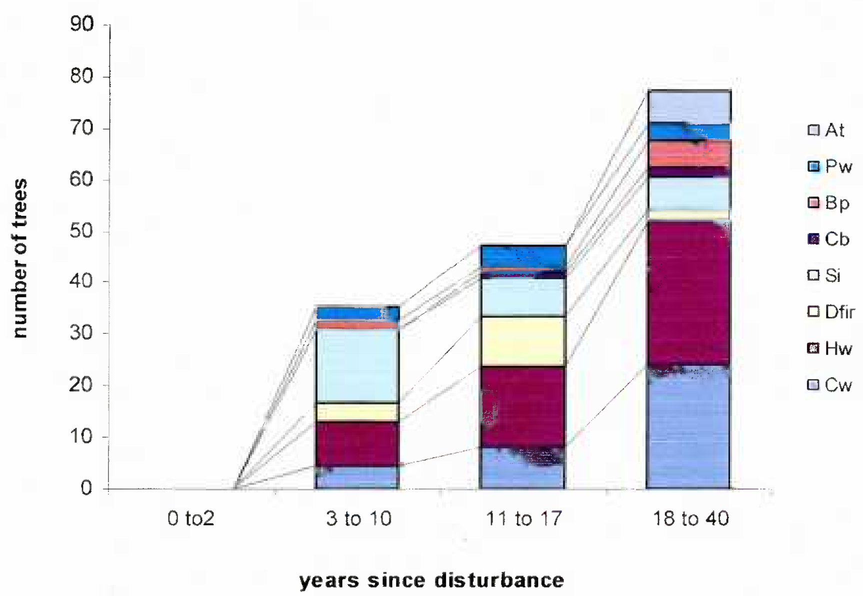
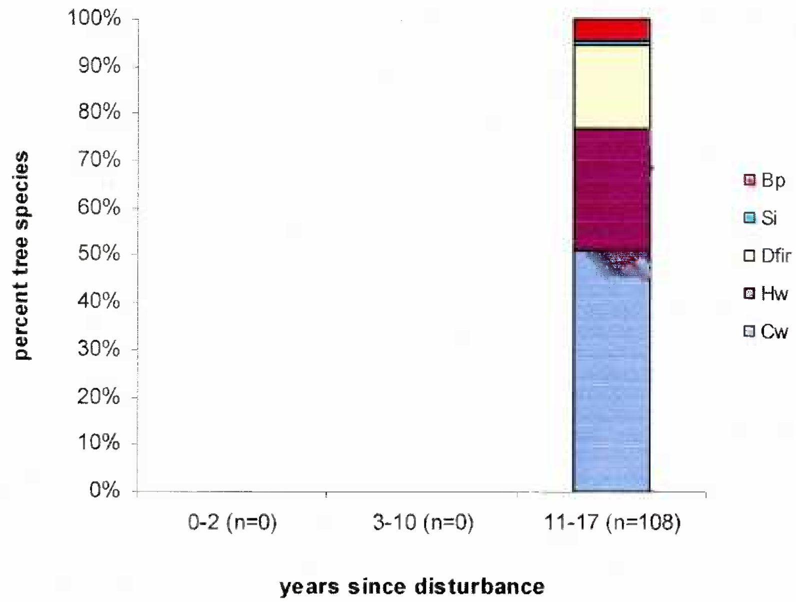


Figure 2.8: Mean number of live overstory trees across fire (a) and clearcut (b) sites, by age class. Note, no information was available for 18 to 40 year-old fires (At = *Populus tremuloides*, Pw = *Pinus monticola*, Bp = *Betula papyrifera*, Cb = *Populus balsamifera*, Si = *Picea engelmannii x glauca*, *Pseudotsuga menziesii* var. *menziesii*, Hw = *Tsuga heterophylla*, Cw = *Thuja plicata*).

The first age class in clearcut sites (Figure 2.9) was entirely composed of western red cedar; however, only one tree was found in all clearcut sites of that age. Excluding this first age class, western red cedar and western hemlock proportions increased over time in the clearcut sites. The proportions, but not always the number, of interior spruce and western white pine decreased over time. Trends in paper birch and Douglas-fir were variable over time. For the 11-17 year age class, fire sites had a much larger proportion of western hemlock, but a smaller proportion of western red cedar than clearcut sites. Douglas-fir proportions were comparable between disturbance types. Regenerating trees in fire sites in this 3rd age class were comprised of western red cedar, western hemlock, Douglas-fir, interior spruce and paper birch. Black cottonwood and western white pine were not present as they had been in clearcut sites. Therefore, there appeared to be differences in overstory species composition and the proportions of each species between disturbance types, and between age classes.

a)



b)

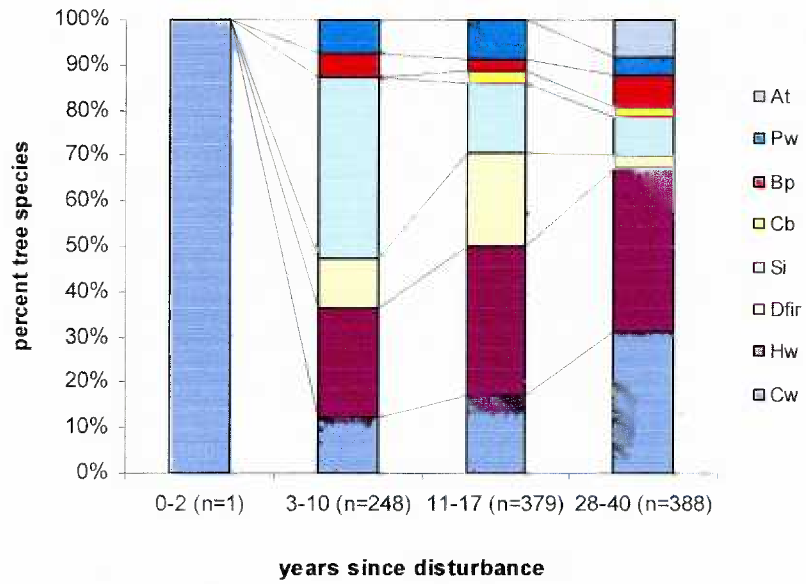


Figure 2.9: Percent live overstory tree species across fire (a) and clearcut (b) sites, by age class. Note, no information was available for 18 to 40 year-old fires (At = *Populus tremuloides*, Pw = *Pinus monticola*, Bp = *Betula papyrifera*, Cb = *Populus balsamifera*, Si = *Picea engelmannii x glauca*, *Pseudotsuga menziesii* var. *menziesii*, Hw = *Tsuga heterophylla*, Cw = *Thuja plicata*).

Overstory trees with pre-disturbance origins (survivors) were uncommon and only occurred in a few early fire sites (Table 2.2). Mean dbh ± standard deviation of survivors was 28.7 ± 9.6cm. Interior Douglas-fir comprised 64% of the surviving trees and had a mean dbh of 31.7 ± 8.5cm.

Table 2.2: Characteristics of surviving overstory trees (above 1.3 m in height) in fire sites.

site number	years since disturbance	species	dbh (cm)
111	1	*P. menziesii* var. *menziesii*	33.8
		P. menziesii var. *menziesii*	19.5
		B. papyrifera	29.5
		P. menziesii var. *menziesii*	36.1
		P. menziesii var. *menziesii*	46.5
		P. menziesii var. *menziesii*	33.5
112	1	*P. menziesii* var. *menziesii*	44.1
		T. plicata	10.2
		T. plicata	15.8
		P. menziesii var. *menziesii*	19.2
		P. menziesii var. *menziesii*	21.9
		P. menziesii var. *menziesii*	35.5
		P. menziesii var. *menziesii*	22.4
		P. menziesii var. *menziesii*	22.4
		T. plicata	13.9
113	1	*P. menziesii* var. *menziesii*	34.3
		P. menziesii var. *menziesii*	40.4
114	1	*B. papyrifera*	32.8
		B. papyrifera	24.0
		P. menziesii var. *menziesii*	32.4
115	1	*B. papyrifera*	18.4
		P. menziesii var. *menziesii*	35.0
122	9	*T. heterophylla*	26.3
		T. heterophylla	39.9
123	9	*P. menziesii* var. *menziesii*	30.0

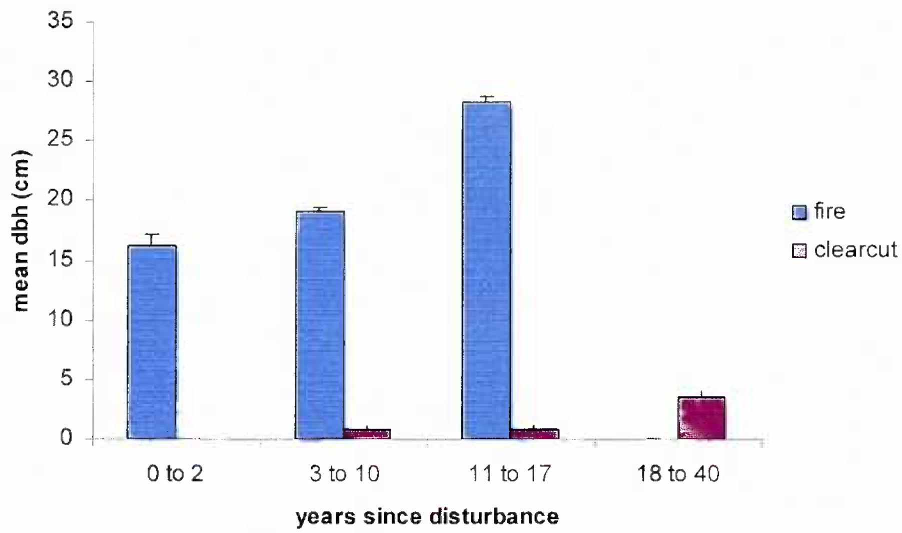
Planting occurred on eight clearcut sites. Only three species were planted: Douglas-fir, interior spruce and western red cedar (Table 2.3). Douglas-fir was planted on 63% of these sites.

Table 2.3: Tree species planted on clearcut study sites.

site number	years since disturbance	planted species
213	1	*P. menziesii* var. *menziesii*
214	1	*P. menziesii* var. *menziesii*
217	1	*P. engelmannii* x *glauca*
231	12	*T. plicata*
232	15	*P. menziesii* var. *menziesii*
236	12	*P. menziesii* var. *menziesii*
237	12	*P. menziesii* var. *menziesii*
244	18	*P. engelmannii* x *glauca*

The mean dbh of snags on fire and clearcut sites tended to be greater with increasing years since disturbance (Figure 2.10a) The regression results indicated an interaction between time and disturbance type, represented as dummy variables ($p=0.0002$), indicating that the trends of snag dbh over time differed between the two disturbance types (Figure 2.10b). Snag diameters remained higher on fire sites than on clearcut sites.

a)



b)

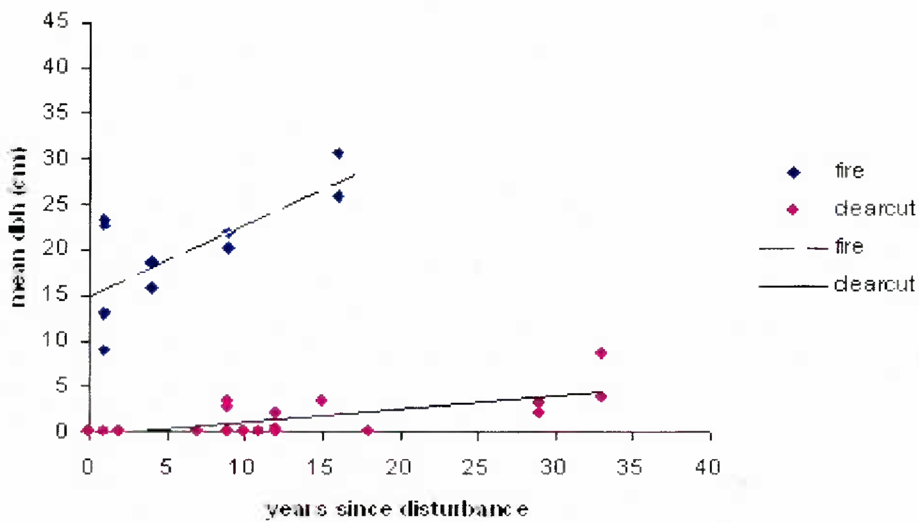
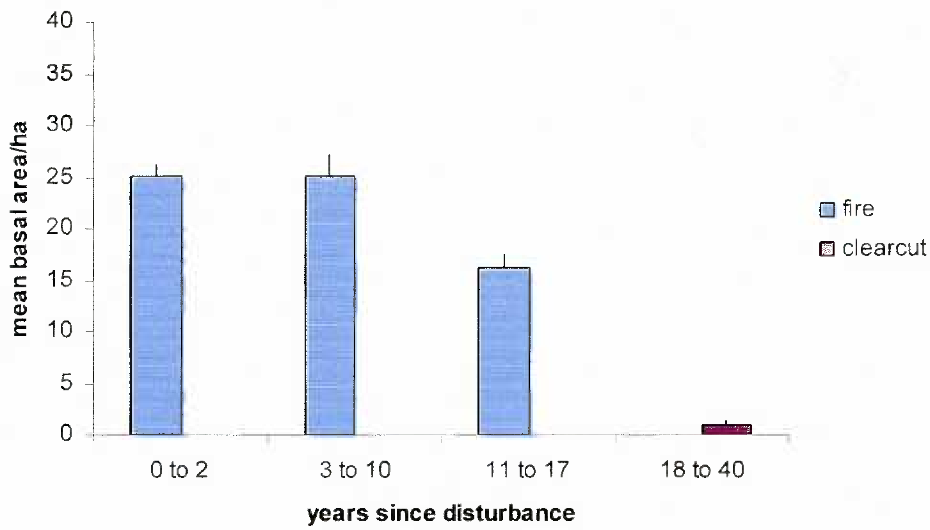


Figure 2.10: a) The mean dbh (cm) of all snags for fire and clearcut sites, by age class. Standard error bars are included. Note that no information was available for sites 18 to 40 years post-fire. b) The mean dbh of snags in all fire and clearcut sites, by years since disturbance, with linear regression lines indicated (n=39).

Mean basal area per ha of snags appeared to begin high and decline over time in fire sites while, in clearcut sites, it was nearly zero until at least 20 years since disturbance (Figure 2.11). A ranked transformation of mean basal area per ha was used to meet the assumptions of linear regression. The ranked mean basal area by age class and linear regression results for ranked mean basal area for each disturbance type were plotted over time. The regression results indicated an interaction between time and disturbance type, represented as dummy variables (p=0.0015), indicating that the trends of basal area over time differed between the two disturbance types.

a)



b)

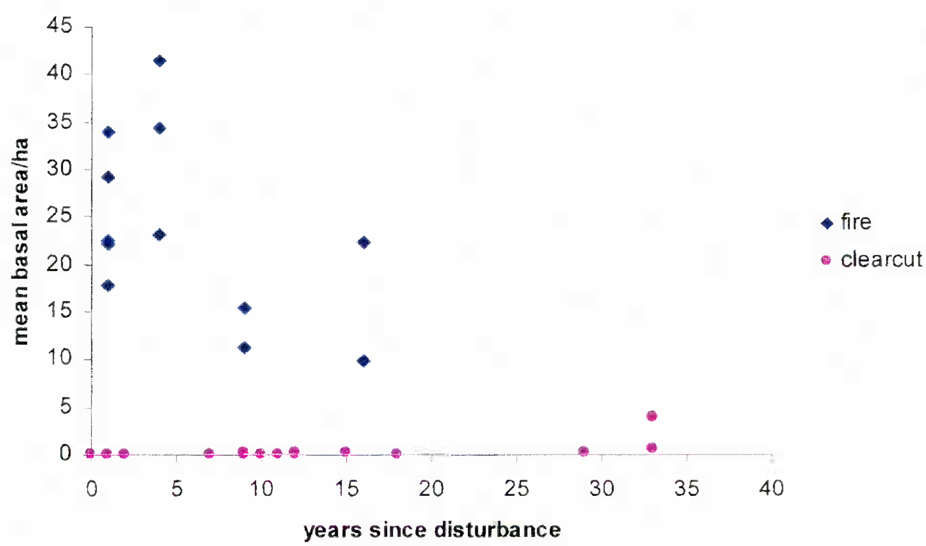
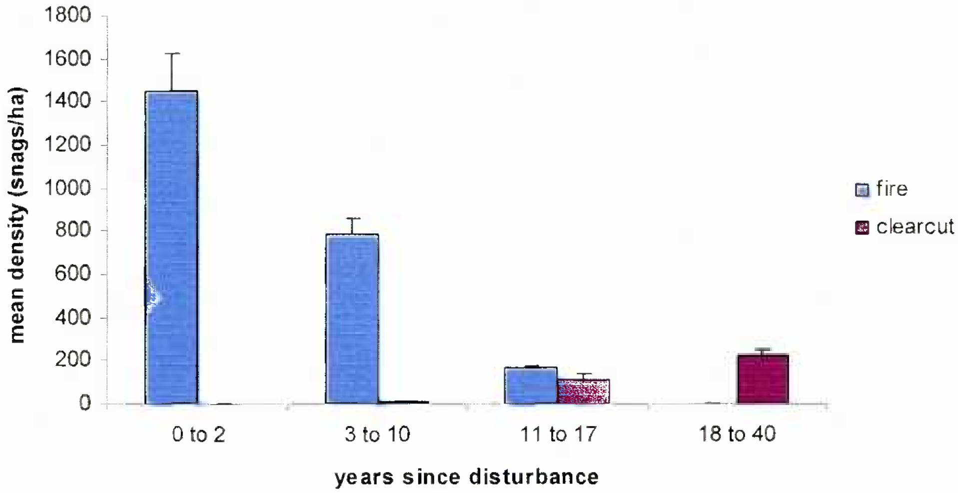


Figure 2.11: a) The mean basal area/ha of all snags for fire and clearcut sites, by age class. Standard error bars are included. Note that no information was available for sites 18 to 40 years post-fire. b) The mean basal area/ha of all snags in all fire and clearcut sites, by years since disturbance (n=39). No regression lines are indicated since the regression was performed on the ranked values of mean site basal area and not on these untransformed values.

A natural logarithm transformation of mean snag density per ha (ln snag density) was used to meet the assumptions of linear regression. The ln snag density by age class and the linear regression results for ln snag density for each disturbance type were plotted over time (Figure 2.12). The regression results indicated an interaction between time and disturbance type, represented as dummy variables ($p=0.0003$), indicating that the trends of snag density over time differed between the two disturbance types. Fire and clearcut sites showed opposite trends over time: snag density on fire sites began very high and declined over time, while snag density on clearcut sites was initially zero and slowly increased over time.

a)



b)

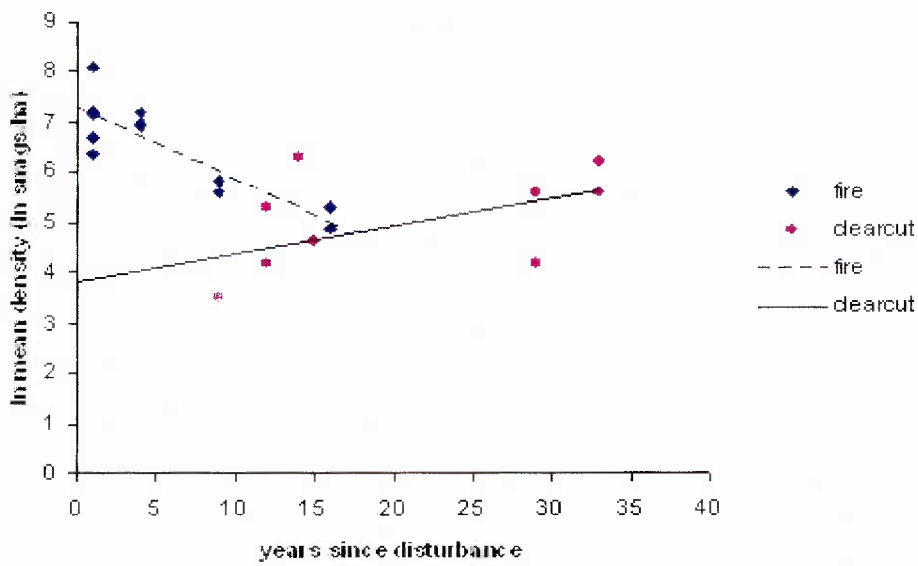
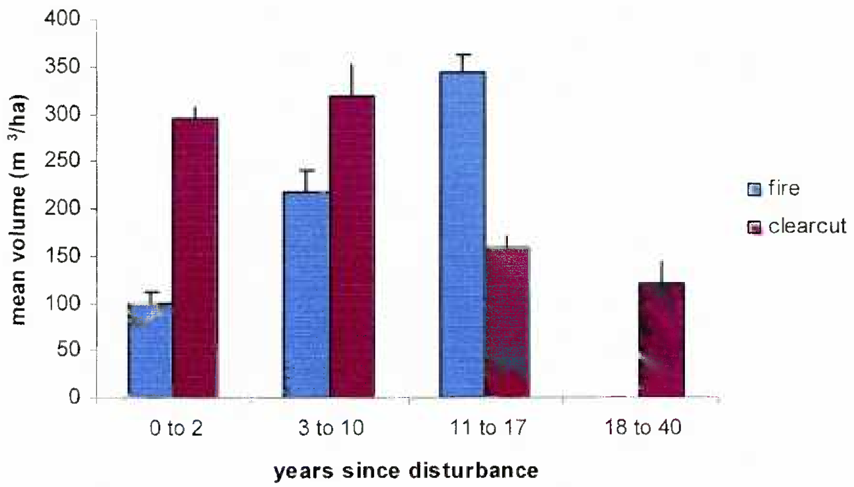


Figure 2.12: a) The mean snag density for fire and clearcut sites, by age class. Standard error bars are included. Note that no information was available for sites, 18 to 40 years post-fire. b) The natural logarithm of mean snag density in all fire and clearcut sites, by years since disturbance, with linear regression lines indicated (n=39).

The maximum coarse woody debris (CWD) volumes occurred on a 9 year old clearcut site (734 m^3/ha) and a 9 year old fire site (460 m^3/ha). The minimum CWD volume occurred on a 29 year old clearcut site (6 m^3/ha) and a 1 year old fire site (38 m^3/ha). The initial difference in CWD volume between fire and clearcut sites was the largest, with mean volumes of 98 m^3/ha and 294 m^3/ha, respectively. Fire and clearcut sites showed opposite trends over time: CWD volume on fire sites was initially low and increased over time, while CWD volume on clearcut sites was initially high and decreased over time (Figure 2.13). A natural logarithm transformation of mean CWD volume was used to meet the assumptions of linear regression. The regression results indicated an interaction between time and disturbance type, represented as dummy variables ($p=0.0001$), indicating that the trends of CWD volume over time differed between the two disturbance types.

a)



b)

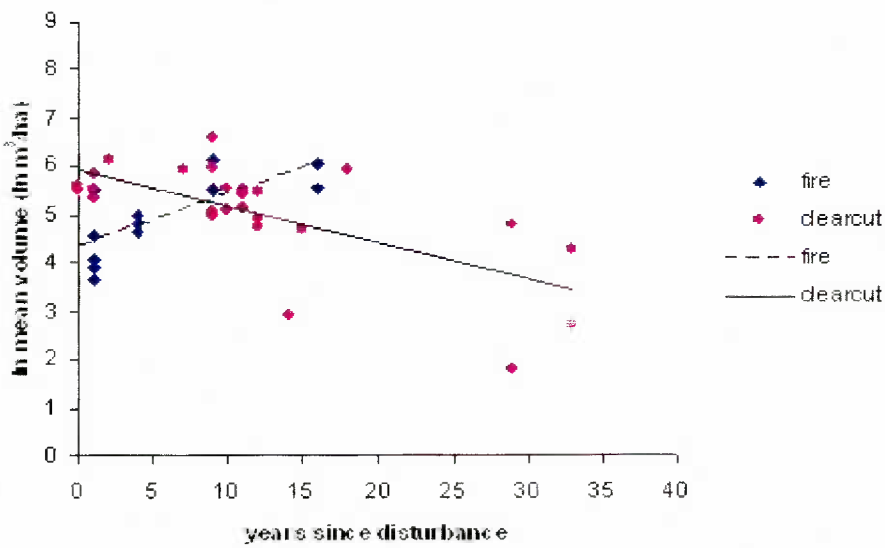


Figure 2.13: a) The mean CWD volume for fire and clearcut sites, by age class. Standard error bars are included. Note that no information was available for sites, 18 to 40 years post-fire. b) The natural logarithm of mean CWD volume (m^3/ha) in all fire and clearcut sites, by years since disturbance, with linear regression lines indicated (n=39).

2.4 Discussion

Limitations

The limitations of this study begin with the lack of potential wildfires within the study area. This limited the sample size of fire sites and yielded no potential fire sites in the oldest age class (18 to 40 years since disturbance). This may have prevented conclusive identification of trends and did prevent comparisons of characteristics between older clearcut and fire sites. Wildfires less than 40 years old in the study area were not numerous, and the few that did exist often failed certain site selection criteria, mainly road accessibility and salvage logging restrictions. Further studies should seek to increase the sample size of wildfires, and if possible, to pair wildfire and clearcut sites in space and time.

A chronosequence was used to identify trends in structural characteristics between disturbances, over time. Site variability (in elevation, aspect and location) can be quite high, especially in regions with varied topography and species composition, such as the area surrounding Revelstoke. This variability may be the underlying cause of variability in site characteristics such as tree species composition. Efforts were made to ensure that the sites were as homogenous in disturbance (type, severity, etc), in pre-disturbance community, and in ecosystem type. However, site selection criteria limited potential sites and consequently, a certain level of site variability was unavoidable. For example, the study includes study sites in two different ICH variants - ICHwk1 and ICHvk1 - which have different climatic characteristics. The ICHvk1 is slightly colder and receives more precipitation than the ICHwk1. This may affect tree growth rates and species composition. Efforts were made to sample in correspondingly similar site series across both variants; however, this was often difficult due to the low availability of potential fire sites and due to lack of accurate mapping to the site series level. The site series of the study plots was as close to zonal as possible, but again, variation was unavoidable, and may have accounted for some of the observed variation in species composition. Variability in aspect and elevation was also unavoidable given the pool of potential sites, which may have influenced tree growth rates. The use of many sites to identify and interpret trends over time is therefore not ideal. However, chronosequence construction is commonly used in successional studies, especially those that deal with long-term processes such as forest succession (ie. Carmona et al., 2002; Passovoy and Fulé, 2006; Uotila et al., 2005). More long-term, permanent plot studies are required to ensure that the trends that appear in these chronosequence studies hold true when monitoring sites through time.

The exploration of light, nutrients and soil moisture as mechanisms that drive the differences in overstory structure and composition was beyond the scope of this study. Only disturbance type (which was defined) and time were analyzed. Further studies should monitor light levels and soil nutrient and moisture availability through time to provide possible causal mechanisms to explain the differences in overstory structure and function that were observed.

Survivors

Surviving trees had some degree of sub-lethal fire damage, which may kill the tree in coming years, but at the time of sampling, these trees had green foliage. The surviving trees were often large Douglas-firs, which usually made up a smaller proportion of the overstory (next to western red cedar and western hemlock). They are more likely to survive than western red cedar and western hemlock because they possess adaptations to fire like thick insulating bark (Lyon and Stickney, 1974).

Overstory Regeneration

In this study, tree diameters, basal areas per hectare, stems per hectare and tree numbers are all essentially indicators of the size and amount of regenerating trees on a site. At least 95% of the overstory was removed on all study sites for both disturbance types. Initial values of zero for these characteristics are therefore to be expected in the first few years following disturbance as regenerating trees need time to establish and reach the minimum 1.3m height that would include them in this study's measurements. The subsequent increases in tree size and abundance through time that were observed are expected as trees begin to regenerate within the sites and re-colonize from outside sources.

Basal area per ha in clearcut sites increased substantially over time but to a lesser extent in fire sites. Though none of the other characteristics had a significant interaction between disturbance type and time, the data suggest that tree regeneration may be delayed in fires sites compared to clearcut sites. Similarly, other studies have found that succession proceeds more rapidly on logged rather than burned sites (Timoney et al., 1997; Rees and Juday, 2002). Accelerated tree regeneration was expected on planted clearcut sites. One of the other mechanisms put forward to explain accelerated plant regeneration on clearcuts is light availability (Timoney et al., 1997; Rees and Juday, 2002). Initially, clearcut sites may have had higher light levels, which gave their successional pathways a head start. Young clearcut sites had no overstory whatsoever, whereas wildfire sites often had occasional mature surviving trees and commonly very high numbers of snags and ladder fuels causing shading. These structural legacies on fire sites may have intercepted enough light to delay tree regeneration by several years.

Differences in other available resources such as nutrient and water availability may also have created this trend of more rapid succession on clearcut sites. Grady and Hart (2006) found that compared to unmanaged ponderosa pine stands, thinned stands had lower *in situ* net N mineralization, while high-severity wildfire stands had 60% higher *in situ* net N mineralization. Therefore, there was greater N availability to plants on fire sites (Grady and Hart, 2006). These results seem to contradict the delayed regeneration observed on fire sites in the present study. However, though increased N supply may assist in vegetative recovery, this increase coincided with relatively low plant and soil microbial biomass, and high rates of N loss via leaching and gaseous N emissions (Grady and Hart, 2006). These large N losses can result in decreased productivity if not offset by N fixation and deposition (Grady and Hart, 2006). It may be that the present study's fire sites had relatively high N amounts, but given the nearly total mortality of trees and ground vegetation on these sites, they were not fully utilized before they began to leave the system. Another possibility is that the relatively high N availability remained on the fire sites, but again, until recolonization occurred, the vegetation could not make use of the beneficial N increase.

In addition to relative nitrogen availability, the impact of survivor trees should be considered. Though few in number, they occurred only on early fire sites, and were large mature trees. These may have deprived establishing seedlings of light, water and nutrient resources at the initial stages of succession, thereby delaying regeneration. With fewer available resources, the growth of seedlings that were established on early fire sites may have been reduced.

Tree regeneration may be slowed in fire sites due to the complete or partial destruction of any tree seeds present in the forest floor and tree canopy. Mechanical damage of soils was minimized on the clearcut sites with the particular harvesting techniques used – cable logging, and skidding in winter only. It is therefore plausible that seeds of tree species may have remained intact and viable in the forest floor or on tree branches following logging. Seeds in clearcuts may then immediately germinate following the disturbance, while the fire sites must be primarily reseeded by outside dispersers and surviving trees for which a good seed year is required – processes that are slower than immediate germination. The success of such off-site colonizers when competing with in-situ survivors (individuals or seeds) in ICH forests may be low, as suggested by Lyon and Stickney (1974), who found that in the cedar-hemlock forests of northern Idaho, individual plants originating from off-site colonization represented only a minimal fraction of the future vegetation following fires.

However, it is difficult to confirm and characterize this trend of accelerated regeneration on clearcuts, as there are no data for older (18 to 40 years) fire sites. It may be that fire sites surpass clearcut sites in tree diameters, basal area, stems per hectare and tree numbers in the 18 to 40 year bracket. It may also be that the study plots from first two age classes (0 to 2 and 3 to 10 years) of fire sites, having no overstory trees at all, did not accurately represent typical fires. With an increase in sample size, and more sampling in later aged fire sites, these trends could be discussed with more certainty.

Overstory Species Richness

Overstory species richness was significantly higher on clearcut sites than on fire sites. Overstory species richness increased over time for both disturbance types. However, this increase occurred in the 2nd age class for clearcut sites and the 3rd age class for fire sites. This again suggests accelerated succession in clearcut sites. In this case, however, these results are ambiguous. In the first two age classes (0-10 years) for the fire sites, there were no trees tall enough to be included in overstory measurements. When there were trees, in the 3rd age class (11-17 years), overstory species richness on fire sites was similar to or higher than that on clearcut sites. Tree species richness may have been similar to that of clearcut sites in younger age classes, but since the tree regeneration on those particular fire sites was slower, the trend was not observed. Therefore, since there were no trees in the earlier fires and since there are no data for later-aged fires, this trend is inconclusive.

Overstory Species Composition

Overstory species composition (by absolute and relative values) was predominantly hemlock and cedar, with a strong component of interior spruce and Douglas-fir, especially in young clearcuts. Western white pine and paper birch were also relatively common on clearcuts. The only comparison between disturbance types can be made in the third age class (11 to 17 years since disturbance) and this shows that fire sites had 40% more western red cedar and very little spruce. Overall, fire sites had fewer species.

Species composition of post-disturbance communities is determined by several factors, including disturbance type, disturbance severity, pre-disturbance community, seed sources (e.g. survivors, dispersal from offsite individuals and soil seed bank), and the characteristics of individual species (Lyon and Stickney, 1974; Cattelino et al., 1979; Shiplett and Neuenschwander, 1994). Since disturbance type, severity and pre-disturbance community were controlled for as much as possible in this study, seed sources and species specific characteristics will be explored as the primary mechanisms driving any differences that were seen.

a) Post-Fire Composition:

Natural post fire succession in the ICH zone has been found to follow several different trajectories. Assuming a mature predominantly cedar and hemlock forest prior to disturbance, Shiplett and Neuenschwander (1994) described the tree species composition following wildfires in the cedar-hemlock forests of northern Idaho. In the first 40 years, there was a dominance of shade intolerants (*Larix* and *Pinus contorta*) with a large component of *Pinus monticola, Pseudotsuga* *menziesii,* and *Abies grandis*. Shade tolerant *Thuja* and *Tsuga* were present but were suppressed in the understory. Stickney (1986) examined early post-fire succession following the Sundance fire in northern Idaho. He described an overstory composed mainly of *Pseudotsuga menziesii* and *Pinus contorta*, with a component of *Betula papyrifera*. Habeck (1968) worked in cedar-hemlock forests in Glacier Park in the U.S.A and found that post-fire, predominantly cedar and hemlock stands were replaced by Douglas-fir and spruce regeneration.

Following fires in this study, the cedar and hemlock components of the overstory do not appear to be in the process of being replaced by lodgepole pine/western white pine/ Douglas-fir (Shiplett and Neuenschwander, 1994), Douglas-fir/lodgepole pine/paper birch (Stickney 1986) or Douglas-fir/spruce (Habeck, 1968) assemblages. This may be due to a cooler, moister climate in the B.C. study area than in the U.S. study areas. The post-fire overstory species composition was predominantly cedar/hemlock/Douglas-fir. These results suggest that the shade-tolerant climax species of the ICH zone, which are usually suppressed in the understory during early succession, were the dominant species in the overstory, and the shade intolerants formed only a minor component. The other studies compared here were all situated in the American portion of the cedar-hemlock forest's range. In these more southern areas, lodgepole pine and western larch are more common and are often the dominant overstory species in many seral communities (Shiplett and Neuenschwander, 1994; Lyon and Stickney, 1974)

The observed species compositions may vary from the literature because of the species and numbers of survivors. The vast majority (~70%) of the overstory species in Lyon and Stickney's cedar-hemlock post-fire succession study (1974) could be accounted for by survivors, which are generally species that have adaptations to fire, such as Douglas-fir, lodgepole pine and paper birch. In the present study, there were few survivors (only 25 individuals were observed on all study plots), and though survivors were usually Douglas-fir (64%), these were only on early fire sites for which we have no species composition data, no regenerating trees having been above 1.3 m in height in these sites. The sites that did provide information on species composition had no survivors whatsoever, and so were necessarily re-seeded from on- and off-site sources. Given that the observed overstory species composition was (in order of relative importance), cedar, hemlock and Douglas-fir, and these have been classified as off-site colonizers (Stickney and Campbell, 2000), it may be inferred that the composition of the overstory following fire is due primarily to off-site colonization rather than on-site survivors as after the Sundance fire (Stickney 1986). This was reinforced by informal field observations that suggested that these sites were surrounded by mature cedar/hemlock/Douglas-fir stands.

Variations in geography, subzones and survivorship could account for the differences in post-fire overstory composition from the literature. However, it is likely that small sample size is a factor. This study's observations are based on only the 3rd age class of fire sites, which had a sample size of only 2, which may be too small to allow an accurate description of overstory composition.

b) Post-Harvesting Composition:

Overstory species composition following clearcut harvesting has not been as extensively studied as natural post-fire species composition in the ICH zone. The lack of mature surviving overstory trees on clearcut sites requires that any regenerating trees originate from the on-site seed bank or from dispersal from off-site sources or understory survivors. The observed trends were an increase in cedar and hemlock proportions over time, a Douglas-fir presence, and interior spruce figuring prominently in the 3 to 10 year age class and subsequently declining. Other species present included western white pine and paper birch, and to a lesser extent black cottonwood and trembling aspen. It is interesting that this post-harvesting composition more closely resembles those observed by Habeck (1968) following wildfire, than the fire site species compositions did. This species composition, with a large proportion of shade-intolerant species initially, and a steady increase in the proportion of the shade tolerant species over time supports a more traditionally accepted view of overstory compositional changes through time (Shiplett and Neuenschwander, 1994; Lyon and Stickney, 1974): light levels were initially very high, allowing fast-growing shade-intolerants to outcompete more shade-tolerant species. With eventual crown closure, shade-intolerant species are expected to be excluded from further regeneration while shade-tolerant species would eventually dominate, but these events were not observed within the timescale of this study.

Planting treatments may have been a confounding factor and may have influenced overstory species composition. Just under one third (29%) of clearcut sites were planted following clearcutting, and, as described earlier, this proportion was similar to the actual proportion of planting that has occurred among clearcut blocks in the study region. Several of these planted sites fell into the first age class (0 to 2 years since disturbance), and these trees were of insufficient height to be considered part of the overstory. Taking this into consideration, only one of the remaining planted sites was planted with interior spruce and three were planted with Douglas-fir. The relatively high proportion of interior spruce and Douglas-fir found on clearcut sites may be accounted for in part, by these planting treatments.

Snags

Clearcut sites in this study had no dead standing trees remaining immediately following the harvesting event (all were mechanically removed). As such, any snags present in clearcut sites occurred during the later age classes when regenerating trees begin to self-thin and selectively die off. Snag basal area, diameters and density on clearcut sites were initially low, and began to increase slightly in the later age classes. Consistent with the present study, Timoney et al. (1997) recorded that snag density following harvesting of boreal forests increased with time at around 30 years since disturbance; and subsequently began to decrease at 150 years since disturbance as the older snags began to decay. Conversely, recent fire sites often had very high numbers of snags initially (Timoney et al., 1997). It has been common in stand-replacing fires of moderate-high severity that most of the overstory trees have been converted to dead-standing snags, accounting for their high numbers.

Snag basal areas, diameters and densities were initially much greater in fire sites. Fire damaged overstory trees can be killed either acutely by the heat damage to the vascular tissues or slowly over time from sub-lethal wounds received during the fire. Mean snag dbh on fire sites increased over time likely because the largest surviving trees likely died slowly from their fire scars and root damage, and therefore did not become snags until the 3rd age class. Or conversely, smaller-sized snags began falling before the large ones.

Snag basal area and density slowly increased in clearcut sites (due to the accumulation of dead post-disturbance regeneration), while snag basal area and density decreased in fire sites over time. Passovoy and Fulé (2006) also recorded a decline in snag density on burned sites in ponderosa pine. Initially most fire-killed trees are present as snags, but they decay and eventually fall and are converted to coarse woody debris; most snags can be expected to have fallen by the 27th year since disturbance (Passovoy and Fulé, 2006). These opposite temporal trends on fire and clearcut sites create widely different early-successional forest structures. The areas of high-density snags created by wildfires are important at the stand and landscape levels. Many organisms rely upon the presence of snags in burned areas for habitat. Snags that have been attacked by insects provide foraging habitat for bark-foraging woodpeckers, nuthatches and other birds. (Stevenson et al., 2006). Though these relatively recently burned ICH forests are not extremely prevalent across the landscape, their existence, their size and their proximity to each other are important factors in determining the range and success of the species that depend on them.

Coarse Woody Debris

Recently disturbed forests often have the highest quantities of CWD than at any other time in succession (Carmona et al., 2002; Feller, 2003). CWD was examined due to its great importance for energy fluxes, for wildlife as habitat and for nutrient cycling in forest ecosystems (Harmon et al., 1986; Carmona et al., 2002; Feller 2003; Stevenson et al., 2006). Initially, fire sites had 67% less CWD volume than clearcut sites. These clearcut sites were usually cable logged, and so their greater CWD volume can be attributed to logging slash from the harvesting operations. Most of the CWD volume on fire sites would have been consumed or partially consumed by the fires, hence the low initial CWD volume. Over time, CWD volume increased on fire sites and declined on clearcut sites. The increase in CWD volume on fire sites is likely due to dead-standing trees falling to the ground (Passovoy and Fulé, 2006). The decrease in volume on clearcut sites is due to the natural decay of the CWD over time. We would similarly expect that in fire sites we would eventually see a gradual decline of CWD volume due to decay (i.e. at year 27, sites had equivalent volumes to 9 year old sites, as Passovoy and Fulé found (2006)), but this trend does not appear within the first 17 years of succession on fire sites. These trends in CWD volume further support the observation that wildfires and clearcuts have very different structural legacies, which can affect ecosystem composition and function. CWD volumes and habitat attributes will decline most dramatically in clearcuts in the long-term (Stevenson et al., 2006). Consequently, the organisms that rely on coarse woody debris for habitat and those responsible for decay, as well as the other nutrient benefits of coarse woody debris may all decline as CWD declines. As such, clearcut sites, with their high initial levels and the subsequent rapid decay of CWD, may not support comparable faunal communities (size and composition) as sites disturbed by wildfire.

Emulation silviculture

Emulation silviculture seeks to utilize forest harvesting practices that have similar effects on ecosystem structure, composition and function as natural disturbances. In the case of the Interior Cedar Hemlock zone of southern B.C., there are both similarities and differences between the effects of clearcut logging and wildfire on the structure and composition of live overstory trees, snags and CWD. Diameters, basal area, stems per hectare and number of trees and species richness all increased over time for both disturbances, but in every case, at a higher rate on clearcut sites, likely due to higher availability of limiting resources and to a more intact seed bank. Overstory species composition varied greatly between clearcut and fire sites, though the principle components were present in each. Snags were common in recent fire sites, and completely absent in recent clearcuts. CWD volume was high on recent clearcuts, and became very high with time since fires when the snags began to fall. Each disturbance type left a different structural legacy which altered the early progression of succession in terms of overstory structure and composition and ground fuels.

The fundamental differences in the nature of each disturbance type create fundamental differences in their ecosystem effects, and in early succession, create different forest types. Whether these differences become more or less pronounced over time is yet to be determined in the ICH zone. Understanding the role that biological legacy plays in long-term site productivity and structural diversity is critical to informed management (Timoney et al., 1997). Managers must specify their goals within emulation silviculture in order to be successful: is the goal to emulate the natural disturbance's effects on structure, function, biodiversity, species composition or all of these? This study identified several differences in tree structural and compositional trends between wildfires and clearcuts during early ICH forest succession. If these initial trends continue their paths and/or deviate from each other further, then the contrasts between wildfire and clearcutting effects may be sufficiently large to merit further research into whether current ICH forest harvesting practices and management are emulating natural disturbances.

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Chapter III: The effects of wildfire and forest harvesting on early-successional understory structure, composition, and diversity in the Interior Cedar-Hemlock zone of British Columbia[3]

3.1 Introduction

Wildfire is the most important natural disturbance type in most North American forest ecosysystems (McRae et al., 2001). Fire is an integral part of ecosystem function, maintaining biodiversity (Rogeau, 2000) and creating a patchy mosaic of stands of different ages, structure and compositions across the landscape (Shiplett and Neuenschwander, 1994; McRae et al., 2001). Suppression activities in the last century have resulted in a widespread build-up of fuels across many forest types (e.g. Albrecht and McCarthy, 2006; Steele et al., 2006; Collins et al., 2007). It is believed that this build-up has often led to a greater frequency and severity of wildfires than some ecosystems have encountered to date (Swetnam et al., 1999), making suppression activities more difficult and costly (e.g. Collins et al, 2007). In addition, there has been a significant increase in forest harvesting (Steele et al., 2006) which is often a major anthropogenic disturbance type. The frequency of forest harvesting (dictated by rotation age and socio-economic factors) is also generally very different from typical fire return intervals (McRae et al., 2001). Consequently, over the last few decades, forested ecosystems may have been exposed not only to an overall increased frequency of disturbance, but also to a completely different, and hitherto un-encountered disturbance type in the form of harvesting. It is imperative that the effects of these changing disturbance regimes are understood by managers in order to conserve biodiversity and to meet other ecological and economic goals (Franklin et al., 2002).

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[3] A version of this chapter will be submitted for publication. Corriveau B.M. and M.C. Feller. 2008. The effects wildfire and forest harvesting on the structure and composition of early successional understory structure, composition and diversity in the Interior Cedar-Hemlock Zone of British Columbia.

Of interest to managers and the public is the conservation of biodiversity and ecological integrity following harvesting operations. A large proportion of the species richness in a forest ecosystem comes from the understory vegetation, yet few research projects have examined all levels of vegetation when examining the effects of disturbance (Roberts, 2007), the emphasis being primarily on the overstory trees for future harvesting purposes. If the conservation of biodiversity is an objective, then a better understanding of how each level of vegetation is affected by natural and anthropogenic disturbances is needed.

There are opposing arguments on whether harvesting and wildfires have similar effects on understory species composition and abundance. Shiplett and Neuenschwander (1994) found that in U.S. cedar-hemlock forests, both wildfire and harvesting tend to increase shrub abundance, though by different mechanisms: the former promoting re-sprouting of certain fire-adapted species and the latter creating more light availability. In spruce forests in Finland, it was found that species richness initially showed the same trend, regardless of disturbance treatment (fire or harvesting) (Uotila and Kouki, 2005). It was also found that the mean number of species for most plant groups varied by stand age, but not by disturbance type, and that disturbance type did not significantly affect species diversity (Uotila and Kouki, 2005). Collins et al. (2007) found that total abundance of native understory plant species was not significantly affected by changes in disturbance type in Sierra Nevada mixed conifer forests. Thus, forest harvesting effects may resemble natural wildfire effects on understory vegetation in some key factors, under certain conditions, depending on fire severity and/or ecosystem.

Despite these general similarities, these disturbance types are fundamentally different in the way they interact with the vegetation complex. Besides varying in inherent characteristics (chemical versus mechanical), wildfires and forest harvesting vary in severity, size, frequency, and homogeneity, resulting in widely contrasting starting points for stand development (Franklin et al., 2002; Rees and Juday, 2002). These contrasts include differing structural legacies, and rates, compositions and density of plant regeneration (Franklin et al., 2002). Different disturbance frequencies may reset succession at different seral stages of the pre-disturbance communities, which is one of the most important factors determining post-disturbance community composition (Shiplett and Neuenschwander, 1994). Further differences in the effects of wildfire and harvesting on understory vegetation were pointed out by Rees and Juday (2002) in the Alaskan upland boreal forest. They found that burned sites had higher species diversity, higher species turn over, and a higher abundance of fire-promoted species than the harvested sites over time (Rees and Juday, 2002). These findings highlight that fire-adapted species are dependant on fire for regeneration, and the lack of fire (ie. during many harvesting treatments) can lead to very different species compositions. They also concluded that, in general terms, logged sites begin and continue succession with a greater share of the original mature forest understory plants while burned sites initiate succession with more distinctive and specialized plant species (Rees and Juday, 2002). It has also been suggested that changes in composition and dominance after logging occur more rapidly than during natural succession in the boreal forest (Timoney et al., 1997). Similarities in the effects of harvesting and wildfire do exist so much as to render them comparable; however, there is ample evidence that many differences in the response of understory vegetation and stand dynamics exist in many forest ecosystems, both at the stand and landscape scales.

Emulation silviculture attempts to imitate natural disturbances such as wildfire (McRae et al., 2001), thereby offering a guiding principle to forest managers, along with an appealing tool set for dealing with ecological issues important to the domestic and international public (McRae et al., 2001). Forest management in B.C. is currently governed by a paradigm that maintains that biological diversity can be preserved by utilizing harvesting regimes that closely mimic "natural" disturbance (Anon., 1995). This is a controversial concept as the successful emulation of natural disturbances via silvicultural techniques appears to vary with ecosystem and harvesting methods (Lindenmayer and McCarthy, 2002; Collins et al., 2007). In most cases where emulation silviculture is practiced or implied, there is a lack of research to confirm that the treatments have similar effects on vegetation.

The Interior Cedar-Hemlock (ICH) forest of southern B.C. is one of these ecosystems where emulation silviculture is presumed but where successional patterns following natural and anthropogenic disturbances are not fully understood. The natural disturbance regime of ICH forest involves relatively infrequent wildfire as the main disturbance type (Shiplett and Neuenschwander, 1994; Lewis and Lindgren, 2000; DeLong et al., 2005), yet harvesting, predominantly clearcutting, has intensified over the last 80 years. Since 1990, more than 184 000 ha have been logged in the ICHmw, ICHwk, and ICHvk subzones (B.C. Ministry of Forests silviculture database, accessed January 2007). Though the community types in the ICH forests of B.C. have been described in impressive detail (Lloyd et al., 1990; Ketcheson et al., 1991), plant succession is still not fully understood. In fact, there is very little research into the effects of wildfires and harvesting on cedar-hemlock forests, and what research there is comes primarily from the Northern Rockies in the USA (e.g. Lyon and Stickney, 1974; Stickney, 1986; Shiplett and Neuenshwander, 1994) as opposed to the ICH zone in B.C..

Given the context of emulation silviculture, this chapter compares the effects of wildfire and forest harvesting on early-successional forest understory vegetation in the ICH zone of southern B.C. More specifically, in this study I test whether disturbance type influences understory vegetation characteristics in early-successional ICH forests, to predict the structure and composition of the forest that will result after 40 years of succession depending on disturbance type, and to provide a better understanding for forest management purposes of early-successional patterns in the ICH following wildfire and harvesting.

The type of wildfire and harvesting activities that were compared were high severity fires and clearcuts as they both result in stand-replacement (Nuguyen-Xuan et al., 2000). High-severity, stand-replacing fires were chosen since severity is the property of fire that most influences forest vegetation and propagules (Stickney and Campbell, 2000), and since fires in the ICH have generally resulted in stand replacement (Shiplett and Neuenschwander, 1994; Anon., 1995; McRae et al., 2001). Fires in cedar-hemlock forests are generally severe, crowning, and kill the existing overstory, thus renewing the successional pathway (Shiplett and Neuenschwander, 1994). Clearcuts are, and have historically been, the most common forest harvesting method used in the ICH (Del Williams, RPF Operations Forester, Revelstoke Community Forest Corporation (RCFC), personal communication; B.C. Ministry of Forests and Range forest cover maps, accessed January 2007). Clearcutting has also been considered most similar to fire of all types of logging, in effects on ecosystems, in terms of living standing trees and effects on surface fuels (Shiplett and Neuenschwander, 1994). Therefore, there is merit in comparing successional pathways of clearcuts and stand-replacing fires in the ICH zone, given their assumed similar influences on ecosystems (McRae et al., 2001).

I hypothesize that:

1) post-disturbance plant species composition, structure and diversity during the first 40 years of succession will differ with disturbance type (wildfire and clearcutting);

2) rates of revegetation and plant species richness will vary with disturbance type;

3) plant successional patterns will differ with disturbance type.

3.2 Methods

The study area was restricted to the Interior Cedar-Hemlock (ICH) zone surrounding Revelstoke, B.C. The ICH zone (Figure 1.1), an inland rainforest which stretches from west central British Columbia south to Idaho and Montana, is found at low to mid elevations (400-1500m) (Ketcheson et al., 1991). In southeastern B.C., it occupies the lower slopes of the Columbia Mountains and the western side of the continental divide along the Rocky Mountains (Ketcheson et al., 1991). This zone's climate is characterized by cool wet winters and warm dry summers. Mean annual precipitation is 500-1200mm, 25% to 50% of which falls as snow (Ketcheson et al., 1991). Average annual temperatures in the ICH zone range from 2 to 8.7 °C, which reflects its latitudinal range (Ketcheson et al., 1991). Soils in zonal ecosystems are primarily Humo-Ferric Podzols, or Brunisolic or Orthic Gray Luvisols with finer textured parent materials (Ketcheson et al., 1991).

The ICH zone has the highest diversity of tree species of any biogeoclimatic zone in the province, and its climax stands are dominated by western hemlock (*Tsuga heterophylla*) and western red cedar (*Thuja plicata*) (Lloyd et al., 1990; Ketcheson et al., 1991). The understory vegetation within wetter, cooler ICH forests contains a diverse mixture of predominantly herbs and shrubs. Commonly found species in the herb layer include bunchberry (*Cornus canadensis*), oak fern (*Gymnocarpium dryopteris*), one-leaved foam flower (*Tiarella unifoliata*), lady fern (*Athyrium felix-femina*), twinflower (*Linnaea borealis*), rosy twisted stalk (*Streptopus roseus*) and queen's cup (*Clintonia uniflora*). Commonly found species within the shrub layer are falsebox (*Pachystima myrsinities*), thimbleberry (*Rubus parviflorus*), oval-leaved blueberry (*Vaccinium ovalifolium*) and devil's club (*Oplopanax horridus*) (Lloyd et al., 1990). The occurrence and relative abundance of these understory species depends on moisture regimes, stand age and light availability.

The ICHwk1 and ICHvk1 variants were chosen for study due to their containing ample potential clearcut sites and the majority of recent ICH wildfires. These variants are characterized by wet-cool and very-wet-cool climates, respectively, which sets them apart from the other drier ICH variants. They occur at mid- to high-elevations (650-1300m), below the Engelmann Spruce – Subalpine Fir (ESSF) zone and above the ICHmw subzone, throughout the wet Columbia and Selkirk mountain ranges (Lloyd et al., 1990). The ICHvk1 occurs upslope of the ICHwk1 and is wetter. The ICHwk1 has a herb-moss dominated understory, with abundant bunchberry, red-stemmed feathermoss (*Pleurosium schreberi*), knight's plume (*Ptilium crista-castrensis*) and step moss (*Hylocomium splendens*) (Lloyd et al., 1990). The ICHvk1 has a smaller herb-moss component in the understory than in the ICHwk1, with a reduction in mosses and with devil's club and lady fern occurring in greater abundance (Lloyd et al., 1990). Appendix I includes further information on ICH subzones and site series.

Disturbance regimes

In ICH forests, many wildfires tend to have high intensities and severities and are therefore stand-replacing (Shiplett and Neuenschwander, 1994; McRae et al., 2001). The Natural Disturbance Type (NDT) of the ICHvk and ICHwk subzones is described as NDT1, which are ecosystems with rare stand-initiating events (Anon., 1995). The mean return interval for these disturbances is generally 250 years (Anon., 1995). Fires in the Revelstoke area of B.C. are typically caused by lightning strikes, usually on steep slopes in mid to high elevations (Glen Burgess, Fire Protection Officer, B.C. Ministry of Forests and Range, Revelstoke B.C., Personal Communication).

Typical clearcut logging in the area varies greatly with slope and road access. When road access is unavailable, helicopter logging is utilized. Cable logging occurs on steep slopes (approximately 30%-40%) with road access. Trees are hand-felled and skidded to a landing using a cable. At the landing, the trees are bucked to length and limbed, and the waste is either piled below the landing or burned in piles on the landing. When slopes are gentle (<30%), ground skidding and machine felling is used, often in the winter to minimize soil damage. The trees are bucked and de-limbed at the landing, as in cable logging. Planting often occurs without any site preparation. Historically, broadcast burning was performed to reduce slash to facilitate planting. However, more recently, public opposition and the size and shape of the cutblocks have prevented burning, so planters must plant through the slash. The proportion of cable logging to helicopter logging to ground skidding used by the RCFC is 70%, 10% and 20% respectively. (Del Williams, RPF Operations Forester, RCFC, personal communication).

Study Site Selection

Study site locations are indicated in Figure 2.2 (Chapter II). Study sites were selected according to certain criteria in order to minimize the confounding of results by factors such as differences in fire severity and ecosystem. These criteria were disturbance type, ecosystem, access, distance from Revelstoke, size of disturbed area, pre-disturbance community, and age. Details are given in Chapter II.

The design involves sampling two disturbance types over time. Time is measured in "years since disturbance" in this case. Sampling occurred in forests where clearcutting or a stand-replacing fire occurred within the last 40 years (1967 to 2007). For sampling purposes, sites were selected within pre-determined age classes. The age classes were defined respectively as: 0-2, 4-10, 11-15, and 20-40 years since disturbance. These age classes were designed to provide appropriate resolution for periods of succession between which rapid changes are predicted to occur (Dr. Suzanne Simard, UBC Forest Sciences Department, personal communication).

Sites were initially located using GIS forest cover maps (Integrated Land Management Bureau, Government of B.C., updated January 2006), B.C. Ministry of Forests and Range forest cover maps (accessed January 2007) and fire location maps for the area around Revelstoke. These methods were supplemented by extensive in-situ ground-based scouting. Study site suitability, age and disturbance type was then assessed from the ground. When an acceptable site was located, elevation and UTM coordinates were noted using a GPS unit (Garmin GPS12). Slope and aspect were also noted. A complete list of the study sites including location, age, biogeoclimatic variant, disturbance type and other information is given in Table 2.1 of Chapter II.

Field Methods

Three 10 x 10m square, non-overlapping, overstory plots (Chapter II) were randomly placed in each study site. The north-west corner of each overstory plot was randomly located within the acceptable area of the site. If a random location was selected for a plot and was deemed unsuitable, because it occurred in a seepage area for example, the plot location was randomly selected again. These plots were buffered by a minimum of 10m from the edges of the cut block or burned area to avoid edge effects. The slope and aspect of each overstory plot were noted.

Four understory vegetation plots were placed in each corner of each 10 x 10m overstory plot. Understory vegetation was sampled using a modified version of the sampling method used by Wetzel and Burgess (2001). These square plots were 2 x 2m, and were numbered in a clockwise manner, beginning in the north-west corner of the overstory plot. In each vegetation plot, the percent cover of each species of tree seedling, shrub and herb below 1.3m in height was visually estimated. In each corner of the understory plots that were adjacent to the overstory plot corners, a 50 x 50cm bryophyte plot was established. The percent cover of each species of moss, lichen and liverwort in these bryophyte plots was visually estimated. The percent cover of arboreal lichens was visually estimated within the 10 x 10m overstory plot using a qualitative scale of 0-5, where zero is negligible coverage and 5 is nearly 100% coverage (on available arboreal substrates). An example of the layout of a study site is shown in Figure 3.1.

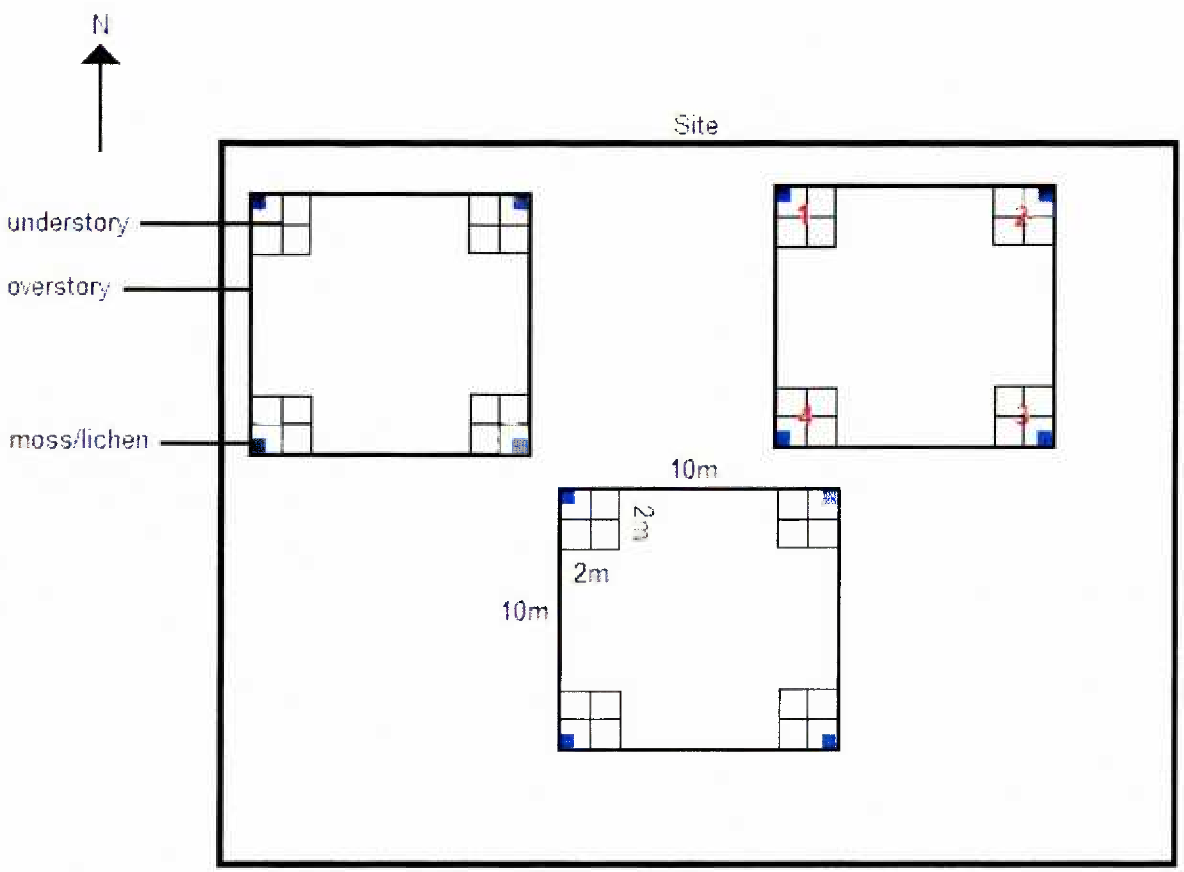


Figure 3.1. Representation of an idealized field site.

Data Analysis

The analysis tested for differences in all measured characteristics between disturbance types over time (at the site level) to assess whether the resulting early-successional plant communities varied with disturbance type and years since disturbance in stand structure and floristic composition. All statistics were performed using SAS 9.1.3 Service Pack 4 (SAS Institute, Inc, 2002-2003).

A chronosequence of understory structural and compositional characteristics was constructed from similar sites of different ages, rather than the same sites monitored over time. Mean percent cover of all vegetation types was analyzed. These types are trees and shrubs (<1.3m tall), herbs (including herbs, grasses and sedges) and bryophytes (a global term used in this study to encompass mosses, lichens and liverworts).

Species composition is presented qualitatively and quantitatively in the form of species richness and species diversity. Species diversity is expressed as the Shannon-Wiener diversity index, due to its common usage in ecological studies and due to its consideration of both species richness and evenness (DeJong, 1975).

Linear regression analysis, with a class variable (ANCOVA with non-homogenous slopes), was used to identify differences in each of these variables between disturbance types, over time. The significance level used throughout was $\alpha=0.05$. Where the assumptions of linear regression (equal variance, linearity, normality) were not met, simple mathematical transformations, such as natural logarithm or square root, were applied to the variables. It should be noted that time in the linear regression analysis was continuous (years since disturbance) rather than discrete (age classes used for even field sampling purposes). However, for presentation purposes and to facilitate comparisons, for certain untransformed variables, time is also presented as discrete age classes.

Following these analyses, the effects of overstory and CWD characteristics (Chapter II) on understory characteristics was explored. Data were merged and subsequently analyzed using a general linear model (linear regression and partial F-Tests) to identify any effects each structural characteristic might have had on vegetation percent covers, species richness and species diversity.

3.3 Results

The complete results of each linear regression analysis (including regression equations and general linear model details) can be found in Appendix III. All linear regressions of understory vegetation characteristics between disturbances, over time, were significant.

Vegetation percent cover

There appears to be an increase in bryophyte mean percent cover (Figure 3.2a) over time to a peak (earlier for fire sites), followed by a decline with no consistent differences between disturbance types. In both disturbance types, herb percent cover increased to a peak (at approximately 7 years) and then began to decline (Figure 3.2b). However, the peak in abundance appeared to be higher for clearcut sites, and the decline slower. Shrub percent cover increased steadily with time for both disturbances (Figure 3.2c). The percent cover of shrubs in the first age class was greater for the clearcut sites, but these inter-disturbance differences appeared to decrease with time. Understory tree percent cover is initially very low for both disturbances and then increased by the second age class (Figure 3.2d).

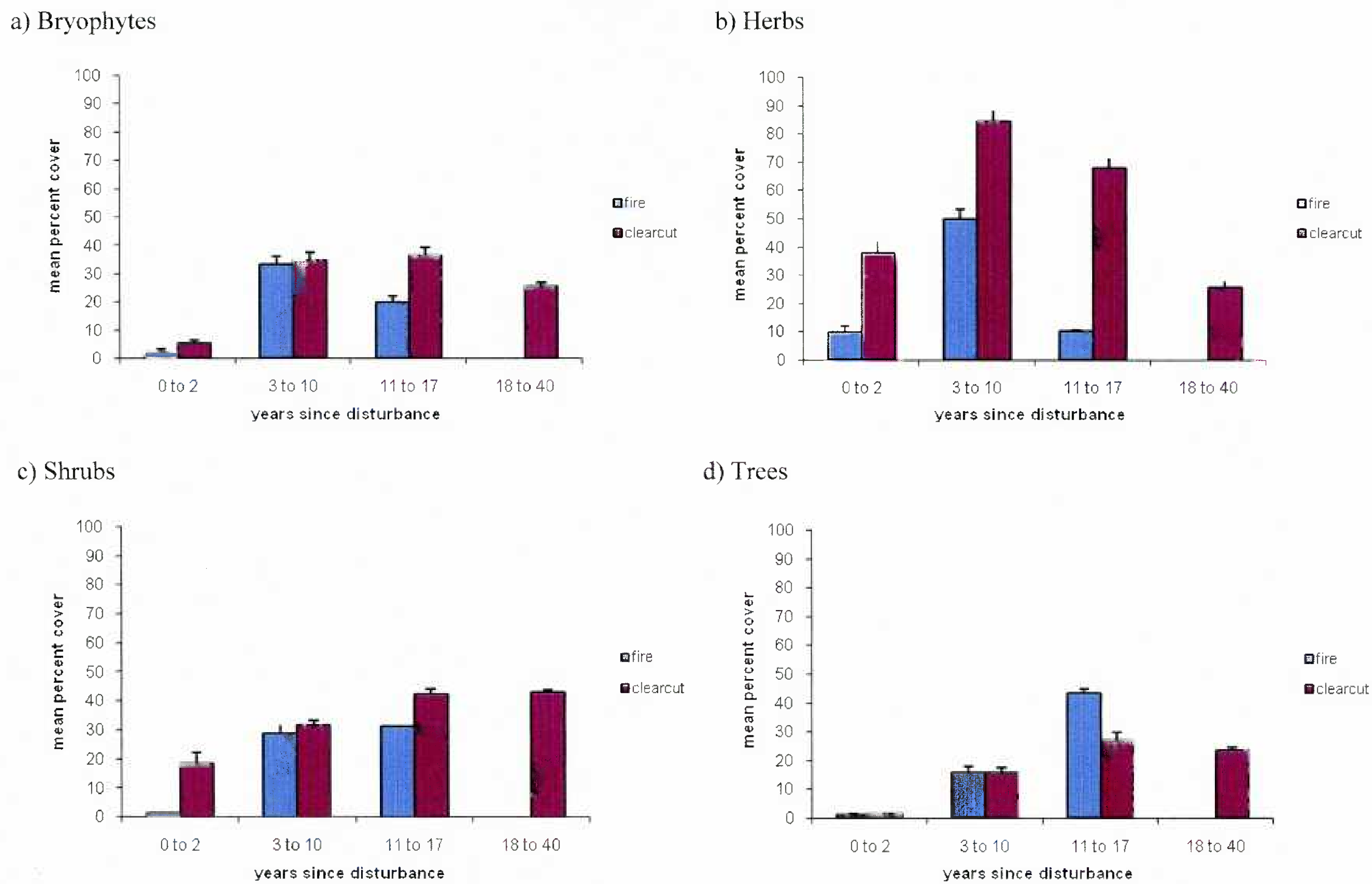


Figure 3.2: The mean percent cover of understory vegetation for fire and clearcut sites, by age class (n=39). Standard error bars are included. Note that no information was available for sites 18 to 40 years post-fire. a) bryophytes (mosses, lichens and liverworts), b) herbs, c) shrubs (<1.3 m in height), d) trees (<1.3 m in height).

To meet the assumptions of linear regression, a parabolic transformation was applied to the x variable (years since disturbance) in the analysis of bryophyte percent cover. The linear regression results for bryophyte percent cover for each disturbance type were plotted over time (Figure 3.3a). The regression revealed a significant interaction between disturbance type and time ($p=0.033$), and a significant interaction between disturbance type and time^2 ($p=0.015$). Therefore, the trends in bryophyte cover over time, indicated above, differed significantly between fire and clearcut sites.
The assumptions of linear regression were met by using a parabolic transformation that was also applied to the x variable (years since disturbance) in the analysis of herb percent cover. The linear regression results for herb percent cover for each disturbance type were plotted over time (Figure 3.3b). The regression results indicated a significant interaction between disturbance type and time ($p=0.024$), and a significant interaction between disturbance type and time^2 ($p=0.008$). Therefore, the trends in herb cover over time, indicated above, differed significantly between fire and clearcut sites.

A square root transformation of shrub percent cover was used to meet the assumptions of linear regression. The linear regression results for square root of shrub percent cover for each disturbance type were plotted over time (Figure 3.3c). The regression results indicated an interaction between time and disturbance type, represented a dummy variable ($p=0.048$), indicating that the trends of square root shrub percent cover over time differed between the two disturbance types. Shrub percent cover was initially much higher on clearcut sites than on fires sites, and then increased at different rates (at a higher rate for fire sites). Interestingly, the increase in shrub percent cover seems to coincide with decline of herbs and bryophyte percent covers.

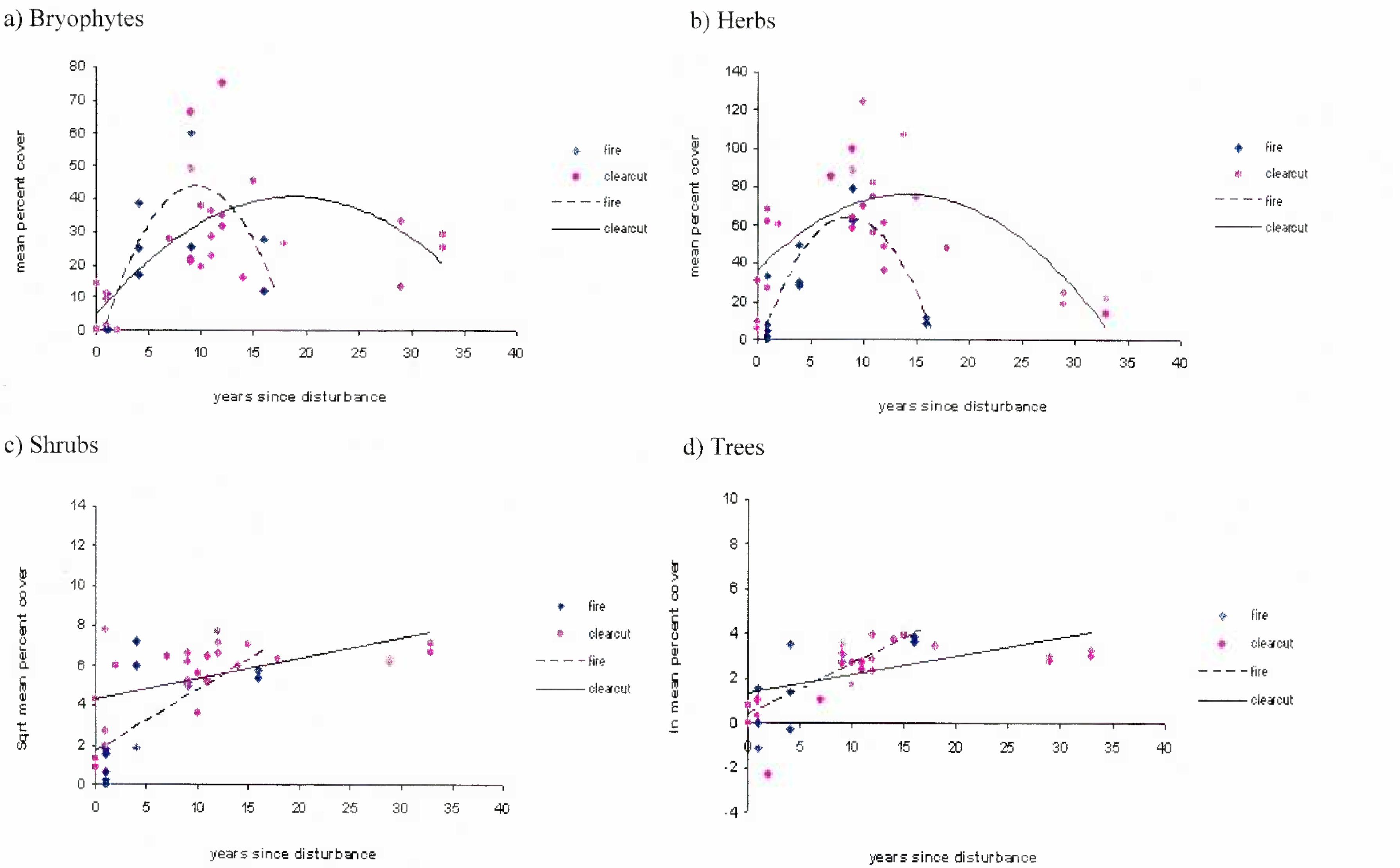


Figure 3.3: The mean percent cover (or transformation thereof) of each understory vegetation type all fire and clearcut sites, by years since disturbance, with linear regressions indicated (n=39). a) bryophytes (mosses, lichens and liverworts), b) herbs, c) shrubs (<1.3 m in height), d) trees (<1.3 m in height).

A natural logarithm of understory tree percent cover was used to meet the assumptions of linear regression. The linear regression results for natural logarithm of tree percent cover for each disturbance type were plotted over time (Figure 3.3d). The regression results resembled those of bryophyte percent cover and indicated that natural logarithm of tree percent cover changed over time (p=0.0004) but this trend over time did not differ significantly between disturbance types.

The cover of different vegetation groups differed in each age class between fire and clearcut plant communities (Figure 3.4). The combined percent cover of all vegetation types was higher in clearcut sites than in fire sites for every age class. This difference was largest in the first age class where clearcut vegetation percent cover was 4.5 times larger than on fire sites. On clearcut sites, herbs had the highest cover, followed by shrubs, bryophytes and trees. On fire sites, herbs still had the highest percent cover, but were followed by shrubs, trees and then bryophytes. Herbs had a larger percent cover on clearcut sites in every age class when compared to fire sites.

a) Fire

b) Clearcut

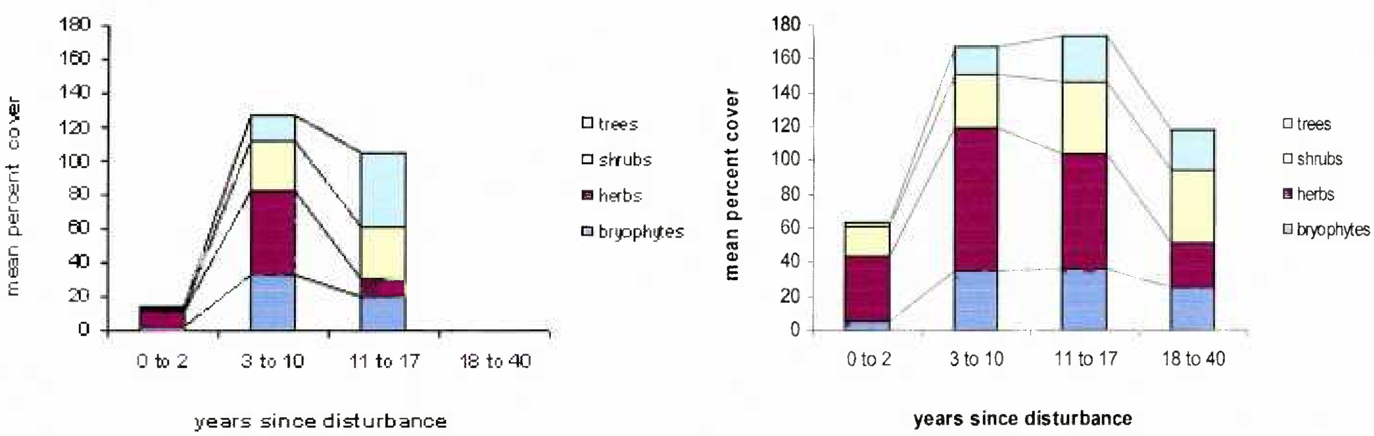
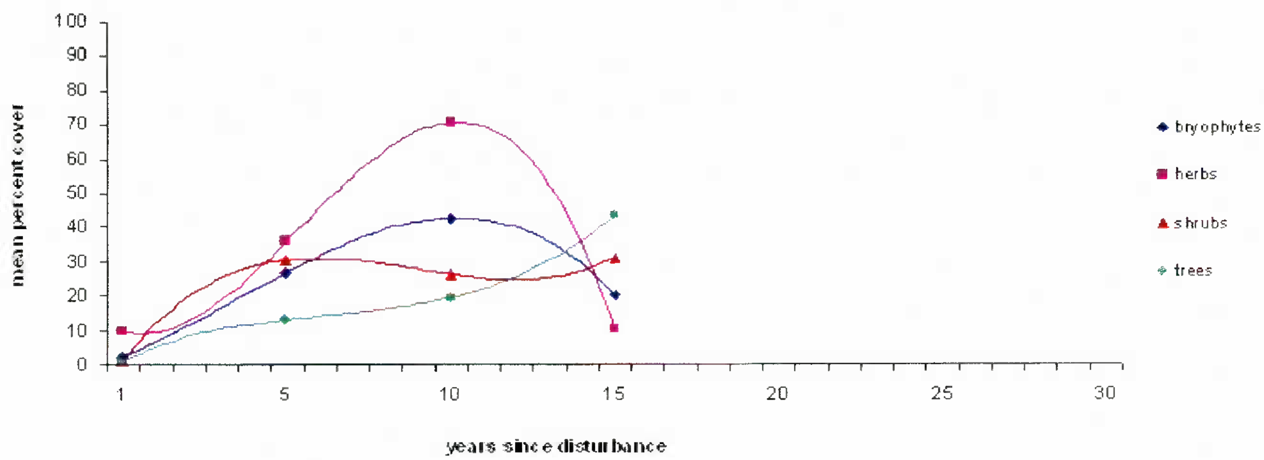


Figure 3.4: Mean percent cover of each vegetation type in fire sites (a) and clearcut sites (b), by age class (n=39). Note that no information was available for sites in the 18 to 40 years post-fire age class.

A chronosequence of early-successional plant group trajectories following fires and clearcuts was plotted using the mean site percent cover data for each vegetation type (Figure 3.5). Years since disturbance were rounded to the nearest 5 to standardize the figures and to facilitate interpretation. The trajectories were similar in that herbs were the most abundant vegetation type for the first 10 to 15 years since disturbance. Trees were the least abundant vegetation type in terms of percent cover until mid-way through the trajectories. Shrub and bryophyte percent covers generally took an intermediate place in both trajectories. The percent covers of all vegetation types were higher on clearcut sites in the first year since disturbance. Herb cover declined at a slower rate on clearcut sites. Tree cover was higher at 15 years in fire sites. Shrub cover surpassed herb cover at approximately 15 years since disturbance for fires and 20 years since disturbance for clearcuts. Tree cover surpassed herb cover in fire sites at 15 years since disturbance, becoming the most abundant vegetation type. Tree cover did not surpass herb cover on clearcut sites until approximately 22 years, at which point shrubs were the most abundant vegetation type. At 10 years since disturbance, bryophytes were notably the second most abundant vegetation type on fire sites, and the third most abundant on clearcut sites. This represents the peak of bryophyte percent cover on fire sites, while this peak occurs at approximately 15 years since disturbance for clearcut sites.

a) Fires



b) Clearcuts

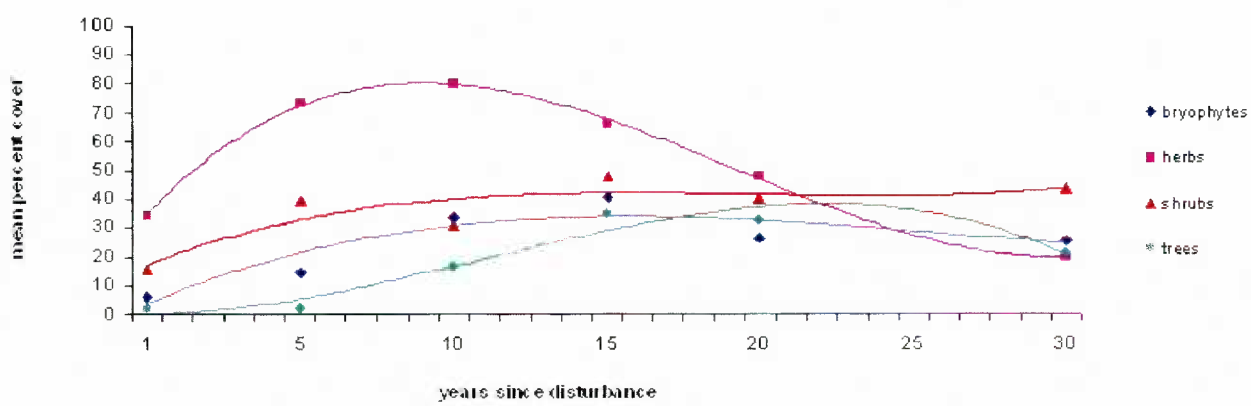


Figure 3.5: Successional trajectories of the mean percent cover of each vegetation type for fire sites (a) and clearcut sites (b) through time, with polynomial trendlines.

Vegetation composition

A list of all understory plant species found during this study is included in Table 3.1. Several species, like 'hawkweeds', included multiple species grouped together here into one 'species' for presentation purposes but were identified separately in the field. Presence data were recorded at the 10 x 10 plot level, and summarized at site and disturbance levels. Included in this table are the

Table 3.1: Species list, including vegetation type, common and scientific names names. The percent incidence of each species is indicated by all sites (percent of all 39 sites in which the species was found) and by fire and clearcut sites (percent of all 36 fire and 81 clearcut overstory plots in which the species was found) specifically. The total overall incidence was calculated as the number of times a species was found in the total 117 overstory plots. Subjective rarity values based on overall incidence are included for each species (VR = very rare = <5 incidences; R = rare = 6-10 incidences; U = unusual = 11-20 incidences; C = common = 21-49 incidences; VC = very common = 50+ incidences). A '*' indicates that the species is exotic but naturalized to B.C. (Qian and Klinka, 1998).

			% incidence				
vegetation type	common name	latin name	site	fire	clearcut	total overall incidence	rarity
bryophyte	apple moss	*Bartramia pomiformis*	12.8	0.0	9.9	8	R
bryophyte	bristly haircap	*Polytrichastrum alpinum*	2.6	0.0	1.2	1	VR
bryophyte	broom moss	*Dicranum scoparium*	10.3	0.0	4.9	4	VR
bryophyte	cladonia spp.	*Cladonia* spp.	53.8	8.3	67.9	58	VC
bryophyte	cow pie	*Diploschistes muscorum*	2.6	0.0	2.5	2	VR
bryophyte	dog pelt	*Peltigera canina*	5.1	8.3	0.0	3	VR
bryophyte	false haircap	*Timmia austriaca*	2.6	0.0	1.2	1	VR
bryophyte	fire moss	*Ceratodon pupureus*	51.3	61.1	18.5	37	C
bryophyte	flapper moss	*Mnium spinulosum*	10.3	0.0	7.4	6	R
bryophyte	four-toothed log moss	*Tetraphis pellucida*	30.8	2.8	23.5	20	U
bryophyte	frog pelt	*Peltigera neopolydactyla*	7.7	0.0	3.7	3	VR
bryophyte	glow moss	*Aulacomnium palustre*	38.5	5.6	32.1	28	C
bryophyte	golden star moss	*Campylium stellatum*	5.1	2.8	1.2	2	VR
bryophyte	hooded moss	*Orthotrichum speciosum*	5.1	8.3	0.0	3	VR
bryophyte	juniper haircap moss	*Polytrichum juniperinum*	64.1	27.8	50.6	51	VC
bryophyte	knights plume	*Ptilium crista-castrensis*	28.2	2.8	19.8	17	U
bryophyte	lepraria spp. 1	*Lepraria* spp.	2.6	0.0	2.5	2	VR
bryophyte	lime dust	*Chrysothrix chlorina*	5.1	0.0	2.5	2	VR
bryophyte	monk's hood	*Hypogymnia physodes*	10.3	0.0	7.4	6	R
bryophyte	pipecleaner moss	*Rhytidiopsis robusta*	17.9	0.0	11.1	9	R
bryophyte	powdered orange	*Xanthoria fallax*	2.6	0.0	1.2	1	VR

Table 3.1 continued:

bryophyte	Schreber's red stem	*Pleurozium schreberi*	76.9	25.0	77.8	72	VC
bryophyte	seepage apple moss	*Philonotis fontana*	2.6	0.0	2.5	2	VR
bryophyte	sickle moss	*Sanionia uncinata*	41.0	8.3	27.2	25	C
bryophyte	step moss	*Hylocomium splendens*	10.3	0.0	8.6	7	R
herb	American vetch	*Vicia americana*	2.6	0.0	2.5	2	VR
herb	baneberry	*Actaea rubra*	17.9	0.0	8.6	7	R
herb	bracken fern	*Hypogymnia physodes*	41.0	11.1	34.6	32	C
herb	bunchberry	*Cornus canadensis*	74.4	25.0	80.2	74	VC
herb	butterweed	**Senecio* spp.	2.6	0.0	1.2	1	VR
herb	Canada thistle	**Cirsium arvense*	10.3	13.9	2.5	7	R
herb	clasping twisted stalk	*Streptopus amplexifolius*	30.8	5.6	18.5	17	U
herb	common dandelion	**Taraxacum officinale*	17.9	8.3	6.2	8	R
herb	common horsetail	*Equisetum arvense*	7.7	2.8	2.5	3	VR
herb	common plantain	**Plantago major*	2.6	0.0	2.5	2	VR
herb	enchanter's nightshade	*Circaea alpina*	20.5	0.0	19.8	16	U
herb	false Solomon's seal	*Smilacina racemosa*	30.8	0.0	22.2	18	U
herb	fireweed	*Epilobium angustifolium*	89.7	91.7	75.3	94	VC
herb	goat's beard	*Aruncus dioicus*	5.1	2.8	3.7	4	VR
herb	Grass spp.	grass	53.8	30.6	34.6	39	C
herb	ground cedar	*Lycopodium complanatum*	7.7	0.0	3.7	3	VR
herb	ground pine	*Lycopodium dendroideum*	10.3	0.0	7.4	6	R
herb	Hawkweed spp.	**Hieracium* spp.	89.7	83.3	74.1	90	VC
herb	heart-leaved arnica	*Arnica cordifolia*	2.6	0.0	1.2	1	VR
herb	lady fern	*Athyrium filix-femina*	56.4	30.6	48.1	50	VC
herb	Lilium spp.	*Lilium* spp.	2.6	0.0	1.2	1	VR
herb	maidenhair fern	*Adiantum pedatum*	5.1	0.0	2.5	2	VR
herb	mountain arnica	*Arnica latifolia*	2.6	0.0	1.2	1	VR
herb	oak fern	*Gymnocarpium dryopteris*	64.1	19.4	71.6	65	VC
herb	one-leaved foam flower	*Tiarella unifoliata*	59.0	19.4	69.1	63	VC

Table 3.1 continued:

herb	one-sided wintergreen	*Orthilia secunda*	2.6	5.6	0.0	2	VR
herb	oxeye daisy	**Leucanthemum vulgare*	2.6	0.0	1.2	1	VR
herb	pathfinder	*Adenocaulon bicolor*	12.8	0.0	9.9	8	R
herb	pearly everlasting	*Anaphalis margaritacea*	51.3	38.9	24.7	34	C
herb	prickly lettuce	**Lactuca serriola*	59.0	63.9	34.6	51	VC
herb	purple-leaved willowherb	*Epilobium ciliatum*	12.8	2.8	6.2	6	R
herb	Pyrola spp.	*Pyrola* spp.	7.7	0.0	8.6	7	R
herb	queen's cup	*Clintonia uniflora*	79.5	19.4	79.0	71	VC
herb	rattlesnake fern	*Botrychium virginianum*	2.6	0.0	2.5	2	VR
herb	rattlesnake plantain	*Goodyera oblongifolia*	17.9	0.0	11.1	9	R
herb	red-stemmed saxifrage	*Saxifraga lyallii*	2.6	0.0	1.2	1	VR
herb	rose twisted stalk	*Streptopus roseus*	69.2	13.9	60.5	54	VC
herb	sitka burnet	*Sanguisorba canadensis*	2.6	0.0	1.2	1	VR
herb	sitka valerian	*Valeriana sitchensis*	7.7	0.0	4.9	4	VR
herb	spiny wood fern	*Dryopteris expansa*	56.4	13.9	59.3	53	VC
herb	spreading dogbane	*Apocynum androsaemifolium*	10.3	0.0	9.9	8	R
herb	sticky geranium	*Geranium viscosissimum*	5.1	16.7	0.0	6	R
herb	stinging nettle	*Urtica dioica*	7.7	5.6	0.0	2	VR
herb	strawberry blight	*Chenopodium capitatum*	2.6	0.0	8.6	7	R
herb	sweet-scented bedstraw	*Galium triflorum*	59.0	27.8	48.1	49	C
herb	twinflower	*Linnaea borealis*	38.5	2.8	39.5	33	C
herb	Viola spp.	*Viola* spp.	64.1	22.2	54.3	52	VC
herb	western meadowrue	*Thalictrum occidentalis*	5.1	0.0	2.5	2	VR
herb	wild ginger	*Asarum caudatum*	30.8	5.6	18.5	17	U
herb	wild sarsaparilla	*Aralia nudicaulis*	51.3	11.1	43.2	39	C
herb	wild strawberry	*Fragaria virginiana*	20.5	16.7	12.3	16	U
shrub	baldhip rose	*Rosa gymnocarpa*	5.1	2.8	1.2	2	VR
shrub	beaked hazelnut	*Corylus cornuta*	25.6	8.3	16.0	16	U
shrub	birch-leaved spirea	*Spiraea betulifolia*	10.3	13.9	2.5	7	R

Table 3.1 continued:

shrub	black gooseberry	*Ribes lacustre*	35.9	19.4	22.2	25	C
shrub	black huckleberry	*Vaccinium membranaceum*	41.0	8.3	30.9	28	C
shrub	black twinberry	*Lonicera involucrata*	17.9	0.0	11.1	9	R
shrub	blue elderberry	*Sambucus caerulea*	2.6	0.0	1.2	1	VR
shrub	cascara	*Rhamnus purshiana*	2.6	0.0	1.2	1	VR
shrub	choke cherry	*Prunus virginiana*	2.6	0.0	1.2	1	VR
shrub	common snowberry	*Symphoricarpos albus*	2.6	0.0	1.2	1	VR
shrub	devil's club	*Oplopanax horridus*	46.2	11.1	40.7	37	C
shrub	douglas maple	*Acer glabrum*	25.6	11.1	13.6	15	U
shrub	dwarf nagoonberry	*Rubus arcticus*	2.6	0.0	2.5	2	VR
shrub	false azalea	*Menziesia ferruginea*	12.8	0.0	7.4	6	R
shrub	falsebox	*Pachistima myrsinites*	48.7	41.7	43.2	50	VC
shrub	five-leaved bramble	*Rubus pedatus*	30.8	2.8	28.4	24	C
shrub	oval-leaved blueberry	*Vaccinium ovalifolium*	51.3	13.9	37.0	35	C
shrub	prickly rose	*Rosa acicularis*	15.4	0.0	7.4	6	R
shrub	princes pine	*Chimaphila umbellata*	15.4	2.8	8.6	8	R
shrub	red elderberry	*Sambucus racemosa* spp. *pubens* var. *leucocarpa*	15.4	0.0	9.9	8	R
shrub	red huckleberry	*Vaccinium parvifolium*	7.7	0.0	6.2	5	R
shrub	red raspberry	*Rubus idaeus*	69.2	44.4	61.7	66	VC
shrub	red-osier dogwood	*Cornus stolonifera*	5.1	0.0	2.5	2	VR
shrub	redstem ceanothus	*Ceanothus sanguineus*	2.6	0.0	1.2	1	VR
shrub	saskatoon	*Amelanchier alnifolia*	10.3	0.0	7.4	6	R
shrub	sitka alder	*Alnus crispa spp. sinuata*	7.7	0.0	9.9	8	R
shrub	sitka mountain ash	*Sorbus sitchensis*	2.6	0.0	1.2	1	VR
shrub	skunk currant	*Ribes glandulosum*	7.7	0.0	3.7	3	VR
shrub	soopalalie	*Shepherdia canadensis*	2.6	0.0	1.2	1	VR
shrub	sticky currant	*Ribes viscosissimum*	5.1	2.8	1.2	2	VR
shrub	tall regon grape	*Mahonia aquifolium*	2.6	0.0	1.2	1	VR
shrub	thimbleberry	*Rubus parviflorus*	76.9	63.9	63.0	74	VC

Table 3.1 continued:

shrub	Utah honeysuckle	*Lonicera utahensis*	30.8	8.3	21.0	20	U
shrub	western mountain ash	*Sorbus scopulina*	17.9	0.0	12.3	10	R
shrub	western teaberry	*Gaultheria ovatifolia*	10.3	0.0	4.9	4	VR
shrub	western yew	*Taxus brevifolia*	30.8	2.8	19.8	17	U
shrub	willow spp.	*Salix* spp.	30.8	47.2	7.4	23	C
tree	black cottonwood	*Populus balsamifera* spp. *trichocarpa*	38.5	36.1	14.8	25	C
tree	grand fir	*Abies grandis*	2.6	0.0	1.2	1	VR
tree	interior Douglas-fir	*Pseudotsuga menziesii* var. *glauca*	53.8	33.3	39.5	44	C
tree	interior spruce	*Picea engelmannii x glauca*	56.4	27.8	44.4	46	C
tree	paper birch	*Betula papyrifera*	33.3	30.6	14.8	23	C
tree	trembling aspen	*Populus tremuloides*	7.7	0.0	3.7	3	VR
tree	western hemlock	*Tsuga heterophylla*	71.8	38.9	65.4	67	VC
tree	western red cedar	*Thuja plicata*	74.4	58.3	70.4	78	VC
tree	western white pine	*Pinus monticola*	28.2	0.0	22.2	18	U
tree	whitebark pine	*Pinus albicaulis*	2.6	2.8	0.0	1	VR

percent incidence by site (percent of all 39 sites in which the species was found), the incidence in each disturbance type (percent of all 36 fire and 81 clearcut overstory plots in which the species was found) and the total overall incidence (number of times a species was found in the total 117 overstory plots) of each encountered species.

A subjective rarity rating was applied to each species based on its total overall incidence in this study, which ranged from very rare to very common (VR = very rare = <5 incidences; R = rare = 6-10 incidences; U = unusual = 11-20 incidences; C = common = 21-49 incidences; VC = very common = 50+ incidences). Overall, there were 47 VR, 26 R, 12U, 19C and 19VC species (Table 3.2). Fire sites only had 21% and 23% of the VR and R species, respectively; while clearcut sites contained 91% and 96% of the VR and R species respectively.

Table 3.2: Number and percentage of species in each rarity class in the study and by disturbance type.

Rarity	Fire		Clearcut		Overall
	#	%	#	%	
VR	10	21	43	91	47
R	6	23	25	96	26
U	9	75	12	100	12
C	19	100	19	100	19
VC	19	100	19	100	19
totals	63		118		123

In total, 123 species were identified (Table 3.3). Sixty three species were found in fire sites and 118 in clearcut sites. Only 6 species were exclusive to fire sites while 60 species were only found on clearcut sites. The most common species found on fire sites was fireweed (*Epilobium angustifolium*) and the most common species on clearcut sites was bunchberry (*Cornus canadensis*). Only seven of the total 123 species were considered exotics but naturalized in B.C (Qian and Klinka, 1998). Clearcut sites contained 100%, and fire sites contained 57%, of the exotics.

Table 3.3: Summary of species presence data.

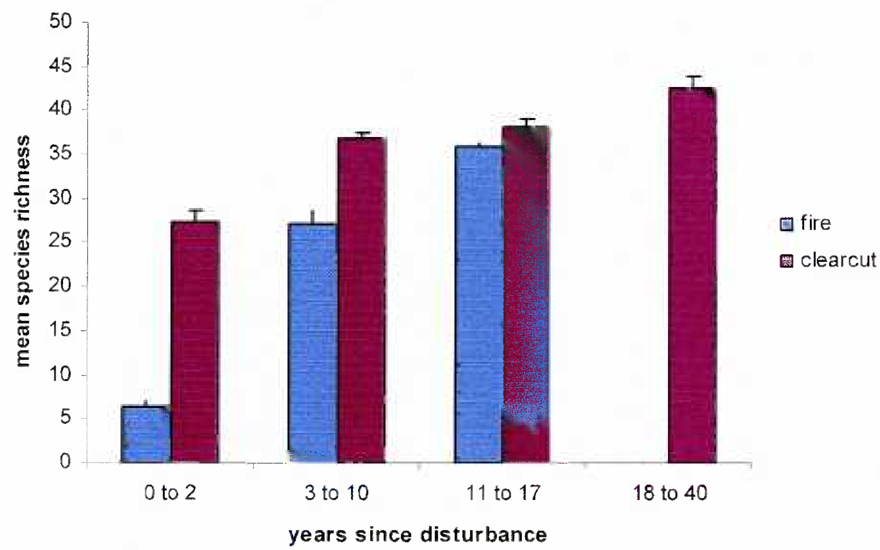
Total number of species:	123
bryophytes	25
herbs	50
shrubs	38
trees	10
Number of species occurring only	
on fire sites:	6
on clearcut sites:	60
Highest site % incidence:	fireweed and hawkweeds (89.7% of sites)
Exotic species: (†=fire sites, ‡=clearcut sites)	butterweed‡, hawkweed†‡, oxeye daisy‡, Canada thistle†‡, common dandelion†‡, common plantain‡, prickly lettuce†‡
Most common species:	fireweed (94 incidences)
fire	fireweed (33 incidences)
clearcut	bunchberry (65 incidences)
Least common species: (all 19 had 1 incidence)	bristly haircap, false haircap, powdered orange, butterweed, mountain arnica, oxeye daisy, red-stemmed saxifrage, sitka burnet, red elderberry, cascara, heart-leaved arnica, choke cherry, common snowberry, sitka mountain ash, redstem ceanothus, soopalalie, tall Oregon grape, grand fir and whitebark pine

Live arboreal bryophytes were almost completely absent from all study sites. The one exception was a 33 year-old clearcut site, in which arboreal bryophytes had an abundance estimate of 1 out of 5 in 2/3 of the 10 x 10m plots. Arboreal bryophytes were therefore very scarce among study sites.

Species richness

Understory plant species richness by age class and the linear regression results for understory species richness were plotted over time (Figure 3.6). The regression results indicated an interaction between time and disturbance type, represented as a dummy variable ($p=0.0005$), indicating that the trends of species richness over time differed between the two disturbance types. Species richness increased with time for both disturbance types but began at a higher value and remained higher in clearcut sites until age 15. However, the rate of increase was higher for fire sites. The maximum understory species richness of 53 was found on a 29 year old clearcut site. The minimum understory species richness was found on two 1 year-old fire sites, each with only three species.

a)



b)

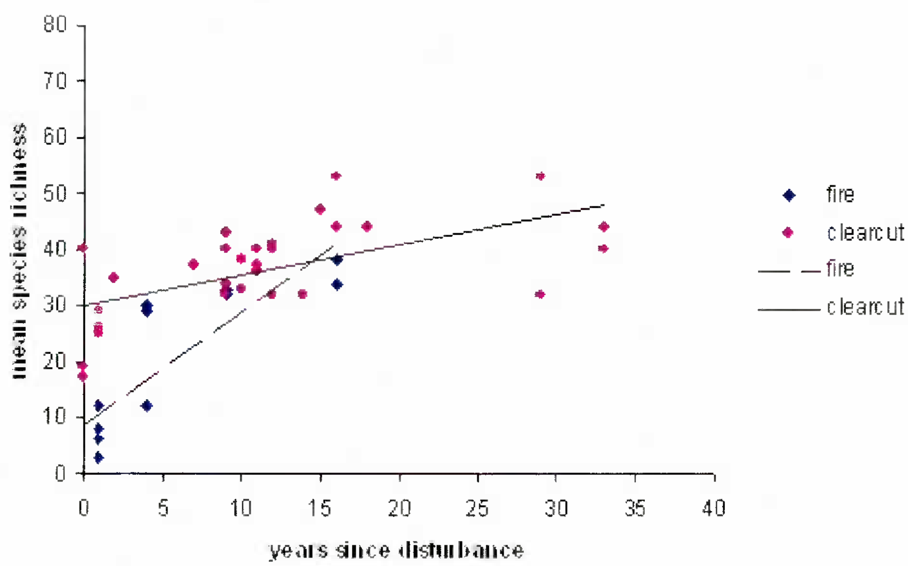
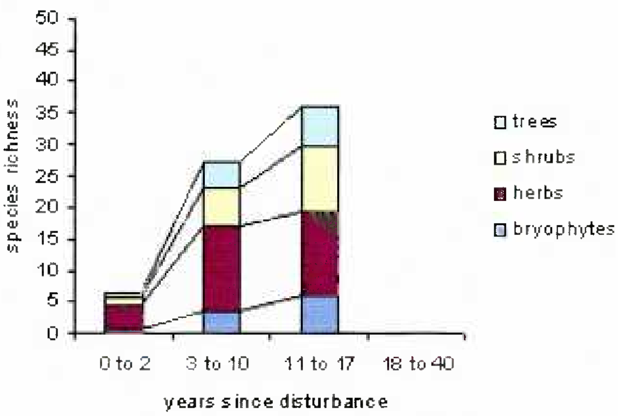


Figure 3.6: a) Understory species richness for fire and clearcut sites, by age class. Standard error bars are included. Note that no information was available for sites, 18 to 40 years post-fire. b) The mean species richness of fire and clearcut sites, by year since disturbance, with linear regression lines indicated (n=39).

The species richness within each vegetation type increased over time for fire sites (Figure 3.7). However, only the shrub and tree species richness increased for clearcut sites over time, while the numbers of herbs and bryophytes remained relatively constant.

a) Fire



b) Clearcut

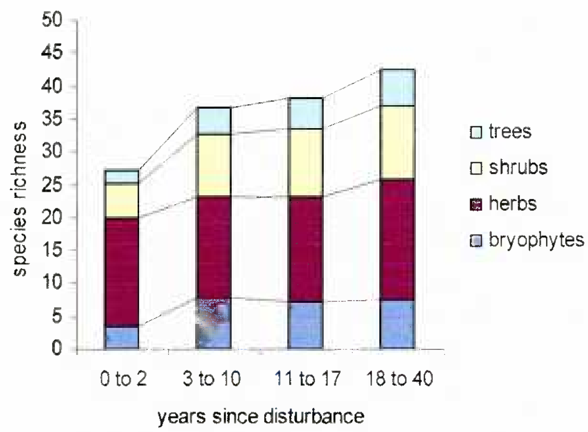
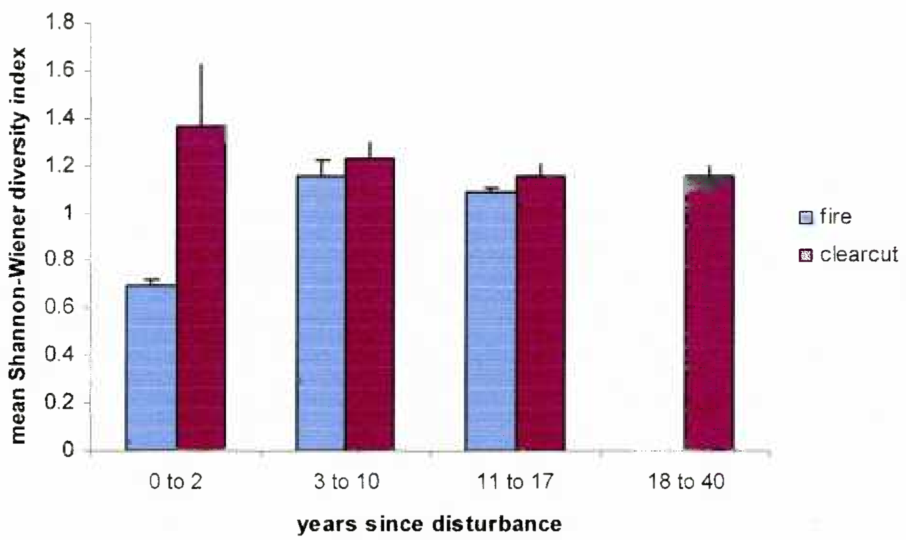


Figure 3.7: Mean site species richness of each vegetation type across fire (a) and clearcut (b) sites, by years since disturbance age classes.

Species Diversity

A rank transformation of the mean Shannon-Wiener diversity index was used to meet the assumptions of linear regression. The ranked Shannon-Wiener diversity index by age class and the linear regression results for the ranked Shannon-Wiener diversity index were plotted over time (Figure 3.8). The ranked Shannon-Wiener diversity index changed significantly with time (p=0.0084), but did not differ significantly between fire and clearcut sites. The minimum diversity was found on a recent clearcut (0 years since disturbance) at 0.12. The maximum diversity of understory plant species was found on a 2 year old clearcut site that had a Shannon-Wiener index of 4.9, which was 2.4 times larger than the next highest site value. This very high diversity site was possibly responsible for the apparently higher initial diversity for clearcut sites, but as the regression revealed, this difference between disturbance types was not significant.

a)



b)

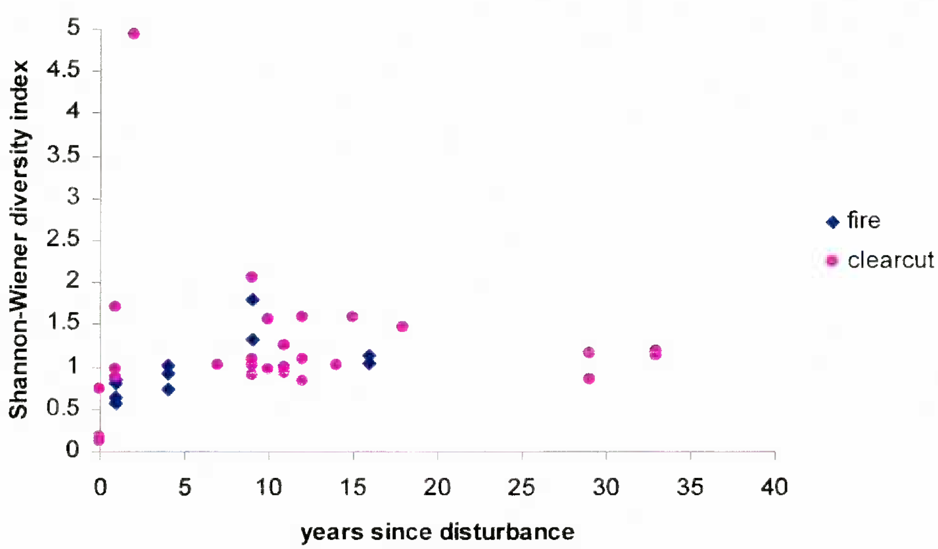


Figure 3.8: a) The mean Shannon-Wiener diversity index for fire and clearcut sites, by age class. Standard error bars are included. Note that no information was available for fire's last age class (18-40 years since). b) The Shannon-Wiener diversity index of fire and clearcut sites, by year since disturbance. No regression lines are indicated since the regression was performed on the ranked values of the Shannon-Wiener diversity index and not on these untransformed values. (n=39).

Merged analysis

Each live overstory structural characteristic (tree and snag diameters, basal area per ha and stems per ha) and CWD volume were tested for effects on understory characteristics (vegetation percent covers, richness and diversity). None of the structural characteristics had any significant effects on understory vegetation cover, richness or diversity.

3.4 Discussion

The recovery of ICH forests from fire and other severe disturbances is a secondary plant succession process (Stickney and Campbell, 2000). Secondary succession in the ICH is the progressive change in species composition and dominance through the processes of colonization, establishment and competition (Stickney and Campbell, 2000). It is initiated by a disturbance that is severe enough to reset succession to an earlier seral stage. The scope of this study was that of an early-successional timescale and it sought to identify differences in the effects of wildfire and clearcutting on understory abundance, composition and diversity within that timeframe.

Limitations

The limitations of this study (discussed in more detail in Chapter II) begin with the lack of potential wildfire study sites. This limited the sample size of fire sites and yielded no potential fire sites in the oldest age class (18 to 40 years since disturbance), thereby preventing comparisons between older clearcut and fire sites. A chronosequence was used to identify trends in plant communities between disturbances, over time. Site variability can be quite high and may be the underlying cause of variability in site characteristics such as species composition. A certain level of site variability was unavoidable and the use of many different sites to identify and interpret trends over time is therefore not ideal. The exploration of light, nutrients and soil moisture as mechanisms that drive the differences in overstory structure and composition was beyond the scope of this study, but may have been useful in providing possible causal mechanisms to explain the differences in understory structure and composition that were observed.

Vegetation Cover

Mean percent cover, examined by vegetation type, increased over time for all types of vegetation except herbs. This increase is a common observation for vegetation abundances during secondary succession. Firstly, fire encourages sprouting and regrowth of many species in interior cedar-hemlock forests (Shiplett and Neuenschwander, 1994). Secondly, both disturbances initially had lower abundances of vegetation than before the disturbance event, and over time, open areas were colonized, thereby increasing the abundance of vegetation. In all study sites, the overstory was completely or almost completely removed, which increased light levels on the forest floor (Shiplett and Neuenschwander, 1994), water availability (Rees and Juday, 2002), short-term nutrient availability (Grady and Hart, 2006), and the availability of other resources. These conditions are very favourable to the colonization and establishment of early-successional (shade-intolerant) species.

After all open areas and niches are filled, the canopy closes, resources become less abundant, and inter- and intra-specific competition intensifies (Shiplett and Neuenschwander, 1994; Timoney et al., 1997; Rees and Juday, 2002). This may explain the slow decline in herb and bryophyte abundances. During secondary succession, herb and bryophyte abundance typically peaks early in the sequence (Shiplett and Neuenschwander, 1994; Stickney 1986; Yang et al., 2005), while light at the ground level is not limiting, competition for resources is not yet great and before its longer lived competitors (shrubs and trees) have time to establish. Shrub percent cover increased at a higher rate on fire sites, most likely due to a fire-induced sprouting response in the fire adapted species (Lyon and Stickney, 1974). This increase in shrub cover coincided with the rapid decline of bryophyte and herb abundance on fire sites. This indicates that shrubs likely outcompeted herbs and bryophytes at that time (3-10 years since disturbance), thus prompting the end of the herb-bryophyte dominated stage and the beginning of the shrub dominated stage. More evidence of this competition is given on clearcut sites, where shrub cover increases at a lower rate on clearcuts, and consequently bryophytes and herb dominance declines at a much slower rate.

The trends in the mean percent cover of herbs, shrubs and bryophytes differed between fire and clearcut sites. Disturbance type therefore appears to have an effect on vegetation cover. The most likely explanation for the disturbance type effects was the widely differing starting points of percent cover between disturbance types, especially where herbs and shrubs are considered. Initially, clearcut sites had a mean percent cover for herbs and shrubs that was 30% and 20% higher than those for fire sites, respectively. The higher covers of herbs, shrubs and bryophytes in clearcut sites are likely due to the actual mechanics of the disturbances themselves. Most (or all) of the bryophyte, herb and shrub layers are consumed during a high severity fire (Feller, 1998), while with logging (especially cable logging), a comparatively large proportion of the plants can survive. Though the same increasing and decreasing trends were observed between disturbance types, these higher initial covers seemed to provide a higher peak vegetation cover as succession proceeded. Whether greater initial covers will ultimately continue to result in higher levels throughout succession was not tested here, indeed there were no data for fire sites beyond 16 years since disturbance from which to draw comparisons (due to lack of potential sites).

There were no observed differences in the mean percent covers of trees between disturbance types. This is most likely due to the very low abundance of trees at such early-successional stages: they require more time after disturbance to establish themselves and/or become dominant (Shiplett and Neuenschwander, 1994). As such, they are relatively uncommon so early in the progression, and disturbance type effects may become more evident at a later point.

It is important to note that the trends in vegetation type discussed above are general trends and some individual species may not obey the overall average. For example, initially increasing herb cover is typical of early-successional shade-intolerant herb species, such as fireweed (Stickney, 1986). More shade-tolerant species that were present initially, such as bunchberry, would theoretically increase in percent cover later in succession, as the shade-intolerant herbs begin to decline. It is therefore possible that more complex, species level dynamics were taking place within the vegetation type trends: the most abundant species within every vegetation type may have been driving the observed trends (Stickney, 1986). However these within-vegetation-type dynamics were not examined in the present study.

The scarcity of arboreal bryophytes throughout this early-successional study was expected. Due to their specific humidity and substrate needs, arboreal bryophytes generally do not become abundant until much later in ICH succession (Campbell and Fredeen, 2007).

Successional Trajectories

The understory community structure diagrams (Figure 3.4) and successional trajectories (Figure 3.5) were based on a chronosequence of mean percent cover by vegetation type, of the study sites for both disturbance types. Community structure and the duration of the dominance of each vegetation type changed with disturbance type since each disturbance has fundamentally different effects on vegetation. The successional trajectory of the fire sites appeared to be a combination of two of the trajectories developed by Stickney (1986) from the secondary succession of ICH forests following the Sundance Forest Fire of 1967 in northern Idaho.

Stickney (1986) described five different vegetation type trajectories (based on vegetation cover) in the first 10 years following the fire disturbance. The present post-fire trajectory appears to be a combination of Stickney's 'extended herb stage succession' and 'herb-tree sequence' in that herbs (namely fireweed) appear to be dominant for the first 10 years (like the former), but that shrub cover is not far behind herbs and tree abundance begins to increase substantially by the 10^{th} year (like the latter). The first 10 years of the successional trajectory of clearcut sites interestingly resembles Stickney's 'extended herb stage succession' quite closely. This is noteworthy as Stickney's successional sequences were all for post-fire succession only. The percent cover trajectories for fire and clearcutting are similar, but not necessarily similar enough to consider clearcutting a substitute for wildfire. However, it is interesting that clearcutting did emulate a relatively common ICH post-fire trajectory in terms of the relative abundance of vegetation types.

Species Composition

Though the trends in vegetation percent covers may have been similar, trends in species composition differed substantially between disturbances. Stickney and Campbell (2000) created a database of early-successional vegetation following forest fires in the cedar-hemlock forests of northern Idaho, in which they classified each species of herb, shrub and tree with regards to their post-fire colonization ability. Fireweed (*Epilobium angustifolium*) is an early colonizer following disturbances in the ICH and, as the name suggests, is especially common in burned areas (Parish et al., 1996). It has been classified as an 'offsite colonizer', and a 'survivor (rhizomes)' following fires in the ICH (Stickney and Campbell, 2000). It is therefore not surprising that it was the most common species found on fire sites. Bunchberry (*Cornus* *canadensis*) is a more shade tolerant species in comparison (Parish et al., 1996). It is classified as 'non-surviving' following fires (Stickney and Campbell, 2000). It was the most common species found on clearcut sites, likely as it survived the logging operations, and subsequently multiplied (presumably vegetatively), forming dense mats (Stickney and Campbell, 2000).

Fire sites had up to 70% fewer rare and very rare species when compared to clearcut sites. Often, these rare and very rare species, such as several mosses, *Pyrola* spp., rattlesnake plantain (*Goodyera oblongifolia*) and western teaberry (*Gaultheria ovatifolia*), were species that are classified as 'non-survivors' of fires (Stickney and Campbell, 2000) and are usually found in mature ICH forest understories. This suggests that although they were killed on the fire sites, they likely survived the clearcutting and were still alive when sampling occurred.

In other cases, the rare and very rare species that were predominantly found on clearcut sites are commonly associated with fields and roadsides (Parish et al., 1996), which was not surprising, as clearcut sites were always directly adjacent to a logging road while most fire sites were at least 200m removed. These species (eg. common plantain (*Plantago major*) and oxeye daisy (*Leucanthemum vulgare*)) are early-successional (Parish et al., 1996) and are characterized by shade-intolerance, rapid growth and good dispersal, which allowed them to quickly establish themselves in the newly disturbed sites. Another reason these species may have been more common on clearcuts is that they are classified as exotics (Qian and Klinka, 1998). It has been found that on newly disturbed sites in mixed conifer forests, clearcutting often increases the presence of exotic species more than fires (Collins et al., 2007). These invaders can drastically alter plant communities and ultimately change ecosystem processes, such as water and nutrient availability (Collins et al., 2007).

As in Rees and Juday's (2002) study on the effects of logging and fire on upland boreal forests in Alaska, certain species were restricted to burned sites and others were restricted to clearcut sites in this study. For example, oak fern (*Gymnocarpium dryopteris*) and twinflower (*Linnaea borealis*), very common and common, respectively, are classified as 'non-survivors' of fire (Stickney and Campbell, 2000), and were exclusively found on clearcut sites. Clearcut sites had 10 times more exclusive species than fire sites. This may be due to there being more clearcut sites sampled than fire sites. However, it could suggest that though the percent cover of vegetation types varied little, species composition during early succession in the ICH varied greatly between disturbance types.

Species Richness

As with percent cover, species richness increased during the first few years of succession due to colonization and regeneration of the various plants. Richness typically levels off or begins to decline as canopy closure begins and light availability is reduced (Rees and Juday, 2002). Rees and Juday (2002) found that vascular species richness in upland boreal forests declined after the stem exclusion phase (13 to 18 years since disturbance). At the equivalent time period in this study, richness had not begun to decline in either disturbance type. Therefore, peak plant species richness may occur at a later time in ICH forests than in boreal forests.

Species richness was initially four times higher on clearcut sites, most likely due to the mechanics of each disturbance type (higher number of surviving understory species after logging than after severe fires). This gave clearcut sites a head start in the successional progression. Succession has been found to proceed more rapidly on clearcuts in terms of vegetation composition (Timoney et al., 1997). One of the mechanisms put forth to explain accelerated plant regeneration on clearcuts is light availability (Timoney et al., 1997; Rees and Juday, 2002). Light availability can influence species richness greatly (Rees and Juday, 2002). Initially, clearcut sites may have had higher light levels due to the lack of large structural legacies such as snags and surviving overstory trees (see Chapter II), which may have increased species richness. However, if this is the case, the merged analysis of the effects of the overstory characteristics on understory species richness does not agree as it revealed no effects. Richness may still be affected by light availability, but this assumed difference in light availability was not tested and could not be attributed solely to overstory structural legacies.

On the contrary, several studies examining the effects of fire and harvesting on vegetation during early succession have found that, rather than increasing species richness, clearcutting reduced it (Roberts 2007; Rees and Juday, 2002). Burned sites had higher species richness during stand initiation (2-5 years), stem exclusion (13 to 18 years) and understory re-initiation (30-38 years) (Rees and Juday, 2002). Initially, this study found the opposite trend: that clearcuts have higher species richness. However, the rate of increase of species richness was much higher on fire sites (higher positive slope). In fact, by the 15th year (end of fire site samples), fire site species richness had overtaken clearcut site species richness (Figure 3.6). Therefore, the trend seen here did not necessarily disagree with the literature; it might only be a matter of timescale. If the trend in fire site species richness were to continue a similar path throughout succession, then despite an initially greater species richness in clearcut sites, fire sites could maintain a higher level of species richness for the rest of early succession (15 to 40 years since disturbance), and potentially beyond that. These results would then agree with those of the other mentioned studies.

Why do clearcut sites generally have initially lower species richness than fire sites? The reason Rees and Juday (2002) suggest for this trend is that the thicker organic layer remaining on logged sites (not burned off, as in fire sites) excluded certain species of off-site colonizers and reduced establishment success in others. Others (Timoney et al., 1997), found that, next to old growth stands, recent clearcuts have the thickest duff depth since the organic matter has not yet begun to decompose. Fire severity specifically refers to the damage that the downward energy of the fire creates, and how much of the forest floor is destroyed. High-severity fires typically consume very large amounts of the forest floor (Feller, 1998). Though this characteristic means that many potential on-site colonizers (ie. soil seed bank) are destroyed, less duff depth facilitates seed establishment by off-site colonizers.

Species Diversity

McRae et al. (2001) pointed out that both fire and harvesting increase diversity in the short term, relative to undisturbed stands. Species diversity increased with increasing time since disturbance most likely for the same reasons that richness and abundance increased over time: initial increased light availability from overstory removal, followed by colonization, competition and niche differentiation. No significant differences in the Shannon-Wiener diversity index were detected between disturbance types. Other similar studies have also found that diversity did not differ with harvesting and fire disturbance treatments during early succession (Uotila and Kouki, 2005). The lack of disturbance type effects in the present study may be due to the high degree of site variability and the relatively small sample size (n=39). The highest and lowest Shannon-Wiener indices recorded for clearcut sites within the first 2 years of succession was 4.9 and 0.12, respectively. The site with 4.9 had unusually high diversity, thus illustrating the potential site variability within the same age class. Timescale should also be considered. This study has only compared plant species diversity in fire and clearcut sites for early succession (the first 15 years). It is possible that there are simply no disturbance-type effects in the first 15 years of ICH succession.

The merged analysis of overstory characteristics and understory vegetation characteristics (mentioned briefly above) revealed that none of the measured structural characteristics (overstory trees, snags or coarse woody debris (CWD)) affected vegetation percent covers, richness or diversity. This is counterintuitive as one would expect that large volumes of CWD and the presence of many snags and trees would reduce ground level light availability and possible establishment sites, thus reducing understory vegetation growth and successful seedling establishment. These counter-intuitive findings may be explained by the lack of overstory. In these early-successional sites, there was little overstory to speak of, when compared to a mature or old-growth forest, where light availability in the understory is very low. Since the majority of the sites (especially the 14 young clearcut sites) had little to no snags or overstory, it follows that there would be no effects. The lack of structural effects may also be explained by timescale and nutrient availability. CWD was shown (Chapter II) to have decayed by approximately half by the 33rd year since disturbance on clearcut sites. CWD volume may therefore have decayed at a sufficient rate that it did not impede the establishment of understory species, and instead may have encouraged growth by inputting nutrients into the soils. On fire sites CWD volume increased with time, and in that case, it may not have impeded the establishment or growth of the understory as the latter may have already been established by the time the CWD began to build up.

Emulation Silviculture

Emulation silviculture seeks to utilize forest harvesting practices that have similar effects on ecosystem structure, composition and function as natural disturbances. In the case of the ICH zone of southern B.C., there are both similarities and differences between the effects of clearcut logging and wildfire on the structure, composition and diversity of understory vegetation. It appears that within the first 15 years of ICH succession, species diversity did not vary with disturbance type. Also, the trajectories of understory percent covers appeared to follow roughly similar trends regardless of disturbance type. It was especially noteworthy that the trajectory for clearcut sites resembled a previously identified, and common, ICH post-fire successional pattern.

Though there was little variation in the above mentioned characteristics, species composition during early succession in the ICH varied greatly between disturbance types. Combined vegetation cover was usually higher in clearcut sites, and herb and shrub percent covers did differ with disturbance type. Furthermore, compositional differences, such as dominant species and incidence, between fire and clearcut sites were obvious and important. Species richness was initially much higher on clearcut sites, but the rate of increase was much higher on fire sites. These differences in composition and richness are important in determining the progression that succession will assume, and the composition of the future forest community.

The scope of this study was limited to an early-successional timescale, and as such, it offers only a small window into the entire process of ICH succession. However, much of the literature (eg. Rees and Juday, 2002; McRae et al., 2001) suggests that clearcutting can drastically alter understory vegetation, reducing richness and diversity. Some studies have suggested that the cover and richness of the understory vegetation of natural forests may never fully recover from clearcutting (McRae et al., 2001). Though clearcutting appears to initially increase richness, and create comparable vegetation coverage and diversity levels, the changes to composition and relative abundance that follow clearcutting may ensure that the resulting mature forest is ultimately significantly different from its natural counterpart. If this is the case, then indeed a forest may never 'recover' its former structure and composition following clearcutting. Further research should examine ICH succession following wildfire and harvesting in older age classes to confirm the direction the early-successional trends are indicating.

The fundamental differences in the nature of each disturbance type create fundamental differences in their ecosystem effects, and in early succession, create very different forest types. Whether these differences become more or less pronounced over time is yet to be determined in the ICH zone. Managers must specify their goals within emulation silviculture in order to be successful: is the goal to emulate the natural disturbance's effects on structure, function, richness, biodiversity, species composition or all of these? If the goal is strictly to increase initial species richness, than clearcut harvesting appears to be a viable option. However, the manager may be increasing species richness to a level beyond that found following natural disturbances and may be changing the ultimate community composition, structure and function. This would no longer be emulation. Extensive research and a firm understanding of the successional trajectories following natural and anthropogenic disturbances should be achieved prior to management decisions regarding emulation silviculture. This study identified several differences in structural and compositional trends between wildfires and clearcuts during early ICH forest succession. If these initial trends continue their paths, then the contrasts between wildfire and clearcutting effects may be sufficiently large to merit further research into whether current ICH forest harvesting practices and management are emulating natural disturbances.

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Chapter 4: Conclusions

4.1 Examining all Levels of Plant Succession

This study focussed on temporal changes in overstory vegetation (Chapter II), surface fuels (Chapter 1) and understory vegetation (Chapter III) following different types of disturbances. It is important for plant succession research to examine all structural levels to gain a more complete understanding of how succession proceeds. Roberts (2007) pointed out that when studies focus solely on the effects of disturbance on the understory, they often further narrow the field by ignoring the herb and bryophyte layers. It may be argued that focussing on only one level of vegetation during a successional study allows for a very complete understanding of the dynamics of that level; however, I would argue that if that research is not coupled with research on the remaining levels, entire processes and interactions may be overlooked. Though, in this case, overstory and CWD appeared to have no significant effects on understory vegetation cover, in other circumstances (e.g. later in succession) it might have, and it is important to have the ability to discount overstory effects on understory patterns.

4.2 Present Study's Findings Summarized

Due to the fundamentally different nature of both disturbance types, structural legacies varied greatly between wildfire and clearcut sites during early plant succession in the ICH zone, especially in coarse woody debris and snag dynamics. This can have significant impacts on later plant succession and wildlife. Clearcut sites, compared to fire sites, exhibited patterns of accelerated succession in several characteristics, such as overstory tree regeneration (i.e. larger trees, greater tree density, etc.), vegetation cover (herb and shrub), and species richness. These are likely due to more rapid regeneration caused by planting treatments and the presence of pre-disturbance relicts such as survivors and intact seed banks. Understory species composition varied greatly between disturbance types, with clearcut sites having more shade-tolerant, later-successional species initially, attributed to survivors and seed source availability. Clearcut sites had higher initial species richness but wildfire sites had a higher rate of increase in species richness, suggesting that plant species richness might be higher on burned areas later in succession. Both disturbances initially had increasing species diversity due to the increased resource availability and the opening of niches following the disturbances, but diversity in early succession did not differ between wildfire and clearcut sites. It is important to note that the diversity index used did not take into account species composition, and that composition varied greatly between disturbances. Therefore, although the levels of diversity were similar between fires and clearcuts, species composition differed between the two disturbance types.

Overstory trees, snags and surface CWD did not influence vegetation cover in either disturbance type during this early stage of ICH succession, most likely because there was relatively little overstory and CWD during the first 40 years.

4.3 Hypotheses Revisited

I hypothesized that disturbance type would be an important determinant of post-disturbance stand structure, fuel volume and understory vegetation characteristics. The many significant differences in these studied characteristics between disturbance types support this premise. Disturbance type appeared to be an especially important determinant of snag dynamics, CWD dynamics, species richness, and species composition. However, understory species diversity was the exception. In Chapter III, I also hypothesized that rates of revegetation would vary with disturbance type, and clearcut sites did exhibit a more rapid succession than fire sites in several characteristics. Finally, I hypothesized that successional patterns (trajectories) would differ with disturbance type. The trajectories, based on vegetation type percent covers, were more similar than expected, but did differ in certain key factors such as initial percent covers and in vegetation type dominance through time. These results suggest that disturbance type is an important factor in determining the progression of succession in the ICH zone, and that clearcut harvesting may not emulate natural early ICH plant succession in any aspect but diversity levels.

4.4 Emulation Silviculture in the ICH Zone

Forest management in B.C. is currently governed by a paradigm that maintains that biological diversity can be preserved by utilizing forest harvesting regimes that closely mimic "natural" disturbance regimes (Anon., 1995). Clearcutting is the most common forest harvesting system in use in the ICH zone near Revelstoke, but a general lack of quantitative data makes it uncertain whether it emulates the local natural disturbance regime, which involves primarily relatively infrequent, high-severity wildfires. Several studies (Lindenmayer and McCarthy, 2002; Rees and Juday, 2002) from a variety of different ecosystems have found that forest harvesting treatments commonly have had very different effects on succession than the local natural disturbances. This study sought to provide at least a portion of the quantitative data that forest managers in the ICH zone would require to ensure that the anthropogenic disturbance regimes emulate natural disturbances.

Assuming that the trends observed in this study are representative of the actual progression of plant succession in the ICHvk1 and ICHwk1 following fire and clearcutting, then there is sufficient evidence to suggest that clearcutting does not fully emulate early, natural plant succession. Though plant species diversity levels were similar (as predicted by the B.C. Ministry of Forests when they specified that harvesting can maintain diversity levels (Anon., 1995)), vegetation structure and composition varied substantially between harvested and burned sites, and these should be considered in any emulation discussion. The composition and structure of early-successional communities necessarily influences the composition and structure of later-successional stages; the species present in the earliest stages of succession will have more influence over the composition of later stages than any off-site colonizers (Stickney and Lyon, 1974). If this assumption is correct, than we expect that the differences in early succession (following fire and clearcutting) found in the present study, would continue and possibly diverge further, in later succession. Clearcutting would then create mature forests that differed significantly from those that followed fire - the dominant natural disturbance.

4.5 Remaining Questions

This study provides a starting point to understanding how harvesting can alter the natural process of succession in ICH forests. However, several questions remain unanswered. The observed trends represent only those of early succession, and due to the lack of potential wildfire sites, could only be compared for the first 15 years post-disturbance. It would be insightful to perform further research to determine whether these trends will continue as they are, diverge, or converge further during later succession. The question of causation could also be explored further. Disturbance type, explored here, is just one of many factors that may influence successional trajectories. Many of the other factors were controlled for as much as possible; however others, such as light, moisture and nutrient availability, were not. These factors are included here in the broad umbrella of 'disturbance type', along with the chemical versus mechanical nature of each disturbance, but it would be interesting to monitor these factors separately, to perhaps infer the mechanisms driving some of the observed differences.

4.6 Future Research

The results obtained for wildfires and clearcuts, were, in my opinion, sufficiently different to warrant further investigation. One of the greatest limitations of this study was the use of a chronosequence instead of continuous measurements of permanent sample plots. Ideally, a long-term experimental study should be attempted to confirm the observed trends, and to obtain information on these trends during later succession. Sampling should occur every year for the first 10 years and then in increasingly longer increments thereafter. However, this may be an unrealistic goal due to the difficulty and cost of maintaining long-term experiments. The following recommended experiment would be more useful if it were conducted over the long-term, but a shorter-term version of it would still be useful. Experimental sites should be established in one or several large areas that are relatively homogenous in aspect, elevation, topography, climate and ecosystem, like the mid-slope, south facing side of one or two east-west valleys. I recommend pairing burned and clearcut sites in space to allow for easy comparisons between the two. The pairing of wildfire and clearcut sites would, however, be very difficult as multiple accessible wildfires within a single ecosystem type are rare in the study area. As such, wildfires themselves would likely have to be eliminated from the experiment and will have to be re-created by prescribed burning at a similar severity and size of a typical wildfire (which may be operationally problematic). Clearcutting methods would be standardized. These burned/clearcut blocks would have to be sufficiently buffered by natural forest to prevent altering the potential pool of off-site colonizers. The same overstory measurements should be taken, with the addition of tree heights. Similar understory vegetation surveys should take place. Light and soil nutrient and moisture availability should be monitored through time.

Ensuring that all study sites are located in areas that are homogenous in ecosystem and site series, with strictly controlled disturbance types, will limit site variability and ensure comparability between sites. However, it may also limit the applicability of the study. It may be useful to explore a range of disturbance severities and ecosystem types within the ICH zone. For example, to have sites in several ICH variants, with repetitions in several site series in each. Or to compare low- or moderate-severity burns to a variety of partial cutting systems. This would provide a very complete database of plant succession following each disturbance type in a variety of conditions. However, if the goal of this research is only to confirm that wildfire and clearcuts result in different forests in terms of structure and composition, then considering differing harvesting systems would not be essential.

4.7 Implications

This study has indicated that there are sufficient major differences in the effects of each disturbance type to warrant future research, and possibly to prompt a re-evaluation of current forest management practices in the ICH zone.

Alterations to current clearcutting practices could allow forest harvesting to more closely emulate ICH wildfires. For example, one of the major differences between disturbance types was CWD dynamics. More larger pieces of CWD could be intentionally left behind after clearcutting to ensure the slow, steady release of nutrients into the soils as they decay, and to ensure the survival of wildlife that rely upon CWD for habitat. Large snags were also non-existent on clearcut sites but plentiful on burned sites. Likewise more snags could be intentionally left behind. Slash burning may be a viable option to destroy the pre-disturbance understory vegetation and promote certain fire activated species to regenerate, as after a natural wildfire. With relatively little effort, a similar volume of wood could be harvested, while ensuring that the structure of the post-harvesting forest is as close to natural as possible. The effectiveness of these treatments in emulating natural wildfires more closely should be explored.

Natural disturbance regimes in most ecosystems have been altered directly or indirectly by human activity. There are many documented cases of the ecological impacts of anthropogenic disturbances, from losses of biodiversity to shifts in ecological equilibria. The concept of emulating natural disturbances to preserve ecosystem structure and function is a forward-thinking and responsible goal. Not only is ecosystem integrity maintained, but humans may still derive from the ecosystem the services that they require, in this case, high quality lumber. Sustainable forestry and emulation silviculture are noble goals, but admittedly lofty ones, due to the complexity of forest ecosystems and due to the costs associated with changes in harvesting practices. If they are to be attempted, a more complete understanding of the acute and long term effects of natural and anthropogenic disturbances should be reached before management policies are implemented.

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Appendix I: Interior Cedar-Hemlock Biogeoclimatic Zone Information

a) Subzone dominant plant species (Lloyd et al., 1990)

Figure a) has been removed due to copyright restrictions. The information removed is a graphical representation of all ICH variants and the mean percent cover of their most common species. It was obtained from: Lloyd D., K. Angrove, G. Hope and C. Thompson. 1990. A guide to site identification and interpretation for the Kamloops Forest Region. Land Management Handbook 23. B.C. Ministry of Forests. Victoria. BC. 400p.

Appendix I: Interior Cedar-Hemlock Biogeoclimatic Zone Information

b) Site series and edatopic grid for the ICHwk1 variant (Lloyd et al., 1990)

Figure b) has been removed due to copyright restrictions. The information removed is a graphical representation of the nutrient and moisture regimes creating each site series in the ICHwk1 variant. It was obtained from: Lloyd D., K. Angrove, G. Hope and C. Thompson. 1990. A guide to site identification and interpretation for the Kamloops Forest Region. Land Management Handbook 23. B.C. Ministry of Forests. Victoria. BC. 400p.

Appendix I: Interior Cedar-Hemlock Biogeoclimatic Zone Information

c) Site series and edatopic grid for the ICHvk1 variant (Lloyd et al., 1990)

Figure c) has been removed due to copyright restrictions. The information removed is a graphical representation of the nutrient and moisture regimes creating each site series in the ICHvk1 variant. It was obtained from: Lloyd D., K. Angrove, G. Hope and C. Thompson. 1990. A guide to site identification and interpretation for the Kamloops Forest Region. Land Management Handbook 23. B.C. Ministry of Forests. Victoria. BC. 400p.

Appendix II: Results of general linear model (linear regressions and ANOVA's) analyses for all overstory tree, snag and CWD characteristics between disturbance types, as a function of 'years since disturbance' (x) (Chapter II).

Table AII-1: Results of linear regressions for all live tree, snag and CWD characteristics.

Live trees:			Model			Statistics				
y variable	disturbance	regression equations	F	p	df	SS	R^2	Coeff var.	rootMSE	mean
sqrt dbh	fire	$\hat{y} = -0.204 + 0.074x$	60.15	**<.0001**	3	34.678	0.841	39.574	0.438	1.108
	clearcut	$\hat{y} = 0.466 + 0.089x$								
sqrt baha	fire	$\hat{y} = -0.094 + 0.034x$	117.79	**<.0001**	3	71.487	0.910	45.27	0.450	0.994
	clearcut	$\hat{y} = -0.357 + 0.153x$								
sph	fire	$\hat{y} = -293.27 + 106.26x$	31.19	**<.0001**	3	3.55E+07	0.728	64.099	615.800	960.680
	clearcut	$\hat{y} = 121.98 + 98.94x$								
richness	fire	$\hat{y} = -0.733 + 0.266x$	39.05	**<.0001**	3	176.857	0.770	49.91	1.229	2.462
	clearcut	$\hat{y} = 0.912 + 0.203x$								
number	fire	$\hat{y} = -8.798 + 3.187x$	31.30	**<.0001**	3	3.20E+04	0.728	64.016	18.498	28.821
	clearcut	$\hat{y} = 3.895 + 2.957x$								
Snags:										
dbh	fire	$\hat{y} = 14.992 + 0.786x$	142.67	**<.0001**	3	3003.18	0.926	38.396	2.649	6.900
	clearcut	$\hat{y} = -0.527 + 0.147x$								
rank baha	fire	$\hat{y} = 1.312 - 0.038x$	55.89	**<.0001**	3	25.252*	0.831*	-2.887*	0.390*	0.000*
	clearcut	$\hat{y} = -0.941 + 0.038x$								
ln density	fire	$\hat{y} = 7.311 - 0.144x$	16.04	**<.0001**	3	24.361	0.728	12.32	0.712	5.776
	clearcut	$\hat{y} = 3.803 + 0.056x$								
CWD:										
ln volume	fire	$\hat{y} = 4.343 + 0.109x$	10.83	**<.0001**	3	18.048	0.482	14.786	0.745	5.039
	clearcut	$\hat{y} = 5.930 - 0.075x$								

* these values are those from a ranked transformation and represent the relative size of snag basal area only.

Appendix II, continued:

Table AII-2: General linear model analysis of the influence of disturbance type and years since disturbance on living overstory tree characteristics (n=39). Significant results are in bold.

	Sqrt (dbh)			Sqrt (baha)			sph		
Predictor variable	df	F	p	df	F	p	df	F	p
Years since disturbance	1	42.4	**<.0001**	1	53.17	**<.0001**	1	34.24	**<.0001**
Disturbance type	1	8.62	**0.0059**	1	1.3	0.2613	1	1.73	0.1965
Interaction	1	0.038	0.5418	1	21.56	**<.0001**	1	0.04	0.836

Table AII-3: General linear model analysis of the influence of disturbance type and years since disturbance on living overstory tree species richness and tree numbers (n=39). Significant results are in bold.

	richness			number of trees		
Predictor variable	df	F	p	df	F	p
Years since disturbance	1	44.83	**<.0001**	1	34.25	**<.0001**
Disturbance type	1	6.86	**0.013**	1	1.81	0.1871
Interaction	1	0.81	0.3729	1	0.05	0.8275

Table AII-4: General linear model analysis of the influence of disturbance type and years since disturbance on transformed snag characteristics (n=39). Significant results are in bold.

	dbh			ranked baha			Ln (density)		
Predictor variable	df	F	p	df	F	p	df	F	p
Years since disturbance	1	38.23	**<.0001**	1	0	0.9983	1	3.89	0.064
Disturbance type	1	130.53	**<.0001**	1	128.14	**<.0001**	1	35.67	**<.0001**
Interaction	1	17.96	**0.0002**	1	11.93	**0.0015**	1	20.22	**0.0003**

Table AII-5: General linear model analysis of the influence of disturbance type and years since disturbance on the transformed mean CWD volume (n=39). Significant results are in bold.

	Ln (volume)		
Predictor variable	df	F	p
Years since disturbance	1	0.65	0.4253
Disturbance type	1	17.35	**0.0002**
Interaction	1	18.71	**0.0001**

Appendix III: Results of general linear model (linear regressions and ANOVA's) analyses for all measured understory characteristics between disturbance types, as a function of 'years since disturbance' (x) (Chapter III).

Table AIII-1: Results of linear regressions for all live tree, snag and CWD characteristics.

Percent Covers:			Model			Statistics				
y variable	disturbance	regression equations	F	p	df	SS	R^2	Coeff var.	rootMSE	mean
bryophyte % cover	fire	$\hat{y} = -7.629 + 10.718x - 0.562x^2$	7.39	<.0001	5	6963.0	0.528	58.394	13.725	23.500
	clearcut	$\hat{y} = 4.848 + 3.794x - 0.1x^2$								
herb % cover	fire	$\hat{y} = -8.153 + 16.625x - 0.962x^2$	12.09	<.0001	5	25733	0.647	43.684	20.635	47.238
	clearcut	$\hat{y} = 36.458 + 5.563x - 0.196x^2$								
shrub sqrt % cover	fire	$\hat{y} = 1.670 + 0.3065x$	10.34	<.0001	3	95.353	0.470	36.267	1.753	4.834
	clearcut	$\hat{y} = 4.318 + 0.1019x$								
tree ln % cover	fire	$\hat{y} = 0.4273 + 0.2281x$	6.74	0.0013	3	29.610	0.403	53.263	1.210	2.272
	clearcut	$\hat{y} = 1.331 + 0.0829x$								
Species Richness:										
richness	fire	$\hat{y} = 8.720 + 2.020x$	28.08	<.0001	3	4113.45	0.7064	22.599	6.988	30.923
	clearcut	$\hat{y} = 30.129 + 0.4952x$								
Shannon-Wiener Diversity Index:										
ranked diversity	fire	$\hat{y} = -1.005 + 0.1198x$	3.44	0.0272	3	8.2640*	0.228*	Infinity*	0.895*	0.000*
	clearcut	$\hat{y} = -0.1071 + 0.0225x$								

* these values are those from a ranked transformation and represent the relative size of diversity only.

Appendix III, continued:

Table AIII-2: General linear model ANOVA analysis of the influence of disturbance type and years since disturbance on transformed mean percent cover of each vegetation type (n=39). Significant results are in bold.

	Bryophytes (mean % cover)			Herbs (mean % cover)		
Predictor variable	df	F	p	df	F	p
yrs_since	1	21.68	**<.0001**	1	22.42	**<.0001**
disturbance	1	1.68	0.2039	1	9.5	**0.0041**
yrs_since*disturbance	1	4.93	**0.0333**	1	5.57	**0.0243**
$(yrs\_since)^2$	1	13.71	**0.0008**	1	18.5	**0.0001**
$(yrs\_since)^2$*disturbance	1	6.66	**0.0145**	1	8.09	**0.0076**

	Shrubs (sqrt mean % cover)			Trees (ln mean % cover)		
Predictor variable	df	F	p	df	F	p
yrs_since	1	16.75	**0.0002**	1	15.81	**0.0004**
disturbance	1	8.72	**0.0056**	1	1.36	0.2521
yrs_since*disturbance	1	4.2	**0.0479**	1	3.45	0.0733
$(yrs\_since)^2$	.	.	.	.	.	.
$(yrs\_since)^2$*disturbance	.	.	.	.	.	.

Table AIII-3: General linear model analysis of the influence of disturbance type and years since disturbance on mean species richness (n=39). Significant results are in bold.

	species richness		
Predictor variable	df	F	p
Years since disturbance	1	40	**<.0001**
Disturbance type	1	35.89	**<.0001**
Interaction	1	14.7	**0.0005**

Table AIII-4: General linear model analysis of the influence of disturbance type and years since disturbance on the ranked Shannon-Wiener diversity index (n=39). Significant results are in bold.

	Ranked Shannon-Wiener index		
Predictor variable	df	F	p
Years since disturbance	1	7.80	**0.0084**
Disturbance type	1	3.84	0.0579
Interaction	1	3.65	0.0642