EVALUATING THE RESILIENCE OF NORTHERN INTERIOR CEDAR-HEMLOCK FORESTS TO WESTERN HEMLOCK LOOPER DEFOLIATION EVENTS

by

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ABSTRACT

Forest response to western hemlock looper outbreaks in the inland temperate rainforest (ITR) can be quite variable. Sixty-three plots sampled 17 years after collapse of the 1991-94 outbreak east of Prince George, British Columbia, revealed multiple aspects of ecosystem resilience. Overstory recovery appears to be greatest in stands with lower site productivity and in stands with a more severe outbreak history. Forest regeneration is strongly constrained by shrub cover, which is promoted by canopy openness and soil nutrients, both of which can be accentuated by defoliators. Site index and soil moisture regime are primarily responsible for niche differentiation among regenerating tree species. Management for tree production should consider differences in site index, site series, post-outbreak canopy density and annual heat:moisture index among stands. These patterns can be mapped and extrapolated throughout the ITR, but forest management options after a defoliation event must be evaluated on a site by site basis.

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TABLE OF CONTENTS

| ABSTRACT | i |
|---|----------|
| ACKNOWLEDGEMENTS | .ii |
| TABLE OF CONTENTS | iii |
| LIST OF TABLES | .v |
| LIST OF FIGURES. | vi |
| | 1 |
| 1.0 Introduction | . 1 |
| 1.1 Herbivory as a disturbance | . [|
| 1.2 Study objectives | .4 |
| 1.3 Biology and ecology of the hemlock looper | .4 |
| 1.4 Hemlock looper as an agent of disturbance | . 6 |
| 1.5 Hemlock looper defoliation history, geography and control | . 8 |
| 1.5.1 Western hemlock looper in British Columbia | . 9 |
| 1.6 Tree mortality, survival and stand development | 11 |
| 1.6.1 Overstory | 11 |
| 1.6.2 Stand development and succession | 14 |
| 1.6.3 Understory | 16 |
| 1.6.3.1 Coarse woody debris in a defoliated stand | 19 |
| 1.7 Nutrients and defoliation | 20 |
| 1.8 Research questions | 22 |
| 2.0 Methoda | 71 |
| 2.0 Methods | 24 71 |
| 2.1 Study alea | 24 |
| 2.5 Data preparation | 20 |
| 2.4 Statistical analyses | 34 |
| 3.0 Results | 41 |
| 3.1 Summary of site variables | 41 |
| 3.2 Summary of overstory | 43 |
| 3.3 Summary of understory | 47 |
| 3.3.1 Plant community | 47 |
| 3.3.2 Regeneration | 51 |
| 3.4 Overstory recovery | 53 |
| 3.4.1 Effect of outbreak severity and site variables | 53 |
| 3.5 Understory recovery | 55 |
| 3.5.1 Effect of outbreak severity | 55 |
| 3 5 2 Effect of site variables | 56 |
| 3 5 3 Plant community | 63 |
| 3 5 3 1 Cluster analysis | 67 |
| 3 5 3 2 Plant community and outbreak severity | 71 |
| 3.5.4 Regeneration | 71 |
| $2.5 \land 1$ Degeneration niche | 95 95 |
| 2.5.4.2 Degeneration substrate | 00 |
| 5.5.4.2 Regeneration substrate | 70 |
| 4.0 Discussion | 95 |

| 4.1 Overstory recovery | |
|--|-----|
| 4.1.1 Effect of outbreak severity and site variables | |
| 4.2 Understory recovery | |
| 4.2.1 Effect of outbreak severity | |
| 4.2.2 Effect of site variables | |
| 4.2.3 Plant community | 101 |
| 4.2.3.1 Cluster analysis | |
| 4.2.3.2 Plant community and outbreak severity | |
| 4.2.4 Regeneration | |
| 4.2.4.1 Regeneration niche | |
| 4.2.4.2 Regeneration substrate | 109 |
| 5.0 Conclusions and synthesis | |
| 6.0 Management of defoliated stands | |
| References | |

LIST OF TABLES

| Table 1. Study-wide summary of site variables measured at each plot (n=63) |
|---|
| Table 2. Overstory density by species. Mean density values are from tree counts in 0.04 ha |
| plots (n=63) |
| Table 3. Overstory basal area by species. All dead trees are trees that likely died directly orindirectly from the WHL defoliation in the 1990s.44 |
| Table 4. All plant species, listed by functional group, found in stands sampled for this study |
| (n=63), with species codes for plant community RDA output interpretation and cluster |
| analysis interpretation |
| Table 5. Total and well-spaced regeneration by species and size class (n=63) |
| Table 6. Total regeneration summaries by species, size class and substrate |
| Table 7. Well-spaced regeneration summaries by species and size class |
| Table 8. Spearman's correlations between Overstory Recovery Index (ORI _{ave}) and site variables 54 |
| Table Q. Snearman's correlations between three understory recovery responses and two |
| indices of defoliation severity, the Defoliation Severity Index (DSI) and the proportion |
| Table 10. Snearman's correlations between understory recovery variables and site variables |
| Table 10. Spearman's conclutions between understory recovery variables and site variables. |
| Table 11 a) Summary of the independent effects of all individual explanatory variables on overall understory plant community composition; b) Summary of the conditional effect of each predictor. |
| Table 12. Summary of plant community ordination forward selection. Only significant $restrictors (n < 0.05)$ were retained (5.5) |
| Table 13. Summary of plant community ordination results from the final constrained RDA. |
| Table 14. Spearman's correlations for the total number of total understory trees by size class and two classes of shrub cover. 75 |
| Table 15. Spearman's correlations between the number of well-spaced understory trees by |
| size class and two classes of shrub cover |
| Table 16. a) Summary of the independent effects of all explanatory variables on overallregeneration density by species and size class; b) Summary of the conditional effect ofeach predictor87 |
| Table 17. Summary of tree regeneration niche ordination results from forward selection. |
| Only significant predictors (p<0.05) were retained |
| Table 18. Summary of results from the final constrained RDA for tree regeneration niche 88 |
| Table 19. Spearman's correlations for regeneration density (stems/ha) on coarse woody |
| debris by size class and two classes of shrub cover |
| Table 20. Spearman's correlations for the proportion of total stems on coarse woody debris |
| by size class and two classes of shrub cover |

LIST OF FIGURES

| Figure 1. Examples of "light", "moderate" and "severe" categories of defoliation, from the |
|--|
| Forest Health Aerial Overview Survey Standards for British Columbia |
| Figure 2. Representation of plot and subplot layout |
| Figure 3. Mean live stems/ha and dead stems/ha tallied according to their health and decay |
| class |
| Figure 4. Mean diameter at breast height of live and dead stems by species (mean, +/- SE). 45 |
| Figure 5. Tree species by diameter at breast height (mean, +/- SE) by subzone: a) live; and b) |
| dead |
| Figure 9. Scatterplots with linear least-squares regression lines for total regeneration density |
| as a function of: a) canopy density; and b) site index |
| Figure 10. Scatterplots with linear least-squares regression lines for well-spaced regeneration |
| density as a function of: a) steepness; b) annual heat: moisture index; c) site index; and |
| d) canopy density |
| Figure 11. a) Redundancy analysis (RDA) correlation biplot for plant community response |
| variables and explanatory variables identified during forward selection; and b) only |
| plant community response |
| Figure 12. Two-way similarity analysis of defoliated stands in the ITR, using a flexible beta |
| linkage method and Sorenson dissimilarity coefficient with PC-ORD |
| Figure 13. Plant community RDA showing the arrangement of understory shrubs and trees |
| and plots in ordination space |
| Figure 15. Scatterplots with linear least-squares regression lines for well-spaced regeneration |
| density and percent competitive shrub cover74 |
| Figure 16. Scatterplots with linear least-squares regression lines for associations between |
| understory regeneration density and percent competitive shrub cover: a) total Tsuga |
| seedlings; b) total Tsuga saplings; and c) total Tsuga (all size classes) |
| Figure 17. Scatterplots with linear least-squares regression lines for associations between |
| understory regeneration density and percent competitive shrub cover: a) total Abies |
| seedlings; b) total Abies saplings; and c) total Abies (all size classes) |
| Figure 18. Scatterplots with linear least-squares regression lines for associations between |
| understory regeneration density and percent competitive shrub cover: a) total seedlings |
| (all species); and b) total saplings (all species) |
| Figure 19. Scatterplots with linear least-squares regression lines for associations between |
| understory regeneration density and percent competitive shrub cover: a) well-spaced |
| Tsuga seedlings; b) well-spaced Tsuga saplings; and c) well-spaced Tsuga (all size |
| classes) |
| Figure 20. Scatterplots with linear least-squares regression lines for associations between |
| understory regeneration density and percent competitive shrub cover: a) well-spaced |
| Abies seedlings; b) well-spaced Abies saplings; and c) well-spaced Abies (all size |
| classes) |
| Figure 21. Scatterplots with linear least-squares regression lines for associations between |
| understory regeneration density and percent competitive shrub cover: a) well-spaced |
| seedlings (all species); and b) well-spaced saplings (all species) |

| Figure 22. a) Redundancy analysis (RDA) correlation biplot for tree regeneration density by species and size class response variables and explanatory variables identified during | у |
|---|----|
| forward selection. | 88 |
| Figure 23. Total regeneration density RDA showing the arrangement of understory tree | |
| species by size class and plots in ordination space | 89 |
| Figure 24. Mean tree regeneration density (± S.E.) by species, size class and substrate | 92 |
| Figure 25. Forest stand types representative of cluster analysis groupings: groups A) to D). | |
| | 05 |

1.0 Introduction

Projections of future climatic conditions in the forests of western North America consistently anticipate greater suitability for outbreaks of both bark beetles and defoliators (Ayres and Lombardero 2000, Haughian et al. 2012, Weed at al. 2013). The western hemlock looper (WHL; *Lambdina fiscellaria* spp. *lugubrosa* Hulst) is a Lepidopteran defoliator that acts as a landscape-scale disturbance in the Interior Cedar-Hemlock (ICH) biogeoclimatic zone (Ketcheson et al. 1991) of British Columbia, Canada, an area also known as the Inland Temperate Rainforest (ITR; Stevenson et al. 2011). The WHL defoliation events of the 1950s and 1990s continue to influence current characteristics of the ITR, and this study aims to ecologically evaluate the consequencess of this natural disturbance, and to forecast the recovery potential of these forests should insect outbreaks become more frequent and more severe, as predicted.

In particular, sampling and analysis was conducted to determine what outbreak, site and stand conditions are associated with stands in which the overstory tree cover has recovered, stands in which tree regeneration or regeneration release has occurred, and stands which have become ingrown with dense shrub cover.

1.1 Herbivory as a disturbance

Herbivory is the consumption of living plant parts by animals (Schowalter 2000). It is a key ecosystem process that reduces density of plants or plant materials, transfers biomass and

nutrients to other trophic levels and eventually the soil, and affects habitat and resource conditions for other organisms (Mattson and Addy 1975, Bardgett et al. 1998, Schowalter 2000). Defoliation by insects is a type of herbivory (also called folivory or phytophagy), and is the direct consumption of photosynthetically active material (Schowalter 2000). It has been argued that phytophagous insects occupy a special "regulator" position in some ecosystems because they affect leaves, the primary site of energy and biochemical synthesis in plants (Mattson and Addy 1975).

Whether herbivory is seen as a normal trophic process (Schowalter 1985, Schowalter and Lowman 1999, Willig and Walker 1999) or a disturbance (Pickett and White 1985), a defoliation event brought about by especially high population densities of an herbivorous insect can dramatically alter ecosystem structure and function over large areas. As a disturbance, the effect of herbivorous insects is not uniform, and varies in severity across forest stands (Stone and Wolfe 1996). Low or moderate levels of herbivory sometimes stimulate productivity through an over-compensation response by plants (McNaughton 1979, Belsky 1986, Dyer et al. 1993, Trumble et al. 1993) or by cascading trophic interactions (Carpenter et al. 1985). Severe herbivory usually results in decreased fitness or mortality (Marquis 1984, Williamson et al. 1989) by reducing a plant's ability to carry out necessary metabolic processes (Kessler and Baldwin 2002).

Entomologists who study the population dynamics of insects have defined some species as "outbreaking" (also known as epidemic) and others as "non-outbreaking" (also known as endemic) (Wallner 1987). This difference has also been described as a matter of population

fluctuation versus population balance (Richards 1961). Outbreak behavior is what distinguishes a disturbance event from the background herbivory that constrains primary productivity.

Herbivory by insects can influence the structure and composition of forest stands by causing mortality among some species or sizes of trees and not others (Evenden 1940, Mattson and Addy 1975, Alfaro et al. 1982, Romme et al. 1986, Knight 1987, Alfaro et al. 1999), thereby reducing the abundance of the host species and allowing other species or cohorts to flourish (Wohlgemuth et al. 2001). In addition to causing the direct mortality of canopy and sub-canopy trees and sometimes shrubs (Jardine 1969, Harris et al., 1982, Alfaro et al. 1999, McCloskey 2007), a defoliating insect outbreak will affect the way a forest develops by reducing plant density, opening up the canopy, stimulating or limiting the growth of plants, transferring nutrients and altering resource conditions for soil organisms (Bardgett et al. 1998, Schowalter 2000). Along with other variables such as light, moisture and temperature, the presence and accessibility of soil nutrients over different scales will have both immediate and gradual consequences for the makeup of plant communities present at any point in time following a defoliation event (Uriarte 2000).

In this study, "defoliation event" and "outbreak" will refer to the years of a sudden increase in population density of an herbivorous insect, including the western hemlock looper. The term "hemlock looper" refers to all subspecies of hemlock looper, *Lambdina fiscellaria*, whereas references to the "WHL" refer specifically to the *lugubrosa* subspecies.

1.2 Study objectives

This study uses previous research and new data to characterize how stands are recovering from the defoliation event that took place between 1991 and 1994 and was motivated, in part, to determine if the short-term trends observed in defoliated stands (Hoggett 2000, Hoggett and Negrave 2001) persist after 20 years of succession. This study aimed to sample documented and mapped WHL outbreaks in the ITR and compile the resulting stand structure, tree regeneration and understory plant composition patterns that have arisen since the event. Moreover, the ambition of this study was to characterize these sites and extrapolate the results to predict the trajectory of forest dynamics on similar sites in the ITR following a WHL outbreak.

1.3 Biology and ecology of the hemlock looper

The hemlock looper (*Lambdina fiscellaria* Guenée) is a native herbivorous insect that goes through cyclic outbreaks in temperate and boreal forests across North America (Otvos et al. 1979, Jobin and Desaulniers 1981, Harris et al. 1982, Hébert et al. 2001). The subspecies *fiscellaria* and *lugubrosa* are the eastern and western forms of this insect, respectively, but studies have been unable to morphologically or genetically distinguish the two (McGuffin 1987, Sperling et al. 1999). A third subspecies, *somniaria*, is found in southwestern B.C. in the Garry oak (*Quercus garryana* Dougl. ex Hook.) ecosystem.

In eastern Canada, the main host trees of the hemlock looper, in order of the observed level of relative feeding "preference," are balsam fir (*Abies balsamea* (L.) Mill.) and eastern hemlock (*Tsuga canadensis* (L.) Carr.) (Carroll 1956, Davidson and Prentice 1967, Martineau 1984, MacLean and Ebert 1999). In western Canada, the hemlock looper feeds on many species including western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), western redcedar (*Thuja plicata* Donn ex D. Don), Sitka spruce (*Picea sitchensis* (Bong.) Carr.), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), white spruce (*Picea glauca* (Moench) Voss), true firs (*Abies* spp.), western white pine (*Pinus monticola* Dougl. Ex D. Don), western larch (*Larix occidentalis* Nutt.), lodgepole pine (*Pinus contorta* ex Loudon.), and some broad-leaved species and understory shrubs (Jardine 1969, Koot 1994, Parfett et al. 1995, Alfaro et al. 1999, McCloskey 2007), although the food species within these latter groups are not named in the literature.

The hemlock looper has one generation per year, with eggs laid on tree branches, lichens, leaves and in bark crevices in September and October (Hopping 1934, Shore 1989, Koot 1994, Alfaro et al.1999, Hébert et al. 2001). Oviposition may also occur in litter on the forest floor, but only at the height of an infestation (Hopping 1934). Hemlock looper eggs overwinter and hatch in May and June, when early instars (stages of larval development) feed on current-year needles and buds on upper tree crowns (Erickson 1984, Koot 1994, Raske et al. 1995, Alfaro et al. 1999).

In July and August, later-instar larvae feed on foliage in all age classes and often do not consume leaves completely (Carroll 1956, Carolin and Lejeune 1967, Otvos et al. 1971,

Furniss and Carolin 1977, Dobesberger 1989, Raske et al. 1995, Carroll 1999). Feeding larvae move down to lower sections of trees during later stages, where they feed voraciously (Koot 1994, Alfaro et al. 1999). In late August, larvae find pupation sites on lower parts of the tree on leaves, tree trunks, on the ground around trees, and on other surfaces, and emerge as adults in 10 to 15 days (Watson 1934, Carroll 1956, Jardine 1969, Ostaff et al. 1974, Raske et al. 1995). Mating occurs soon after (Jardine 1969, Ostaff et al. 1974) and females lay eggs, likely near their emergence site (Thomson 1958).

1.4 Hemlock looper as an agent of disturbance

Little is known about the factors that facilitate WHL population growth and bring a population to outbreak levels (McCloskey et al. 2009). Climatic factors have been linked to vacillations in population densities of Lepidoptera, with above-average temperature and below-average precipitation being associated with WHL outbreaks (McCloskey 2007). A favourable climate may allow high survival and fecundity (McCloskey et al. 2009) and may lead to synchronous outbreaks over wider areas (Williams and Liebhold 1995, Myers 1998). Spatially independent outbreaks of WHL have developed in B.C. in the same years in the past, suggesting that regional climate is a factor influencing the start of an outbreak (Parfett et al. 1995, McCloskey et al. 2009).

During a defoliation event, trees may be stripped of leaves in one season, or they appear orange-to-brown with the surrounding ground littered with needles that were chewed at their base and then fell to the forest floor, while other needles were partially chewed, dried out and

then fell (Koot 1994, Alfaro et al. 1999). Outbreaks often last three years, and extensive tree mortality may occur after the first and second years of a defoliation event (Watson 1934, Otvos et al. 1979, Jobin and Desaulniers 1981, Alfaro et al. 1999, Bordeleau 2000, Hébert et al. 2001). A WHL outbreak leaves the soil and forest floor undisturbed (Hoggett 2000).

Populations may become limited by wasp parasitism or by one or more of the 47 viruses that affect all life stages on this insect (Torgersen 1971, Turnquist 1991, Koot 1994, Otvos 2004, Whittome-Waygood et al. 2009). The fungal pathogen *Entomophthora* sp. has been a significant natural control agent of the hemlock looper (Koot 1994), as have the common parasitic wasps *Aoplus velox occidentalis* (Harrington), *Telenomus dalmani* (Ratzeburg) and *Trichogramma minutum* (Riley), and the nucleopolyhedrovirus (Torgersen 1971, Otvos 2004, Whittome-Waygood et al. 2009). In situations when foliage becomes a limiting factor, larval starvation may end an outbreak, and there is speculation that heavy precipitation and cool weather during the adult flight and egg-hatching periods can also lead to population collapse (Koot 1994). Some bird species prey on the larval and pupal stages of the hemlock looper, but their effect on population densities during outbreak periods is unknown and unlikely to be limiting (Otvos et al. 1979).

In B.C., mature *Tsuga heterophylla* dominated forests were considered to be most susceptible to WHL defoliation (Kinghorn 1954, Koot 1994). Forests previously defoliated by hemlock looper are at high risk for future defoliation (Borecky and Otvos 2001).

Western hemlock looper outbreaks are said to be less damaging than eastern hemlock looper outbreaks (Harris et al., 1982), but to date no study specifically comparing the severity and consequences of outbreaks of each subspecies has been carried out.

1.5 Hemlock looper defoliation history, geography and control

Macrofossil and dendroecological data suggest that there was a major decline in eastern hemlock abundance across its entire range about 5000 years before present (Bhiry and Filion 1996, Foster 2000). Because this decline was only experienced by one tree species over a wide area at the same time, it has been suspected to be a result of an outbreak of a defoliating insect like the hemlock looper, as opposed to climate change or aboriginal impact (Davis 1981, Bhiry and Filion 1996, Foster 2000). Lending support to this hypothesis is evidence in the paleoecological record of large numbers of looper fossils in sediments from the same period in which pollen and macrofossils indicate a hemlock decline (Bhiry and Filion 1996).

Hemlock looper outbreaks have been recorded in all the Atlantic provinces (Hudak et al.1978, Otvos et al., 1979, Clarke and Carew 1987, Magasi 1990, Hartling et al. 1991, Carter and Hartling, 1992, Iqbal and MacLean 2010, Iqbal et al. 2011), Quebec (Jobin 1980, MacLean and Ebert 1999, Martel 1999, Chouinard and Filion 2005), Ontario (Carroll 1956, Torgersen 1971) and B.C. (Kinghorn 1954, Alfaro et al. 1999, McCloskey 2007, McCloskey et al. 2009). Alaska, Oregon and Washington, Idaho and Montana, Michigan and Wisconsin have also been subject to hemlock looper outbreaks in the past (Graham 1956, Torgersen and

Baker 1967, Johnson et al. 1970, Furniss and Carolin 1977, Western North American Defoliator Working Group 2002).

Efforts to control hemlock looper outbreaks with such agents as *Bacillus thuringiensis* var. *kurstaki* (commonly known as B.t.), dichlorodiphenyltrichloroethane (DDT), lead and calcium arsenates, carbaryl and phosphamidon have been documented (Buffam 1965, Carolin and Thompson 1967, Turnquist 1991, Koot 1994, Fuxa et al. 1998, Charles 2000), and the introduction of naturally occurring pathogens has also been studied (Wood and Van Sickle 1993, Levin et al. 1997, Whittome-Waygood 2009). Early tests of the general effectiveness of B.t. found that its effectiveness is in proportion to the concentration applied to infested trees (Buffam 1965), but limited success was found in achieving high levels of mortality of hemlock looper when it was applied to control an infestation (Fuxa et al. 1998). Aerial sprayings of DDT and lead arsenate have been found to curtail the adverse effects of feeding forest insects, including hemlock looper (Paananen et al. 1987), but have other unacceptable environmental effects.

1.5.1 Western hemlock looper in British Columbia

In B.C., WHL outbreaks have occurred primarily south of 56 degrees latitude, in valleybottom stands with a high proportion of mature open-growing *Tsuga heterophylla* (Parfett et al. 1995). The biogeoclimatic units most frequently attacked by the WHL in B.C. are wet cool (wk), very wet cool (vk) and moist warm (mw) subzones of the Interior Cedar-Hemlock zone (ICHvk, ICHwk, ICHmw), and the wk and very wet cold (vc) subzones of the Engelmann Spruce – Subalpine Fir (ESSF) zone, known as the ESSFwk and ESSFvc (Ketcheson et al. 1991, Coupe et al. 1991, Parfett et al. 1995), all of which are in the interior of the province. Most infestations have only lasted for one to two years in any one area; however, two small coastal areas (east of Indian Arm and south of Lake Cowichan) have defoliation records showing four-year long outbreaks (Parfett et al. 1995). The first recorded WHL outbreak in B.C. was in 1911 in Stanley Park, Vancouver (Harris et al. 1982, Parfett et al. 1995).

WHL infestations with the highest proportion of trees killed have occurred in coastal and interior wet belt regions, principally in mature hemlock and hemlock-cedar stands (Alfaro et al. 1999). In coastal B.C., major outbreaks have been documented on Vancouver Island and the South Coast (1945-1946, 2000-2003). In interior B.C., major outbreaks have taken place in the Upper Fraser River valley (1954-1955, 1991-1994), the north Thompson (1976 and 1991-1992), Arrow Lakes (1972-1973), Shuswap Lake (1983-1984), Horsefly Lake-Quesnel Lake (1946, 1984, 1991-1992), and Revelstoke (1945-1947, 1972-1973, 1982-1983, 1991-1993) areas (Thomson 1958, Turnquist 1991, Duncan 2006, McCloskey et al. 2009). The fifteen distinct outbreaks in 100 years have increased in size, distribution and intensity over that period, particularly those in the Interior (Borecky and Otvos 2001, McCloskey 2007). Some research suggests that outbreak patterns differ between interior and coastal forests of B.C. due to differences in regional climate and tree species composition (McCloskey 2007).

In the ITR of the Upper Fraser River valley, a WHL outbreak in 1954 and 1955 affected 45,500 ha of forest at Eaglet Mountain, Lunate Creek, Penny and McBride (Harris et al.

1982, Parfett et al. 1995). Another defoliation event over 39,000 ha took place forty years later from 1991 to 1994 (Taylor 1996).

1.6 Tree mortality, survival and stand development

1.6.1 Overstory

Tree death is often the consequence of multiple factors (Franklin et al. 1987). Defoliation affects the growth and vigour of individual trees (McCloskey 2007), but secondary attack by bark beetles, root rot such as *Armillaria mellea* (Vahl. ex. Fr.) and dwarf mistletoe (*Arceuthobium* spp.) has been thought to exacerbate tree stress further and eventually kill defoliated trees (Kinghorn 1954, Kulman 1971). A WHL defoliation will kill some trees and not others, increasing heterogeneity at the stand scale, with variation in tree mortality producing distinct patches of defoliated trees at the landscape scale (McCloskey 2007). Sometimes defoliation can help tree survival; grand fir (*Abies grandis* Douglas ex. D. Don Lindl.) seedlings defoliated by the western spruce budworm (*Choristoneura occidentalis* Freeman) showed higher survival during a period of drought stress than non-defoliated seedlings (Parks 1993), possibly due to the reduced demands of water and nutrient uptake of defoliated plants (Webb 1978).

In the context of forest disturbance research, disturbance severity typically refers to the proportion of trees killed during a more or less discrete disturbance event (Frelich and Reich 1999). In general, WHL-induced tree mortality is related to defoliation level, tree species and

tree size (Alfaro et al. 1999, Hoggett and Negrave 2001), and usually happens after a tree has been defoliated for two consecutive seasons (McCloskey 2007). It has been found that low levels of defoliation only slowed the growth of *Tsuga heterophylla* in the canopy, and severe defoliation resulted in the death of hemlock in the canopy (Alfaro et al. 1999). Generally, all species of trees that are 100% defoliated by WHL are killed outright, while trees 50% or more defoliated have a high degree of mortality due to subsequent stresses to the weakened trees (Kinghorn 1954, Turnquist 1991). Mortality can continue to occur up to three years following the collapse of an infestation (Kinghorn 1954, Turnquist 1991).

In a study in the submontane variant of the very wet maritime subzone of the Coastal Western Hemlock biogeoclimatic zone (CWHvm1; Pojar et al. 1991), the most severely defoliated stands had been dominated by *Tsuga heterophylla*, and the most lightly defoliated sites had the lowest proportion of living *T. heterophylla* pre-defoliation (McCloskey 2007). Four years after the outbreak had ended, *T. heterophylla* had the highest cumulative mortality, with amabilis fir (*Abies amabilis* (Dougl. ex Loud.) Dougl. ex J. Forbes) and *Thuja plicata* suffering the least mortality, thus increasing their proportion in the surviving canopy (McCloskey 2007). A study examining mortality ten years post-disturbance in stands with similar overstory composition found comparable results (Kinghorn 1954). The consequence of this differential mortality on overstory composition was reduced absolute and relative abundance of *Tsuga heterophylla* and increased relative abundance of other species (McCloskey 2007).

A study that contained elements analogous to the coastal study began approximately six years following the end of the 1991-1994 WHL outbreak in the ITR. Within the Goat variant of the wet cool subzone of the Interior Cedar Hemlock biogeoclimatic zone (ICHwk3), *Abies lasiocarpa* and *Tsuga heterophylla* had the highest mortality following the outbreak, while *Thuja plicata* and *Picea engelmanii* x *glauca* suffered the least mortality (Alfaro et al. 1999, Hoggett and Negrave 2001). However, stands with a high basal area composition of *Tsuga* and *Abies* did not always experience commensurately high mortality; high variability in mortality between stands masked these species-related mortality differences within stands (Hoggett and Negrave 2002).

In both coastal and interior rainforests, the effects of WHL are more severe for sub-canopy trees than for canopy trees, with smaller-diameter trees showing significantly higher levels of mortality than larger trees (McCloskey 2007, Hoggett and Negrave 2001). Although Hoggett and Negrave (2001) reported high variability in mortality among diameter classes in defoliated stands in the Interior, in general the largest diameter classes suffered the lowest rates of mortality. Trees with a diameter at breast height (DBH) of greater than 50 cm had significantly less mortality than those in smaller size classes (Hoggett and Negrave 2001). Forest floor depth was one measured site factor that was found to be significantly associated with the severity of the WHL defoliation; there was a strong negative relationship between forest floor depth and *Thuja plicata* mortality (Hoggett and Negrave 2001).

In the Interior, a strong positive correlation between total live basal area, proportion of trees to survive and mean live cover with the basal area of live *Thuja plicata* suggested that

overstory tree survival in stands was closely linked with the presence and survival of *Thuja* (Hoggett 2000). Furthermore, the mean DBH and height of live canopy trees was positively correlated with the basal area of *Thuja*, meaning that stands with greater proportions of *Thuja* tended to have surviving canopies that consisted of taller and larger trees (Hoggett 2000). Changes in plant community composition following a defoliation event happen partially as a result of differences in survival rates among different tree species (Kinghorn 1954, Alfaro et al. 1999, McCloskey 2007).

1.6.2 Stand development and succession

Defoliation events are an important instrument of succession (Bhiry and Filion 1996). A study that examined two mid-Holocene hemlock looper outbreaks in eastern North America using paleoecological methods showed a long-term decline in eastern hemlock in areas where an outbreak was severe (Bhiry and Filion 1996, Fuller 1998). This defoliation was described as a "major biotic and biostratigraphic event" (Oswald and Foster 2011) that initiated a successional process that led to stands with entirely different species compositions than pre-disturbance ones (Fuller 1998, Foster 2000).

Succession is a directional change in the composition of a plant community over time (Pickett et al. 1987, Barbour et al. 1999). Mechanisms of change in plant species dominance following a disturbance can reflect interactions such as competition or herbivory, a limitation of a particular resource, the availability of propagules, life history differences, changes in environmental factors or canopy architecture (Pickett et al. 1987, Veblen 1992). Since neither the soil nor the propagules within it are disrupted by a WHL defoliation event, the series of plant community changes following an outbreak of this kind can be described as secondary succession, which occurs following a perturbation that is not severe enough to kill all plants or the existing seed bank (Connell and Slayter 1977, Barbour et al. 1999). Some ecological models describing succession in forested ecosystems have included the influence of herbivores (Dyer and Shugart 1992, Fuhlendorf and Smeins 1997, Tester et al. 1997, Blatt et al. 2001, Seidl et al. 2011). Insect herbivores influence competitive interactions within a plant community and therefore affect plant species composition (Dyer and Shugart 1992, Blatt et al. 2001, Hartley and Jones 2004). Changes in the proportion and vigour of overstory trees following a WHL defoliation have been found to lead to increased dominance of understory shrub species in some stands, while in other stands understory densities of climax tree species are greater. Different stands follow different successional pathways following a WHL disturbance (McCloskey 2007), and one of the primary objectives of this study is to determine why this is the case.

The WHL defoliation event in coastal B.C. increased structural and compositional diversity within stands by increasing the density of snags, thinning the forest canopy, shifting the relative composition of canopy trees and modifying biomass and competition in the understory plant community (McCloskey 2007). These effects likely depend on the severity of the defoliation event, including the role of biological legacies such as standing dead trees (Turner et al. 1998, Franklin et al. 2000). Canopy openness increases significantly with increasing severity of defoliation, and a severe defoliation event may slow the redevelopment of a closed-canopy forest because young trees are killed and a dense understory plant

community is created, often with little or no tree regeneration (McCloskey 2007). This pattern was also found in the ITR, where increased canopy mortality was associated with increasing cover of understory shrub species, which in turn was negatively correlated with tree regeneration density (Hoggett and Negrave 2001).

1.6.3 Understory

In a four-year post-outbreak study of a 2000 to 2003 WHL defoliation in coastal (CWHvm1; Pojar et al. 1991) forests, it was found that more severely defoliated stands (>65% visible defoliation) were significantly richer in shrub, fern and herbaceous species, and had higher shrub cover than lightly or moderately defoliated stands (McCloskey 2007). Conversely, there was lower tree seedling and sapling cover with increasing defoliation severity (McCloskey 2007). Red elderberry (*Sambucus racemosa* L.) and salmonberry (*Rubus spectabilis* Pursh) are known to dominate sites following WHL disturbances in coastal forests, with salmonberry being particularly responsive and persistent (Kinghorn 1954). The dense canopies of these shrub species limit the regeneration of trees, and one study predicted that it would take decades for coniferous trees to become re-established unless management actions were taken to control shrubs in these stands (Kinghorn 1954). It is not known whether the dominating shrub and fern species originated from growth release of preestablished plants, from propagule reservoirs in the soil, or an input of propagules from elsewhere.

Five years after the 1991-1994 ITR WHL outbreak, sampled stands in the ICHwk3 generally had two distinct, co-existing understory layers: a lower layer made up of climax community species, and an upper layer made up of species more common on disturbed sites, such as *Sambucus racemosa*, fireweed (*Epilobium angustifolium* L.) and red raspberry (*Rubus idaeus* L.) (Haeussler et al. 1990, Hoggett 2000, Wilhelm 2004). Devil's club (*Oplopanax horridus* (Sm.) Miq.), a species usually associated with later seral stages (Mason 1990) also occurred in the upper understory layer. In areas of higher canopy mortality, the development of this upper understory layer was pronounced (Hoggett 2000, Wilhelm 2004). In a study of sites with 100% canopy mortality, *Rubus idaeus* had a higher cover and frequency than other species (Wilhelm 2004).

The development of the tall shrub understory layer was associated with a decrease in regeneration density (Hoggett 2000). Regeneration density was highly variable among plots (between 1,000 stems/ha to 12,000 stems/ha) but was found to be associated with higher levels of living canopy cover (Hoggett 2000). In stands where there was tree regeneration, *Tsuga heterophylla* seedlings and saplings occurred at the highest densities, with somewhat less *Thuja plicata* and minor amount of *Abies lasiocarpa*, while paper birch (*Betula papyrifera* Marsh.) and spruce were absent (Hoggett 2000).

In light of these results, Hoggett and Negrave (2001) identified two possible trajectories for stands following a WHL disturbance in the ITR: stands with moderate mortality and a sparse shrub understory should recover to a full tree canopy in the medium term (not defined), while stands with high levels of mortality (>60%) and strong shrub understory development (>90%)

cover) would enter a period of shrub dominance. Hoggett and Negrave (2001) and Wilhelm (2004) -- both working in the ICHwk3 -- and McCloskey (2007) -- working in the CWHvm - - noted that a period of understory dominance by shrubs and ferns appears to be part of the natural dynamic of heavily defoliated stands affected by WHL in B.C. A white spruce under-planting trial set up immediately after the 1991-1994 WHL outbreak in the ICHvk2 in a severely defoliated stand found that seedlings had low growth rates and height-to-diameter ratios in the first three years following the plantings (Coopersmith et al. 1998). These results were likely due to low light levels due to competition from understory plants and shade from *Tsuga heterophylla* and *Thuja plicata* snags (Coopersmith et al. 1998).

Severe defoliation in CWHvm and ICHwk3 stands altered canopy structure and understory composition in ways that are expected to delay the re-development of a closed canopy (Hoggett and Negrave 2002, McCloskey 2007). As observed in moderately and severely defoliated stands, the death of subcanopy trees means a loss of opportunity for trees to recruit from subcanopy to overstory strata and replace the canopy trees killed by defoliation (McCloskey 2007). Thus, there will most likely be a prolonged period of open canopy and a lag in canopy closure as new seedlings establish in the understory and recruit to the canopy (Hoggett and Negrave 2002, McCloskey 2007). This effect was exacerbated in severely defoliated stands where the understory plant community was already well developed prior to defoliation (McCloskey 2007).

1.6.3.1 Coarse woody debris in a defoliated stand

Coarse woody debris (CWD) in the ITR provides habitat for wildlife (Stevenson et al. 2006). Some of the existing CWD in this ecosystem is likely the result of defoliated trees that have died and fallen to the forest floor, creating a potential substrate for regenerating trees. Coarse woody debris may help regenerating trees avoid competition with species on the forest floor (Harmon and Franklin 1989, Daniels and Gray 2006) and could also function to hide or block access to regenerating trees from browsing ungulates (Ripple and Larsen 2001). Both of these possibilities facilitate tree regeneration, although the rate of falling and decay in looperdefoliated trees may limit the availability of this substrate.

Defoliated trees have reduced decay resistance; trees that become stressed due to prolonged defoliation lose both their capacity to block rot fungi from entering, and their ability to prevent their spread to other parts of the tree by compartmentalizing (Engelhardt 1957, Neely 1970, Shortle et al. 1977, Wargo 1977, Shortle 1979, Shortle and Ostrovsky 1983). In a wet coastal forest, standing looper-defoliated trees deteriorated much faster than dead trees on the ground not killed by WHL over a similar period (Johnson et al. 1970). Additionally, 20% of the wood volume of trees killed by WHL can be expected to show advanced decay after only two years, whereas dead trees on the ground for the same period will suffer only slight losses after the same amount of time (Johnson et al. 1970). Decay rates of post-WHL trees are useful to an understanding of recovery and regeneration in defoliated stands and are an important consideration in determining their carbon balance.

1.7 Nutrients and defoliation

The delivery of frass and partially-eaten leaves to the forest floor is one of the ways forest canopies and soils are linked by the process of herbivory (Chew 1974, Mattson and Addy 1975, Swank et al. 1981, Seastedt and Crossley 1984, Grace 1986, Hollinger 1986, Schowalter et al. 1991, Risley and Crossley 1993, Lovett and Ruesink 1995, Reynolds et al. 2000, Reynolds and Hunter 2001, Hunter 2001, Reynolds et al. 2003). A defoliation event can modify the functional attributes of a forest stand by changing conditions of soil nutrients, light and moisture in a way that may shape the direction of succession and recovery (Assmann 1970, Franklin et al. 1987, Hicke et al. 2012). Defoliating insects affect the total amount of nutrients available to plants and also cause temporal and spatial variation in that availability (Hartley and Jones 2004). An outbreak also increases canopy openness, thereby increasing forest floor temperatures and decomposition rates (Schlesinger 1991, Reynolds and Hunter 2001).

Defoliators such as the hemlock looper will consume the carbohydrates and proteins in leaves and release large fluxes of nitrogen, carbon and other nutrients into forest ecosystems through frass (feces), partially eaten "greenfall," dead insects, and exuviae (Mattson and Addy 1975, Swank et al. 1981, Grace 1986, Hollinger 1986, Schowalter 2000, Frost and Hunter 2004, Hicke et al. 2012). Also, defoliation can increase the nutrient content of precipitation as it falls through the forest canopy ("throughfall") (Schowalter et al. 1991, Hunter 2001). Increased canopy openness results in higher forest floor temperatures, which

in combination with more moisture availability from throughfall, facilitates decomposition and nutrient cycling (Gabriel and Kellman 2011).

There appears to be no consistent trend in soil nutrient availability to plants in insect defoliated stands (Stadler et al. 2004). Some authors have observed increased nitrogen mobilization brought about by enhanced frass and litter inputs (Swank et al. 1981, Hollinger 1986, Christensen et al. 2002), and others report nitrogen immobilization in reponse to greater levels of carbon compounds (Lovett and Ruesink 1995, Michalzik and Stadler 2000, Lovett et al. 2002). This might be due to site-specific factors such as the microbial soil community, nutrient status (e.g., N saturation,) litter quality (Stadler et al. 2004), or other abiotic variables.

At non-outbreak densities, defoliating insects don't have an especially important effect on the decomposer system, with significant effects occurring mainly during short, intense outbreak periods (Wardle and Bardgett 2004). At non-outbreak densities, frass has not been found to affect soil respiration or litter decomposition rates, even though frass inputs stimulate micro-arthropod densities (Reynolds and Hunter 2001, Reynolds et al. 2003). Thoughfall and greenfall associated with a defoliation event have been found to reduce soil respiration, likely because soil microbes were outcompeted by mycorrhizal fungi for uptake of the added mineral nitrogen (Reynolds and Hunter 2001).

Below ground, plants can increase root exudation in response to herbivory, and this may have effects on soil fauna (Wardle 2002), which in turn may affect nutrient availability to

plants (Bardgett and Chan 1999). The physiological responses of plants to above-ground herbivory may be important in influencing both soil organisms and key soil processes such as decomposition and nutrient mineralization in terrestrial ecosystems (Bardgett et al. 1998), although there is limited research on this effect in forest ecosystems.

Importantly, differences among studies of what happens to nitrogen or other nutrients following a defoliation event can be the result of differences in soil parent material, local topography, edaphic conditions, soil fauna, variation in forest age, quality of frass, and other factors (Hunter 2001, Christenson et al. 2002). In addition to nutrient inputs and nutrient availability, light availability, soil moisture and temperature changes may influence the quality of litter by affecting leaf chemistry and its decomposition dynamics (Strand et al. 1999). These effects can create stand-specific defoliation outcomes.

1.8 Research questions

With this study spanning a wide range of site types approximately two decades after the WHL outbreak, I can meet the objectives identified in Section 1.2 by answering the following four research questions about the resilience of defoliated stands in the ICHwk3 and ICHvk2:

1. Is greater canopy recovery after defoliation significantly related to site productivity or climate factors?

2. Are different levels of shrub cover more closely associated with differences in site productivity factors (e.g., soil moisture availability), climate or canopy openness?

3. Are tree regeneration densities more closely associated with canopy openness, shrub cover, site productivity or climatic factors?

4. To what degree does understory plant community composition reflect site productivity, climatic factors, WHL outbreak history or current canopy conditions?

2.0 Methods

2.1 Study area

Plots were located within the vk2 and wk3 variants of the Interior Cedar-Hemlock biogeoclimatic zone (ICH; Ketcheson et al. 1991). The ICHvk2 occurs between elevations of 680 and 1,180 m in the valley of the Fraser River between Dome Creek and Sinclair Mills, and includes areas around the Torpy and MacGregor Rivers, Slim Creek and Purden Lake (DeLong 2003). Mean annual precipitation in this variant is about 840 mm and mean annual temperature is approximately 3.3°C. The ICHwk3 occurs at elevations between 670 and 1,225 m between Dome Creek and McBride, has a mean annual temperature of approximately 3.1°C (Meidinger et al. 1988), and is slightly drier than the ICHvk2 (DeLong 2007).

Soils in the ITR are mostly of the Podzolic order, with Brunisols and Regosols occurring on unstable slopes and in areas of recent fluvial deposition, and Luvisols forming where there are morainal deposits (Stevenson et al. 2011). Forest floors in the ITR can be two to four times thicker than in drier forest types to the west in central B.C. (Arocena and Sanborn 1999). Mormoders, Humimors and Hemimors tend to be the dominant humus forms in the vk2 and wk3 variants (Green et al. 1993).

Sixty-three plots were placed in stands that had been defoliated by the WHL between 1992 and 1994. Only stands that had been classified and mapped as 'moderately' or 'severely'

defoliated by Forest Health Aerial Overview Surveys (CFS and MoF 2000) and had remained unharvested were sampled. Stands in the 'moderate' defoliation class are defined as having trees with pronounced discoloration, thin foliage, the top third of trees defoliated, and some trees completely stripped (CFS and MoF 2000; Figure 1). Stands in the 'severe' defoliation class are defined as having trees with bare branch tips, completely defoliated tops and where most trees sustain more than 50% total defoliation (CFS and MoF 2000). Maps provided by the B.C. Forest Service were used to locate plots in stands that met these criteria.

McCloskey (2007) found that lightly defoliated stands (<25% defoliated) do not differ substantively from the surrounding non-disturbed landscape, and so only stands that experienced higher defoliation levels were sampled. Only stands mapped as having been defoliated in the 1990s, but not in the 1950s, were sampled in order to isolate the effects of the more recent defoliation event and to avoid obscuring the circumstances under which regeneration and succession are occurring.

Plots were located in stands that had been sampled previously by other researchers, as well as in some stands with no history of having been sampled in the past. Plots were placed in stands sampled by Deschamps et al. (Walker Creek, unpublished 1994), Alfaro et al. (1999), Hoggett and Negrave (2002), Conder (unpublished 2006), and Konchalski (unpublished) that met the sampling criteria for this study. Maps, latitude/longitude coordinates and UTM coordinates provided by these researchers were used to find the plots they had sampled, and new plots were placed in the same stands when possible. When an attempt to find a

previously sampled plot location in the field was unsuccessful, a new plot was placed within the same forest cover polygon, based on the B.C. Forest Service maps of the study area.

Additional plots accessible by road were located to capture the ecological variation of stands within the study area. After walking into a stand (away from the nearest road) 170-250 m, a random number between zero and 360 generated in advance using MS Excel was used as a compass bearing then followed for 70 paces. All plots were at least 100 m from a road except for three plots located at Walker Creek, which were approximately 30 m away from the Highway 16 right-of-way. Plots were at least 30 m away from any cut tree sighted.



Figure 1. Examples of "light", "moderate" and "severe" categories of defoliation, from the Forest Health Aerial Overview Survey Standards for British Columbia (CFS and MoF 2000). Copyright (c) Province of British Columbia. All rights reserved. Reproduced with permission of the Province of British Columbia. www.ipp.gov.bc.ca

2.2 Plot layout and sampling design

The centre of each 400 m² circular, fixed-area plot was marked with a flagged wire 'pigtail' pin. Three 100 m² circular subplots, each with a nested 50 m² circular subplot, were located along the edge of the main plot at 20° ("North"), 140° ("Southeast") and 260°("Southwest") azimuths from plot centre; see Figure 2. Within each 400 m² plot, the following site data were collected: slope, aspect, elevation and UTM coordinates. Stand data collected within each plot were: percent canopy cover (using a concave spherical densiometer in each subplot for a total of three readings), the species and DBH of all live trees >7.5 cm DBH, and a visual estimate of their current percent defoliation were recorded. This included trees with tops that had snapped off. Percent defoliation values were not assigned to *Betula papyrifera*.



Figure 2. Representation of plot and subplot layout.
Dead trees were also tallied by species, measured for DBH, and recorded as being "standing," "leaning," "snapped" or "fallen." Coarse woody debris (CWD) classes 4 and 5 and snag classes 6 and up (Maser et al. 1979) were excluded from this count, so that the dead trees counted are assumed to have died directly or indirectly from the 1990s WHL defoliation. This method is consistent with studies determining the relationship between decay and time of tree death (Daniels et al. 1997). We did not, however, look for or record evidence of butt rots, root rots, bark beetles or other causes of tree damage or death, none of which are recorded as being widespread forest health issues in the Robson Valley during the 1990s. We took four digital photographs, one in each cardinal direction, from the centre of every 400 m² plot.

A 50 cm deep soil pit was dug in every plot and the following data were collected: soil texture class, per cent coarse fragments, effective rooting depth, humus form, mesoslope position, whether there was gleying or mottling, and a determination of soil nutrient regime and soil moisture regime (DeLong 2003, 2007). Soil nutrient regime (SNR), soil moisture regime (SMR) and site series (Pojar et al. 1987) were validated using a combination of soils data and plant cover data (DeLong 2003, 2007).

Although no charcoal particles were found in soil pits to indicate fire activity, these particles are difficult to observe without a trained eye (P. Sanborn pers. comm.). There is datable evidence of fires as recently as 182 years ago in both forest floors and buried soil profiles in climax stands sampled in the ICHwk3 (Sanborn et al. 2006) so it is likely that some of the 63 stands sampled for this study have fire in their history. This study considers the effects of the WHL defoliation in isolation from their possible fire history.

All saplings (>1.3 metres in height to 7.5 cm DBH) were tallied by species in each 100 m² subplot. In each 50 m² subplot, all seedlings (10 cm to <1.3 metres in height) and germinants (<10 cm in height) were searched for and tallied by species as well. Germinants were likely under-counted because of their small size. Two tallies were done for each subplot: one for total regeneration and one for only well-spaced regeneration. Well-spaced germinants, seedlings and saplings were the tallest and most vigorous of each size class and at least 0.5 m from other individuals. For total regeneration tallies, the substrate on which each germinant, seedling, and sapling was growing was recorded. It is not necessarily possible to correctly identify the establishment substrate of a sapling because of the time elapsed since the establishment of trees in that size class. All regeneration was assigned to one of three substrate categories: forest floor, coarse woody debris and mineral soil.

A prism sweep using a glass wedge prism having a basal area factor (BAF) of 4 m²/ha, of all overstory trees was taken from the centre of each subplot to determine local basal area for overstory trees by species. Canopy density was also measured from the centre of each subplot using a spherical densiometer. Subplot data were aggregated so that there was one value per plot for basal area and canopy density.

Vegetation cover for all vascular plant and bryophyte species that could be seen on the forest floor was visually estimated in 50 m^2 subplots. Some lichen species in some stands were

recorded in this study, but lichens were not sampled reliably, and therefore not included in any analyses. It was observed that terricolous lichens were uncommon and most lichens were epiphytic. For more information on this functional group in the ITR see Goward and Arsenault (2000), Benson and Coxson (2002), Radies (2008), Radies et al. (2009), Spribille et al. (2009) and MacDonald (2013).

2.3 Data preparation

Canopy density, regeneration densities, vegetation cover and basal area data were aggregated by calculating the arithmetic mean for each variable at the plot level.

In order to analyze plots in both subzones together, I created a synthetic index for relative soil moisture using SMR categories and their correspondence to absolute soil moisture regime (ASMR) values (DeLong et al. 2011a). Absolute Soil Moisture Regime is an estimate of water availability on a site, considering climatic as well as terrain influences (DeLong et al. 2011a) and these values were used to compare moisture levels in both subzones. Plots in this study fell into SMR categories 3 to 6 ('submesic' to 'hygric') in the wk3 biogeoclimatic variant and categories 3 to 7 ('submesic' to 'subhydric') in the vk2. The synthetic index, standardized to ICHwk3 relative moisture, captures the range of soil moisture possibilities within the plots in this study; the driest category (3) includes submesic plots in the wk3, while the wettest category (8) includes subhydric plots in the vk2. The intermediate categories (4-7) include plots in both subzones because moisture levels in this range likely

overlap. In general, relative moisture regimes in the ICHvk2 were offset by one relative SMR unit to correspond to approximately the same ASMR score.

A frost hazard rating was assigned to each plot using the Stand Level Frost Hazard Assessment and Management Tool (DeLong et al. 2011b). Using latitude, slope and aspect, potential direct incident radiation (referred to hereafter as simply "radiation") was estimated for each plot (McCune and Keon 2002). Estimates of mean annual precipitation (MAP), mean annual temperature (MAT) and annual heat:moisture index (AHM) were estimated for each plot using ClimateWNA ver. 4.71 (Wang et al. 2012). ClimateWNA calculates sitespecific climate data based on 30-year climate norms using geo-referenced interpolations, correlations, and elevation adjustment (Wang et al. 2012). Those variables were selected for inclusion because their coefficients of variation were the highest among the 21 climate variables produced by ClimateWNA for the 63 plot locations, and hence should have the greatest potential for distinguishing plot differences.

Site index, a measure of site productivity, was included in this analysis in order to compare the productivity potential among stands (MoFR 2011). Site index values were assigned to each sampled stand on the basis of biogeoclimatic variant and site series, using values published by MoFR (2011). Site index, as used here, is the mean reported height (m) for dominant trees across five species (*Picea engelmanii* x glauca, *Pinus contorta*, *Abies lasiocarpa*, *Tsuga heterophylla* and *Thuja plicata*) in stands at 50 years of age. Data collected in Forest Health Aerial Overview Surveys in the years 1992, 1993 and 1994 were used to create an independent index of defoliation severity (Defoliation Severity Index, DSI). Based on estimates of living canopy cover, Forest Health Aerial Overviews Surveys assigned an annual damage classification rating, such as "moderate" or "severe" to defoliated parts of the landscape during the 1991-1994 outbreak (CFS and MoF 2000). These damage ratings and their duration were integrated to create an ordinal index with four classes of cumulative defoliation severity. MacLean and Ebert (1999), in studying eastern hemlock looper outbreaks, suggest that two years of moderate defoliation have a similar effect as one year of severe defoliation, so I make comparable assumptions of additive cumulative impacts here. Consequently, one year only of moderate defoliation was assigned a DSI score of 1, stands with two years of moderate defoliation or one year only of severe defoliation were assigned a DSI score of 2, stands with one year of moderate defoliation and one year of severe defoliation were assigned a score of 3, while DSI = 4 for stands with two years of severe defoliation. Nine sample plots which clearly had experienced a history of WHL did not have multi-year damage classification ratings from the Forest Health Overview Surveys, so these plots were assigned an index score that reflected the mapped severity according to the Pest Infestation polygons provided by B.C.'s Land and Resource Data Warehouse. Where both sources of information were available, those Pest Infestation polygons generally corresponded to the 1994 defoliation survey results, but could only be scored as DSI=1 or DSI=2, so may underestimate the disturbance severity experienced by those nine plots.

A second indicator of defoliation severity -- the proportion of dead stems per hectare -- was calculated using the number of dead stems (including fallen, leaning and snapped trees in

snag classes 3 to 5; Maser et al. 1979) and the number of live stems in sampled stands. Using the proportion of dead stems as an index of severity assumes that this is a measure of net canopy impact or "final" severity. This plays down the situation where some stems may have been defoliated for one or more years, but have since recovered fully or partially.

The damage classes reported in Forest Health Aerial Overviews Surveys were also used to infer their converse, namely the proportion of unaffected trees as documented during the 1992-1994 outbreak. With a damage class of "moderate" denoting 11-29% defoliation, its midpoint is 20% defoliation and its converse is implied to portray a forest stand that was 80% intact at that time; "severe" damage portrays 30-100% defoliation, with a midpoint of 65%, and a converse of 35% intact trees.

An index was developed to denote the relative recovery or deterioration of the forest canopy from the peak of the outbreak, as estimated at the time. An average Overstory Recovery Index (ORI_{ave}) divides percent live stems in 2012 by the mean of intact stem percentages inferred for 1992, 1993 and 1994, assuming 100% vigour of stands not mapped as moderately or severely defoliated in a particular year. High values of these ORI scores – more green trees now compared to the past -- indicate a higher level of tree recovery, while low ORI values denote poorer tree recovery at the plot or stand level.

"Competitive shrub cover" refers to the percent cover of shrubs considered competitive with tree regeneration and associated with soils that are higher in nitrates (as per Haeussler et al. 1990). These shrubs include *Rubus idaeus*, thimbleberry (*Rubus parviflorus* Nutt.), Sambucus racemosa and Oplopanax horridus. "Tall shrub cover" refers to cover of all nondwarf shrub species found in sampled stands.

2.4 Statistical analyses

To explore how overstory recovery is related to defoliation severity, ORI_{ave} scores were tested against cumulative damage class ratings (i.e., "moderate" or DSI=1, "moderate-moderate" or "severe" for which DSI=2; "moderate-severe" or DSI=3, and "severe-severe" or DSI=4) in a Spearman Rank correlation. This non-parametric test does not assume that variables are drawn from a normal distribution. All correlations were performed using Stata version 12.1 (Stata Corporation 2011). For significant correlations, linear least-squares regression was used to characterize the relationship. Significant results are shown in figures.

An exploratory Spearman Rank correlation analysis was done to test associations between the ORI_{ave} and 13 site variables (excluding canopy density) to explore how overstory recovery is associated with site variables.

To explore how basic understory attributes are associated with measured and inferred defoliation severity, Spearman Rank correlations were performed to test three understory recovery variables – shrub cover, total regeneration density and well-spaced regeneration density -- against two indices of 1990s WHL outbreak severity, the ordinal DSI and percent dead stems.

A Spearman Rank correlation analysis was done to test associations between understory recovery variables (shrub cover, total regeneration density and well-spaced regeneration density) against all 14 site variables. Where visual inspection revealed a unimodal or parabolic distribution, a quadratic term (x^2) was added to the regression model. Where log-transformed values of the dependent variable or the independent variable resulted in a higher R^2 value, only the regression based on the log-transformed variable is reported.

To examine understory plant community patterns and the relationships between species composition and site characteristics in defoliated stands in the ITR, redundancy analysis (RDA; Rao 1964, van den Wollenburg 1977) was performed. Redundancy analysis is a canonical ordination method, and is the direct extension of multiple regression to the modelling of multivariate response data (Legendre and Legendre 2012). All RDA analyses were conducted using CANOCO 5.0 (ter Braak and Smilauer 2012).

Redundancy analysis represents the variation of a data matrix in a reduced number of dimensions. A plant community data matrix composed of percent cover for all individual vascular plant and bryophyte species in defoliated stands was tested against an explanatory data matrix made up of site variables. Prior to RDA analysis, I removed from the plant community data matrix any species that occurred in fewer than 5% of plots in order to reduce noise and enhance the detection of relationships between community composition and site variables (McCune and Grace 2002).

Species gradient lengths are a measure of the heterogeneity in community composition along an ordination axis (McCune and Grace 2002, Lepš and Šmilauer 2003). To determine whether the plant community dataset was appropriate for a linear ordination method such as RDA, rather than a unimodal method, I used detrended correspondence analysis (DCA) in PC-ORD 6.07 (McCune and Mefford 2011) to determine the longest species gradient length. Plant community data had a gradient <3.0 standard deviation units long and thus was appropriate for a linear method (ter Braak and Smilauer 2002). A linear technique was also recommended by CANOCO 5.0 (ter Braak and Smilauer 2012).

For all multivariate plant community analysis, plant cover data were first converted using the Hellinger transformation:

$$Y'_{ij} = \sqrt{(Y_{ij}/Y_{i+})}$$

where Y'_{ij} = Hellinger transformed abundance value, Y_{ij} =% cover of a species at a site, i=sites (rows), j =species (columns), and Y_{i+} = row sums (Legendre and Gallagher 2001). The Hellinger transformation allows the use of Euclidean-based ordination methods such as RDA without having to deal with the problems associated with Euclidean distance (Legendre and Gallagher 2001).

To reduce the asymmetry of distributions of site variables and dampen the influence of outliers (Legendre and Legendre 2012), some of these variables were transformed where appropriate. Percent live stems and canopy density (both proportions) were transformed using arcsine square root, and elevation, steepness, live total basal area, mean annual temperature, mean annual precipitation and annual heat:moisture index were square root transformed. The variables slope position, radiation, soil nutrient regime, soil moisture index, site index and frost hazard were not transformed.

I used a modified forward selection procedure that corrects for the overestimation of the proportion of explained variance, which often occurs in forward selection (Blanchet et al. 2008). A 'global' test of the relation between the plant community and the whole set of 14 site variables was run using a constrained ordination using RDA (ter Braak and Smilauer 2012). The overall statistical significance of the whole model was evaluated using Monte Carlo permutation tests (n=999). Two stopping criteria used for the forward selection of variables were the model-adjusted R^2 and a variable retention permutation p-value (stopping significance value) of 0.05 (Blanchet et al. 2008).

Stepwise selected variables had to have variance inflation factors (VIF) < 10 (Borcard et al. 2011). Site variables were tested for multi-collinearity in Stata v. 12.1. Only mean annual temperature (MAT), mean annual precipitation (MAP) and annual heat:moisture index (AHM) were multicollinear (VIF>10). Mean annual precipitation was pulled out of the forward selection process in RDA because it was not significant and had a low percent contribution (<5%) to the regression model. Axis scores derived from the global RDA for plant community were graphed in order to examine relationships among all explanatory variables. A final parsimonious RDA model was run after stepwise selection of the combined data set. This process identified the smallest number of significant predictors necessary to

model plant community and regeneration trends. Final biplots (two RDA axis scores plotted orthogonally to each other) were created to display the results of the most parsimonious model.

Spearman Rank correlations were performed to explore how the proportions of competitive shrub cover (*Rubus idaeus*, *Oplopanax horridus*, *Rubus parviflorus* and *Sambucus racemosa*) and tall shrub cover (all shrub species except *Rubus pedatus* Sm.) associated with overall regeneration density (total and well-spaced), and regeneration densities of each tree species by size class (total and well-spaced). Where log-transformed values of the dependent variable or the independent variable resulted in a higher R^2 value, only the regression based on the log-transformed variable is reported.

Redundancy analysis was used also to examine relationships between environmental variables and the composition of the regenerating tree assemblage among defoliated stands in the ITR. This regeneration RDA followed the same methodology as the plant community RDA (i.e., treating size classes as well as species of tree regeneration in the manner analogous to individual plant species), including gradient length determination, transformation of variables and forward selection procedure.

In order to investigate possible vegetation trends in the plant community RDA analysis as related to defoliation severity, a Kruskal-Wallis analysis of variance was used to test the first three RDA axis scores against cumulative damage classification ratings. Spearman Rank correlations were used to evaluate how the proportion of total regeneration on coarse woody debris relates to both competitive and tall shrub cover, and how the individual proportions of tree species by size class on coarse woody debris related to both shrub groups. Availability of each substrate (coarse woody debris, forest floor, mineral soil) was not accounted for in this study and so it is not possible to quantitatively determine the relative importance of each substrate to regenerating trees in defoliated stands.

Cluster analysis is a tool used to objectively identify groups of sample units that are similar in composition (Peck 2010). A hierarchical cluster analysis was accomplished using PC-ORD 6.07 (McCune and Mefford 2011) to group defoliated stands in terms of their similarity based on the relative abundance of species in the understory. This analysis was produced using Sorensen/Bray-Curtis distance coefficients and a flexible beta linkage method (beta value of =-0.25), and was applied to cluster samples (stands), not species. Only understory species that occurred in more than 5% of the sampled stands were included. A dendrogram portraying multivariate compositional relatedness of stands is used to portray the output of this analysis.

A second examination of possible groupings among stands according to their recovery response was also undertaken. Using the plant community RDA biplot, stands were simply colour-coded according to their site series and the resulting output was scrutinized for any clustering among stands. Using the same technique, the regeneration RDA biplot was colourcoded in order to better visualize regeneration patterns by site series. Collectively, these

clustering techniques facilitated distinction of the two main understory development trajectories, namely dominance by shrubs or by regenerating trees.

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3.0 Results

3.1 Summary of site variables

Site variables measured at each plot are listed, described and summarized in Table 1. It is worth noting that those with the greatest variability (coefficient of variation, CV, > 30%) are steepness, live basal area, percent live stems, and frost hazard.

| Variable | Full variable name and | Measurement | Units | Mean | CV | Min. | Max. |
|------------|-------------------------------|-----------------------------|--|-------|------|------|-------|
| | description | method | | | (%) | | |
| elev | Elevation. Distance above | GPS unit | Metres | 837.6 | 12.6 | 653 | 1,145 |
| | mean sea level | (Magenan Meridian Basic) | | | | | |
| steepness | Steepness. Horizontal slope | Clinometer | % | 11.5 | 90.3 | 0 | 51 |
| | gradient | (Suunto PM5/360PC) | | | | | |
| slopepos | Slope position. Relative | Visual | Index | 1.8 | 25.3 | 1 | 3 |
| | mesoslope position (Banner | estimation in the | | | | | |
| | et al. 1993) | field and Google | | | | | |
| radiation | Radiation Potential annual | Equation $\# 1$ in | $M1 \mathrm{cm}^{-2} \mathrm{vr}^{-1}$ | 0.57 | 13.0 | 0.32 | 0.78 |
| Taulation | direct incident radiation | McCune and | IVIS CIII yI | 0.57 | 15.0 | 0.52 | 0.78 |
| | | Keon (2002) | | | | | |
| | | using folded | | | | | |
| | | aspect, slope and | | | | | |
| | | latitude, | | | | | |
| [| | collected in the | | | ĺ | | |
| | | field | | | | | |
| snr | Soil nutrient regime. A | From key in | Index | 4.4 | 23.4 | 2 | 0 |
| | relative scale of available | Delong (2003, 2007) | | | | | |
| ismr | Indexed Soil Moisture | Assigned index | Index | 53 | 16.8 | 3 | 8 |
| | Regime. A synthetic index | based on | | 0.0 | | | Ű |
| | of soil moisture regime, a | Drought | | | 1 | | |
| | relative scale of available | Assessment Tool | | | | | |
| | water for plant growth | (DeLong et al. | | | | | |
| | | 2011a) | | | | | |
| Site index | Site index. A measure of site | Estimates by site | m height at | 18.6 | 8.7 | 12.6 | 19.8 |
| | productivity | series, from | DU yrs. | | | | |
| | | (2011) | five-species | | | | |
| | | | mean (Tsuga | | | | |
| | | | heterophylla. | | | | |

Table 1. Study-wide summary of site variables measured at each plot (n=63).

| Variable | Full variable name and description | Measurement method | Units | Mean | CV (%) | Min. | Max. |
|----------------|---|--|---|-------|-----------|------|------|
| | | | Thuja plicata, Abies lasiocarpa, Picea glauca x engelmanii and Pinus contorta) | | | | |
| lba_tot | Live basal area. Live total basal area of all overstory tree species taken from centre of regeneration subplots | Wedge prism, basal area factor 4 | m²ha⁻¹ | 34.0 | 55.0 | 2 | 81.3 |
| %live stems | Percent live stems. Proportion of living stems of all live and dead overstory trees | Counted in the field in fixed area (400 m ²) plots | % | 49.3 | 48.4 | 5.2 | 92.1 |
| canopdens | Canopy density. The proportion of area that is covered by a crown of trees. | Spherical densiometer (Lemmon Model C) | % | 80.3 | 19.8 | 40.0 | 95.1 |
| frsthaz | Frost hazard rating | Assigned index based on Stand Level Frost Hazard Assessment and Management Tool (DeLong et al. 2011b) | Index | 2.14 | 40.0 | 1 | 4 |
| MAT | Mean annual temperature | For 1960-1999, interpolated using ClimateWNA ver. 4.71 (Wang et al. 2012) | °C | 3.0 | 11.2 | 1.7 | 3.6 |
| МАР | Mean annual precipitation | For 1960-1999, interpolated using ClimateWNA ver. 4.71 (Wang et al. 2012) | mm | 825.2 | 5.9 | 751 | 969 |
| АНМ | Annual heat:moisture index, (MAT+10)/(MAP/1000)) | For 1960-1999, interpolated using ClimateWNA ver. 4.71 (Wang et al. 2012) | Index | 15.8 | 6.1 | 13.7 | 17.3 |

3.2 Summary of overstory

A summary of overstory tree density is presented in Table 2. *Tsuga heterophylla* had the highest mean density among live and dead trees, while *Betula papyrifera* had the lowest mean density in sampled stands. Overstory basal area by species is displayed in Table 3 and shows that among live trees, *Thuja plicata* had the highest mean basal area and *Tsuga heterophylla* had the highest mean basal area among dead trees.

Figure 3 presents the current health class distribution of stems in sampled stands. Most living trees of all species are in the highest health class (have the highest percentage of live canopy), and *Tsuga heterophylla* has the highest mean number of stems in the highest decay class (fallen trees). Most dead trees of all species are in the lowest decay class (standing). Figure 4 shows mean DBH of live and dead stems by species. The mean DBH of dead *Tsuga heterophylla* was greater than that of live individuals, whereas the abundance of larger-stemmed *Thuja plicata* implies that they had greater WHL survivorship than stems with a lower DBH. This information is further divided to display mean DBH of live and dead stems by subzone (ICHvk2 and ICHwk3: Figures 5a and 5b, respectively).

Table 2. Overstory density by species. All dead trees are trees that likely died directly or indirectly from the WHL defoliation in the 1990s. Older dead trees (snag classes 6 and greater; Maser et al. 1979) were excluded from tree counts in this study. Mean density values are from tree counts in 0.04 ha plots (n=63).

| | Overstory density (stems ha ⁻¹) | | | | | | |
|------------|---|--------|-------|------|-------|-----------------------|-----------------------|
| Live | mean | median | SD | min. | max | 1st quartile (25%) | 3rd quartile (75%) |
| Tsuga | 159.1 | 50.0 | 192.7 | 0.0 | 775.0 | 25.0 | 225.0 |
| Thuja | 121.8 | 75.0 | 137.0 | 0.0 | 775.0 | 25.0 | 200.0 |
| Abies | 70.2 | 0.0 | 151.3 | 0.0 | 800.0 | 0.0 | 50.0 |
| Picea | 49.2 | 25.0 | 74.7 | 0.0 | 450.0 | 0.0 | 75.0 |
| Betula | 18.7 | 0.0 | 55.4 | 0.0 | 300.0 | 0.0 | 0.0 |
| Subtotal | 419.0 | | | | | | |
| Dead | | | | | | | |
| Tsuga | 182.9 | 150.0 | 188.4 | 0.0 | 975.0 | 50.0 | 250.0 |
| Thuja | 89.7 | 75.0 | 93.8 | 0.0 | 375.0 | 25.0 | 125.0 |
| Abla | 83.3 | 50.0 | 93.8 | 0.0 | 450.0 | 25.0 | 100.0 |
| Picea | 9.5 | 0.0 | 15.8 | 0.0 | 75.0 | 0.0 | 25.0 |
| Betula | 4.0 | 0.0 | 15.0 | 0.0 | 75.0 | 0.0 | 0.0 |
| Subtotal | 369.4 | | | | | | |
| % of total | 46.9 | | | | | | |

Table 3. Overstory basal area by species. All dead trees are trees that likely died directly or indirectly from the WHL defoliation in the 1990s. Old trees (snag classes 6 and greater; Maser et al. 1979) were excluded from tree counts in this study. Basal area values are from wedge prism (BAF 4) sweeps, three per each 0.04 ha plot, (n=63) averaged for each plot.

| | Overstory basal area (m²/ha) | | | | | | |
|------------|------------------------------|--------|------|------|------|-----------------------|-----------------------|
| Live | mean | median | SD | min. | max | 1st quartile (25%) | 3rd quartile (75%) |
| Tsuga | 8.7 | 4.7 | 10.3 | 0.0 | 41.3 | 1.3 | 14.3 |
| Thuja | 17.4 | 10.0 | 17.3 | 0.0 | 72.0 | 2.7 | 26.3 |
| Abies | 3.1 | 1.3 | 4.5 | 0.0 | 18.7 | 0.0 | 4.0 |
| Picea | 4.0 | 2.0 | 5.4 | 0.0 | 26.0 | 0.0 | 6.0 |
| Betula | 0.4 | 0.0 | 1.0 | 0.0 | 4.0 | 0.0 | 0.0 |
| Subtotal | 33.6 | | | | | | |
| Dead | | | | | | | |
| Tsuga | 7.6 | 5.3 | 8.7 | 0.0 | 38.7 | 1.3 | 11.3 |
| Thuja | 7.4 | 4.7 | 8.1 | 0.0 | 36.0 | 1.0 | 11.0 |
| Abla | 2.7 | 2.0 | 2.9 | 0.0 | 11.3 | 0.3 | 4.0 |
| Picea | 0.5 | 0.0 | 1.0 | 0.0 | 3.3 | 0.0 | 0.7 |
| Betula | 0.0 | 0.0 | 0.1 | 0.0 | 0.7 | 0.0 | 0.0 |
| Subtotal | 18.2 | | | | | | |
| % of total | 35.1 | | | | | | |



Figure 3. Mean live stems/ha (above '0' line) and dead stems/ha (below '0' line) tallied according to their health (if live) and decay (if dead) class. Health classes go from highest to lowest percentage of live canopy (1=76-100%, 2=51-75%, 3=26-50%, 4=0.1-25%). Decay classes go from least decayed to most decayed (1=standing, 2=leaning, 3=snapped, 4=fallen). Dead trees are trees that likely died directly or indirectly from the WHL defoliation in the 1990s. Coarse woody debris classes 4 nd 5 and snag classes 6 and up (Maser et al. 1979) were excluded from this count.



Figure 4. Mean diameter at breast height of live and dead stems by species (mean, +/- SE).





Figure 5. Tree species by diameter at breast height (mean, +/- SE) by subzone: a) live; and b) dead.

3.3 Summary of understory

3.3.1 Plant community

Eighty-seven species of vascular and non-vascular plants were found in plots sampled in this study. Table 4 presents a list of the plant species encountered, with mean abundance and frequency by species. Five trees, 19 shrubs, 41 forbs, five ferns, two grasses, one sedge, 10 mosses and one clubmoss species were identified across the 63 plots sampled. In terms of frequency, the most common tree species was *Tsuga heterophylla*, with germinants and/or seedlings and/or saplings growing in 97% of plots. The next most common tree species was *Thuja plicata*, which was present in 94% of plots.

The most common shrubs were five-leaved bramble (*Rubus pedatus* Sm.), which was found in 97% of plots, and *Oplopanax horridus*, which occurred in 95% of plots. Rosy twistedstalk (*Streptopus lanceolatus* (Aiton) Reveal var. *curvipes* (Vail) Reveal) was found in all plots, and other common herbs were foamflower (*Tiarella* spp.) and bunchberry (*Cornus canadensis* L.), found in 98% and 97% of plots, respectively. Oak fern (*Gymnocarpium dryopteris* (L.) Newman) and lady fern (*Athyrium filix-femina* (L.) Roth ssp. *cyclosorum* (Rupr.) C. Chr.) were the most common ferns, appearing in 100% and 86% of plots, respectively. Knight's plume moss (*Ptilium crista-castrensis* (Hedw.) De Not.) occurred in 90% of plots and red-stemmed feather moss (*Pleurozium schreberi* (Brid.) Mitt.) occurred in 87% of plots. All plots sampled had some regenerating trees in the understory. *Tsuga heterophylla* was regenerating in 97% of plots and *Thuja plicata* regeneration was found in 94% of plots. *Abies lasiocarpa* and *Picea engelmannii* x *glauca* were less common, occurring in 71% and 43% of plots, respectively. Forest floor was the most frequent substrate used by regenerating trees in all plots. Coarse woody debris was used as a substrate by regenerating trees in 96% of plots. Exposed mineral soil, typically resulting from tree tip-ups, was a substrate used by regenerating trees in fewer than 5% of plots. As a size class, saplings (>130 cm tall) were the most frequent, occurring in all plots, whereas germinants (<10 cm tall) were the least frequent, occurring in 43% of plots. Among all size classes and species on any substrate, *T. heterophylla* saplings on forest floor were found in the most plots (81%).

Table 4. All plant species, listed by functional group, found in stands sampled for this study (n=63), with species codes for plant community RDA output interpretation and cluster analysis interpretation. Presented in this table are the mean, coefficient of variation, median, minimum and maximum values for percent cover (abundance values) of each species. Species highlighted in blue occurred in fewer than 5% of plots sampled and were thus not included in the plant community RDA analysis or the cluster analysis. Three lichen genera found in plots are underlined in this list but this functional group was not reliably sampled in this study.

| Species | code | Mean | C.V. | Med. | Min. | Max. |
|----------------------------|-------|------|------|------|------|-------|
| Trees | | | | | | |
| Abies lasiocarpa | tabla | 1.21 | 2.22 | 0.17 | 0.00 | 16.83 |
| Betula papyrifera | tbepa | 0.34 | 3.24 | 0.00 | 0.00 | 6.67 |
| Picea engelmannii x glauca | tpigl | 0.45 | 2.31 | 0.00 | 0.00 | 5.00 |
| Thuja plicata | tthpl | 2.81 | 1.46 | 1.33 | 0.00 | 23.00 |
| Tsuga heterophylla | ttshe | 6.90 | 1.26 | 3.08 | 0.00 | 34.00 |
| Shrubs | | | | | | |
| Acer glabrum | sacgl | 1.09 | 3.52 | 0.00 | 0.00 | 27.00 |
| Alnus tenuifolia | | 0.03 | 5.77 | 0.00 | 0.00 | 1.33 |
| Amelanchier alnifolia | | 0.01 | 6.52 | 0.00 | 0.00 | 0.67 |
| Cornus sericea | | 0.01 | 7.94 | 0.00 | 0.00 | 0.50 |
| Lonicera involucrata | sloin | 0.80 | 2.65 | 0.00 | 0.00 | 11.00 |

| Species | code | Mean | C.V. | Med. | Min. | Max. |
|-------------------------|---------|-------|------|------|------|-------|
| Menziesia ferruginea | smefe | 0.28 | 2.54 | 0.00 | 0.00 | 3.33 |
| Oplopanax horridus | sopho | 17.31 | 1.08 | 9.67 | 0.00 | 66.67 |
| Ribes glandulosum | srigl | 0.25 | 2.33 | 0.00 | 0.00 | 3.50 |
| Ribes lacustre | srila | 2.08 | 1.23 | 1.08 | 0.00 | 13.00 |
| Rubus idaeus | sruid | 2.31 | 1.51 | 0.67 | 0.00 | 15.50 |
| Rubus parviflorus | srupa | 3.70 | 2.02 | 0.33 | 0.00 | 38.00 |
| Rubus pedatus | srupe | 2.25 | 1.28 | 1.50 | 0.00 | 15.50 |
| Rubus pubescens | | 0.12 | 6.39 | 0.00 | 0.00 | 5.83 |
| Sambucus racemosa | ssara | 1.35 | 1.99 | 0.13 | 0.00 | 15.17 |
| Sorbus scopulina | ssosc | 0.11 | 2.93 | 0.00 | 0.00 | 2.00 |
| Vaccinium membranaceum | svame | 0.48 | 2.00 | 0.17 | 0.00 | 5.92 |
| Vaccinium ovalifolium | svaov | 2.55 | 1.53 | 0.92 | 0.00 | 20.33 |
| Vibernum edule | svied | 0.11 | 3.87 | 0.00 | 0.00 | 2.50 |
| Herbs | | | | | | |
| Actea rubra | hacru | 0.40 | 2.39 | 0.00 | 0.00 | 4.50 |
| Aquilegia formosa | | 0.01 | 7.94 | 0.00 | 0.00 | 0.50 |
| Aralia nudicaulis | harnu | 1.19 | 1.88 | 0.07 | 0.00 | 9.17 |
| Arnica spp. | | 0.00 | 7.94 | 0.00 | 0.00 | 0.03 |
| Aruncus dioicus | hardi | 0.23 | 3.24 | 0.00 | 0.00 | 4.00 |
| Asarum caudatum | | 0.01 | 5.23 | 0.00 | 0.00 | 0.23 |
| Aster spp. | | 0.02 | 4.33 | 0.00 | 0.00 | 0.50 |
| Chimaphila umbellata | hchum | 0.02 | 4.46 | 0.00 | 0.00 | 0.75 |
| Circaea alpina | hcial | 1.04 | 2.36 | 0.00 | 0.00 | 11.83 |
| Cirsium palustre | hcipa | 0.20 | 3.29 | 0.00 | 0.00 | 4.33 |
| Clintonia uniflora | hclun | 0.99 | 1.67 | 0.08 | 0.00 | 7.17 |
| Cornus canadensis | hcoca | 5.36 | 1.05 | 4.00 | 0.00 | 31.00 |
| Epilobium angustifolium | hepan | 1.52 | 2.70 | 0.00 | 0.00 | 22.83 |
| Equisetum arvense | heqar | 0.82 | 2.53 | 0.00 | 0.00 | 10.17 |
| Equisetum pratense | | 0.03 | 7.94 | 0.00 | 0.00 | 1.67 |
| Equisetum sylvaticum | heqsi | 1.07 | 1.81 | 0.33 | 0.00 | 9.83 |
| Galium triflorum | hgatr | 0.76 | 1.41 | 0.18 | 0.00 | 3.83 |
| Geum macrophyllum* | | 0.02 | 4.98 | 0.00 | 0.00 | 0.75 |
| Goodyeraa oblongifolia | hgoob | 0.09 | 3.89 | 0.00 | 0.00 | 2.50 |
| Impatiens noli-tangere | | 0.01 | 7.94 | 0.00 | 0.00 | 0.67 |
| Linnaea borealis | hlibo | 0.45 | 2.58 | 0.00 | 0.00 | 6.33 |
| Listera cordata | hlico | 0.08 | 4.10 | 0.00 | 0.00 | 2.42 |
| Lysichiton americanus | | 0.00 | 7.54 | 0.00 | 0.00 | 0.25 |
| Maianthemum racemosa | hmara | 0.46 | 1.69 | 0.07 | 0.00 | 4.75 |
| Mitella spp. | hmitell | 0.29 | 3.24 | 0.00 | 0.00 | 4.67 |
| Moneses uniflora | hmoun | 0.02 | 3.06 | 0.00 | 0.00 | 0.37 |
| Orthilia secunda | horse | 0.23 | 2.02 | 0.00 | 0.00 | 2.33 |

| Species | code | Mean | C.V. | Med. | Min. | Max. |
|-----------------------------------|---------|------|--------|------|------|-------|
| Petasites palmatus | | 0.03 | 5.57 | 0.00 | 0.00 | 1.08 |
| Platanthera dilatata | | 0.00 | 7.94 | 0.00 | 0.00 | 0.08 |
| Platanthera orbiculata | | 0.00 | 5.60 | 0.00 | 0.00 | 0.08 |
| Pyrola asarifolia | hpyas | 0.28 | 3.55 | 0.00 | 0.00 | 6.67 |
| Pyrola grandiflora | | 0.01 | 5.68 | 0.00 | 0.00 | 0.20 |
| Senecio triangularis | | 0.02 | 7.94 | 0.00 | 0.00 | 1.00 |
| <i>Spiraea</i> spp. | | 0.24 | 6.10 | 0.00 | 0.00 | 10.75 |
| Streptopus amplexifolius | hstam | 0.33 | 1.53 | 0.13 | 0.00 | 2.17 |
| Streptopus roseus | hstro | 3.68 | 0.95 | 2.67 | 0.05 | 16.67 |
| Thalictrum occidentale | | 0.00 | 7.94 | 0.00 | 0.00 | 0.07 |
| Tiarella spp. | htiarel | 4.86 | 1.01 | 2.83 | 0.00 | 19.00 |
| Valeriana sitchensis | | 0.03 | 7.94 | 0.00 | 0.00 | 1.83 |
| Veratrum viride | hvevi | 0.64 | 2.27 | 0.00 | 0.00 | 6.42 |
| Viola spp. | hviola | 0.17 | 2.95 | 0.00 | 0.00 | 3.17 |
| Ferns, fern allies, mosses, grass | ses and | | | | | |
| lichens | | | ······ | | | |
| Athyrium filix-femina | fatfi | 6.41 | 1.24 | 2.83 | 0.00 | 31.67 |
| Botrychium virginianum | | 0.00 | 7.94 | 0.00 | 0.00 | 0.17 |
| Calamagrostis canadensis | gcaca | 0.13 | 2.31 | 0.00 | 0.00 | 1.58 |
| <u>Cladina spp.</u> | | | | | | |
| <u>Cladonia spp.</u> | | | | | | |
| Dicranum polysetum | mdipo | 0.11 | 2.36 | 0.00 | 0.00 | 1.67 |
| Dryopteris expansa | fdrex | 2.02 | 1.32 | 0.67 | 0.00 | 9.50 |
| Glyceria elata | gglel | 0.08 | 3.67 | 0.00 | 0.00 | 2.00 |
| Gymnocarpium dryopteris | fgydr | 7.41 | 1.13 | 3.83 | 0.13 | 46.67 |
| Hylocomnium splendens | mhysp | 9.15 | 2.25 | 1.00 | 0.00 | 86.67 |
| Lycopodium annotinum | mlyan | 0.81 | 2.43 | 0.07 | 0.00 | 14.00 |
| Mnium spp. | mmnium | 0.72 | 3.21 | 0.03 | 0.00 | 17.00 |
| <u>Peltigera</u> spp. | | | | | | |
| Pleurozium schreberi | mplsc | 1.78 | 1.33 | 0.83 | 0.00 | 11.00 |
| Polytrichum juniperum | mpoju | 0.04 | 3.57 | 0.00 | 0.00 | 0.67 |
| Ptilium crista-castrensis | mptcr | 2.34 | 1.23 | 1.33 | 0.00 | 12.00 |
| Racomitrium spp. | | 0.01 | 7.03 | 0.00 | 0.00 | 0.67 |
| Rhytidiadelphus triquetrus | mrhtr | 0.94 | 1.92 | 0.17 | 0.00 | 9.33 |
| Sphagnum spp. | msphag | 0.22 | 4.09 | 0.00 | 0.00 | 6.00 |
| Thelypteris phegopteris | fthph | 0.60 | 2.78 | 0.00 | 0.00 | 10.17 |

*Species mistakenly left out of plant community RDA

Trees regenerating in defoliated stands of the ITR were mostly *Tsuga heterophylla*, followed by *Thuja plicata* (Table 5) in both total and well-spaced tallies. The mean number of germinants of *Tsuga heterophylla* was greater than all other species. Germinants, as a size class, constituted the majority of regeneration.

Table 6 summarizes total regeneration by species, size class and substrate. There was a greater mean number of germinants on coarse woody debris (CWD) than other size classes, and *Tsuga heterophylla* as a species was found in higher densities on this substrate than other species. Mineral soil was the least-used substrate for all size classes and tree species. These general findings were similar for well-spaced regeneration (Table 7).

| | | | Reg | eneration der | nsity (stern | s ha ⁻¹) | |
|----------|-------------|---------|-------|---------------|--------------|----------------------|-------|
| | | Germ | inant | Seed | ling | Sapl | ing |
| | | Mean | S.E. | Mean | S.E. | Mean | S.E. |
| Tsuga | Total | 992.6 | 514.3 | 627.5 | 158.5 | 649.2 | 92.8 |
| | Well-spaced | 255.0 | 123.3 | 171.4 | 46.8 | 322.2 | 43.6 |
| Thuja | Total | 159.8 | 122.2 | 346.0 | 62.4 | 267.7 | 43.6 |
| | Well-spaced | 23.3 | 15.2 | 120.6 | 22.4 | 157.7 | 27.7 |
| Abies | Total | 5.3 | 3.5 | 221.2 | 47.3 | 216.4 | 56.4 |
| | Well-spaced | 2.1 | 1.5 | 78.3 | 16.1 | 117.5 | 30.9 |
| Picea | Total | 4.2 | 2.6 | 41.3 | 13.6 | 36.5 | 11.1 |
| | Well-spaced | 2.1 | 1.5 | 18.0 | 6.1 | 23.8 | 7.7 |
| All | | | | | | | |
| conifers | Total | 1,161.9 | 534.5 | 1,236.0 | 187.8 | 1,169.8 | 123.6 |
| | Well-spaced | 282.5 | 125.3 | 388.4 | 61.3 | 621.2 | 59.2 |

Table 5. Total and well-spaced regeneration by species and size class (n=63).

| | Mean | C.V. | Min. | Max. |
|---------------------|---------|------|------|--------|
| Tsuga germinants | 992.6 | 4.1 | 0 | 28,867 |
| Tsuga seedlings | 627.5 | 2.0 | 0 | 8,267 |
| Tsuga saplings | 649.2 | 1.1 | 0 | 2,600 |
| Thuja germinants | 159.8 | 6.1 | 0 | 7,600 |
| Thuja seedlings | 346.0 | 1.4 | 0 | 2,600 |
| Thuja saplings | 267.7 | 1.3 | 0 | 1,733 |
| Abies germinants | 5.3 | 5.2 | 0 | 200 |
| Abies seedlings | 221.2 | 1.7 | 0 | 2,333 |
| Abies saplings | 216.4 | 2.1 | 0 | 2,800 |
| Picea germinants | 4.2 | 4.8 | 0 | 133 |
| Picea seedlings | 41.3 | 2.6 | 0 | 733 |
| Picea saplings | 36.5 | 2.4 | 0 | 533 |
| Germinants on CWD | 1,130.2 | 3.7 | 0 | 29,000 |
| Germinants on FF | 31.7 | 2.9 | 0 | 467 |
| Germinants on MS | 0.0 | n/a | 0 | 0 |
| Seedlings on CWD | 644.4 | 1.7 | 0 | 6,333 |
| Seedlings in FF | 590.5 | 1.1 | 0 | 2,800 |
| Seedlings on MS | 1.1 | 7.9 | 0 | 67 |
| Saplings on CWD | 448.1 | 0.9 | 0 | 1,433 |
| Saplings on FF | 720.6 | 1.0 | 0 | 2,833 |
| Saplings on MS | 1.1 | 7.9 | 0 | 67 |
| Tsuga on CWD | 1,680.4 | 2.5 | 0 | 28,900 |
| <i>Tsuga</i> on FF | 586.8 | 1.1 | 0 | 2,900 |
| Tsuga on MS | 2.1 | 5.6 | 0 | 67 |
| <i>Thuja</i> on CWD | 366.1 | 2.6 | 0 | 7,333 |
| <i>Thuja</i> on FF | 407.4 | 1.3 | 0 | 2,667 |
| <i>Thuja</i> on MS | 0.0 | n/a | 0 | 0 |
| Abies on CWD | 123.3 | 1.8 | 0 | 1,267 |
| Abies on FF | 319.6 | 1.9 | 0 | 3,867 |
| Abies on MS | 0.0 | n/a | 0 | 0 |
| Picea CWD | 52.9 | 3.0 | 0 | 1,133 |
| Picea on FF | 29.1 | 2.2 | 0 | 300 |
| Picea on MS | 0.0 | n/a | 0 | 0 |
| All conifers | | | | |
| Germinants | 1,161.9 | 3.6 | 0 | 29,000 |
| Seedlings | 1,235.9 | 1.2 | 0 | 8,867 |
| Saplings | 1,169.8 | 0.8 | 33 | 4,267 |
| On CWD | 2,222.7 | 1.9 | 0 | 29,200 |
| On FF | 1,342.8 | 0.8 | 33 | 5,300 |
| On MS | 2.1 | 5.5 | 0 | 67 |

Table 6. Total regeneration summaries by species, size class and substrate. All numbers are in stems/ha, and were obtained by tally.

| | Mean | C.V. | Min. | Max. |
|------------------|-------|------|------|-------|
| Tsuga germinants | 255.0 | 3.8 | 0 | 6,867 |
| Tsuga seedlings | 171.4 | 2.2 | 0 | 2,200 |
| Tsuga saplings | 322.2 | 1.1 | 0 | 1,267 |
| Thuja germinants | 23.3 | 5.2 | 0 | 933 |
| Thuja seedlings | 120.6 | 1.5 | 0 | 933 |
| Thuja saplings | 157.7 | 1.4 | 0 | 1,167 |
| Abies germinants | 2.1 | 5.6 | 0 | 67 |
| Abies seedlings | 78.3 | 1.6 | 0 | 667 |
| Abies saplings | 117.5 | 2.1 | 0 | 1,500 |
| Picea germinants | 2.1 | 5.6 | 0 | 67 |
| Picea seedlings | 18.0 | 2.7 | 0 | 267 |
| Picea saplings | 23.8 | 2.6 | 0 | 400 |
| All conifers | | | | |
| Germinants | 282.5 | 3.5 | 0 | 6,933 |
| Seedlings | 388.4 | 1.2 | 0 | 2,600 |
| Saplings | 621.2 | 0.7 | 0 | 2,266 |

Table 7. Well-spaced regeneration summaries by species and size class. All numbers are in stems/ha, and were obtained by tally.

3.4 Overstory recovery

3.4.1 Effect of outbreak severity and site variables

There was a significant relationship between overstory recovery (ORI_{ave}) and defoliation severity (DSI) in defoliated stands ($r_s = 0.35$, P=0.004). Figure 6 shows that overstory recovery was greatest in stands with a more severe outbreak history. There was a significant negative correlation between the ORI_{ave} and site index ($r_s = -0.39$, P=0.001; Table 8). Figure 7 shows that overstory recovery was greatest in stands with lower site productivity.



Figure 6. Scatterplot with linear least-squares regression line relating Overstory Recovery Index (ORI_{ave}) to Defoliation Severity Index (DSI) and the Overstory Recovery Index (ORI_{ave}). y=0.12x + 0.36, $R^2=0.14$, p=0.002.

| ····· | 0 | RI _{ave} |
|------------------------------|----------------|-------------------|
| | r _s | р |
| elevation | -0.1699 | 0.1831 |
| site index | -0.3913 | 0.0015* |
| steepness | -0.1940 | 0.1277 |
| slope position | 0.0374 | 0.7713 |
| radiation | -0.0626 | 0.6257 |
| soil nutrient regime | -0.0766 | 0.5508 |
| indexed soil moisture regime | 0.0532 | 0.6790 |
| frost hazard | 0.0579 | 0.6520 |
| mean annual temperature | -0.0941 | 0.4632 |
| mean annual precipitation | 0.2361 | 0.0625 |
| annual heat:moisture index | -0.2164 | 0.0884 |
| | | |

Table 8. Spearman's correlations between Overstory Recovery Index (ORI_{ave}) and site variables.

*Correlation is significant at $\alpha = 0.05$.



Figure 7. Scatterplot with linear least-squares regression line relating Overstory Recovery Index (ORI_{ave}) to site index. y=-0.09x + 2.47, $R^2=0.18$, p<0.001.

3.5 Understory recovery

3.5.1 Effect of outbreak severity

There was no relationship between shrub cover and damage class as defined by the Defoliation Severity Index (DSI), nor between either of the two groups of regeneration density (total and well-spaced) and the DSI. Shrub cover increased with the proportion of dead stems ($r_s = 0.46$, p<0.001), while in contrast, both total and well-spaced regeneration densities were negatively associated with the proportion of dead stems ($r_s = -0.34$, p=0.006; Table 9).

| DS | SI | % dead stems | | |
|----------------|--------|--|--|--|
| r _s | P | rs | P | |
| -0.0582 | 0.6504 | 0.4645 | < 0.001* | |
| 0.0093 | 0.9426 | -0.3445 | 0.005* | |
| -0.0165 | 0.8979 | -0.3415 | 0.006* | |
| | Ds | DSI <u>rs</u> <u>P</u> -0.0582 0.6504 0.0093 0.9426 -0.0165 0.8979 | $\begin{array}{c c c c c c c c c c c c c c c c c c c $ | |

Table 9. Spearman's correlations between three understory recovery responses and two indices of defoliation severity, the Defoliation Severity Index (DSI) and the proportion of dead stems.

*Correlation is significant at $\alpha = 0.05$.

3.5.2 Effect of site variables

There was a significant positive relationship between shrub cover and site index ($r_s = 0.70$, p<0.001) and slope steepness ($r_s = 0.42$, p<0.001), and a significant negative relationship with canopy density ($r_s = -0.56$, p<0.001; Table 10). On the other hand, there are indications that shrub cover peaks under conditions of 50% to 90% canopy density (Figure 8a) and less steep sites (Figure 8b). Perhaps the most practical revelation of this analysis is that shrub cover appears to be at a minimum at site index 16 (Figure 8c), although the lack of shrub cover data points for lower site indices suggests that this result should be interpreted cautiously.

Surprisingly, total regeneration density was positively associated with canopy density (r_s =0.46, p<0.001; Figure 9a) and negatively associated with site index (r_s =-0.34, p=0.006; Figure 9b). A regression analysis confirms that total regeneration decreases with site index, however, this variable explains little of the variation in total regeneration density (R^2 =0.06).

Well-spaced regeneration was similarly correlated with canopy density in a positive manner ($r_s = 0.44$, p<0.001), and also with annual heat:moisture index ($r_s = 0.29$, p=0.018), and

negatively associated with site index ($r_s = -0.33$, p=0.006) and slope steepness ($r_s = -0.27$, p=0.03). There was more well-spaced regeneration on sites of lower steepness (Figure 10a) and on warmer sites (Figure 10b). Again, well-spaced regeneration appears to decrease with site index (Figure 10c) and to increase with canopy density (Figure 10d).

Relationships between tree regeneration densities and shrub cover are reported later in this chapter.

| | % Shrub cover | | Total regeneration (stems ha ⁻¹) | | Well-spaced regeneration (stems ha ⁻¹) | |
|----------------------------------|----------------|---------|--|---------|--|---------|
| | | | | | | |
| | r _s | р | r _s | р | r _s | р |
| elevation | -0.0875 | 0.4953 | -0.1227 | 0.3382 | -0.0592 | 0.6449 |
| site index | 0.7070 | <0.001* | -0.3413 | 0.0062* | -0.3369 | 0.0069* |
| steepness | 0.4252 | <0.001* | -0.2184 | 0.0854 | -0.2726 | 0.0307* |
| slope position | -0.1617 | 0.2054 | -0.1414 | 0.2691 | -0.0891 | 0.4873 |
| radiation | -0.1335 | 0.2969 | -0.0852 | 0.5067 | -0.0150 | 0.9069 |
| soil nutrient regime | 0.1428 | 0.2641 | 0.0899 | 0.4835 | 0.1170 | 0.3610 |
| indexed soil moisture regime | 0.0281 | 0.8269 | 0.1169 | 0.3616 | 0.1467 | 0.2512 |
| canopy density | -0.5645 | <0.001* | 0.4646 | <0.001* | 0.4427 | <0.001* |
| frost hazard | -0.0725 | 0.5723 | 0.0468 | 0.7158 | 0.0873 | 0.4963 |
| mean annual temperature | -0.0492 | 0.7016 | 0.1602 | 0.2099 | 0.1469 | 0.2506 |
| mean annual precipitation | 0.0509 | 0.6922 | -0.1193 | 0.3515 | -0.2396 | 0.0585 |
| annual heat:moisture index | -0.0940 | 0.4638 | 0.1892 | 0.1376 | 0.2963 | 0.0184* |

Table 10. Spearman's correlations between understory recovery variables and site variables.

*Correlation is significant at $\alpha = 0.05$.







Figure 8. Scatterplots with linear least-squares regression lines for competitive shrub cover as a function of: a) canopy density; b) steepness; and c) site index. a) $y = -0.05x^2 + 7.386x - 202.02$, $R^2 = 0.32$, p=0.003; b) log y= 0.027x + 0.66, $R^2=0.11$, p=0.007; c) log y=0.37x - 6.04, $R^2=0.51$, p<0.001.



Figure 9. Scatterplots with linear least-squares regression lines for total regeneration density as a function of: a) canopy density; and b) site index. a) $\log y= 0.009x + 2.55$, R²=0.13, p=0.002; b) $\log y=-0.06x + 4.56$, R²=0.06, p=0.04.





a)

7000



Figure 10. Scatterplots with linear least-squares regression lines for well-spaced regeneration density as a function of: a) steepness; b) annual heat: moisture index; c) site index; and d) canopy density. a) log y=-0.01x + 3.09, R²=0.09, p=0.01; b) log y=0.14x + 0.64, R²=0.15, p=0.001; c) log y=-0.06x + 4.20, R²=0.08, p=0.02; d) log y= 0.01x + 2.29, R²=0.13, p=0.003.

3.5.3 Plant community

An overall test of significance in the RDA showed that the canonical relationship between species composition and the explanatory variables was highly significant (p=0.001 after 999 permutations; pseudo-F=3.3 on all axes), meaning that there was a relationship between the explanatory variables and plant community composition. Table 11 shows the explanatory influence of each variable and its contribution to the model.

The forward selection process identified nine of the 14 predictors as a sufficient subset: site index, total live basal area, index of soil moisture, slope position, MAT, AHM, steepness, percent live stems and soil nutrient regime (Table 12). I included these nine variables in the final constrained RDA analysis (Table 13). The first two axes summarize about 26% of the variation in the plant community data from defoliated stands. Only these two axes are represented in correlation biplots (Figures 11a and 11b).

The nine site variables accounted for 43.1% of the total variation in the plant community of defoliated stands. The explained variation (adj. R^2) of this final model (which included all the site variables) was 33.5% (pseudo-F=4.5, p=0.001).
Table 11 a) Summary of the independent effects of all individual explanatory variables on overall understory plant community composition; b) Summary of the conditional effect of each predictor, representing the variation and significance explained by a predictor after accounting for the effect of the predictors placed above it in the list. The predictors were chosen in the order of their decreasing explained variation.

| a) Independent Term Effects | | | |
|------------------------------|------------|----------|-------|
| Variable | Explains % | pseudo-F | p |
| site index | 16.6 | 12.2 | 0.001 |
| canopy density | 8.2 | 5.5 | 0.001 |
| % live stems (all) | 7.2 | 4.7 | 0.001 |
| total live basal area | 6.3 | 4.1 | 0.001 |
| steepness | 5.9 | 3.8 | 0.002 |
| annual heat:moisture index | 4.5 | 2.9 | 0.008 |
| slope position | 4.1 | 2.6 | 0.016 |
| frost hazard | 3.7 | 2.3 | 0.027 |
| elevation | 3.6 | 2.3 | 0.024 |
| mean annual temperature | 3.5 | 2.2 | 0.025 |
| mean annual precipitation | 3.4 | 2.1 | 0.027 |
| soil nutrient regime | 3.0 | 1.9 | 0.057 |
| indexed soil moisture regime | 2.8 | 1.7 | 0.073 |
| radiation | 1.8 | 1.1 | 0.284 |

| b) Conditional Term Effects: | | | |
|------------------------------|------------|----------|-------|
| Variable | Explains % | pseudo-F | р |
| site index | 16.6 | 12.2 | 0.001 |
| total live basal area | 5.5 | 4.2 | 0.001 |
| indexed soil moisture regime | 4.3 | 3.5 | 0.001 |
| slope position | 3.9 | 3.2 | 0.001 |
| mean annual temperature | 3.4 | 2.9 | 0.002 |
| annual heat:moisture index | 2.7 | 2.4 | 0.003 |
| steepness | 2.7 | 2.5 | 0.010 |
| % live stems (all) | 2.1 | 1.9 | 0.021 |
| soil nutrient regime | 1.9 | 1.8 | 0.041 |
| mean annual precipitation | 1.2 | 1.2 | 0.260 |
| elevation | 1.1 | 1.1 | 0.347 |
| radiation | 1.1 | 1.0 | 0.416 |
| frost hazard | 1.0 | 0.9 | 0.498 |
| canopy density | 1.1 | 1.0 | 0.435 |

| Variable | Explains % | Contribution % | pseudo-F | р |
|------------------------------|------------|-----------------------|----------|-------|
| site index | 16.6 | 34.2 | 12.2 | 0.001 |
| total live basal area | 5.5 | 11.3 | 4.2 | 0.001 |
| indexed soil moisture regime | 4.3 | 8.9 | 3.5 | 0.002 |
| slope position | 3.9 | 7.9 | 3.2 | 0.001 |
| mean annual temperature | 3.4 | 7 | 2.9 | 0.002 |
| annual heat:moisture index | 2.7 | 5.5 | 2.4 | 0.001 |
| steepness | 2.7 | 5.6 | 2.5 | 0.005 |
| % live stems (all) | 2.1 | 4.3 | 1.9 | 0.028 |
| soil nutrient regime | 1.9 | 3.9 | 1.8 | 0.031 |

Table 12. Summary of plant community ordination forward selection. Variables are in selection order and the model adjusted R^2 after inclusion of each successive variable is shown. Only significant predictors (p<0.05) were retained.

Table 13. Summary of plant community ordination results from the final constrained RDA.

| Statistic | Axis 1 | Axis 2 | Axis 3 | Axis 4 |
|---|--------|--------|--------|--------|
| Eigenvalues | 0.2059 | 0.0643 | 0.0567 | 0.042 |
| Explained variation (cumulative) | 20.59 | 27.01 | 32.68 | 36.88 |
| Pseudo-canonical correlation | 0.8355 | 0.8619 | 0.8309 | 0.8586 |
| Explained fitted variation (cumulative) | 47.72 | 62.62 | 75.75 | 85.49 |







b)

Figure 11. a) Redundancy analysis (RDA) correlation biplot for plant community response variables and explanatory variables identified during forward selection; and b) only plant community response, to show more clearly the positioning of understory species in ordination space. Shown in a) are the two first axes of a canonical ordination of 63 sites, Hellinger-transformed percent cover data for 59 understory plant species and nine significant explanatory variables. Explanatory variables are shown as vectors and species names are coded. The longer the vector arrow, the stronger the inferred correlation between the explanatory variable and the species (ter Braak and Smilauer 2002). Species codes are given in Table 4. The four competitive shrub species are in dark red and the remaining tall shrubs are purple to show their position in ordination space. The five tree species are in dark green.

3.5.3.1 Cluster analysis

Four somewhat dissimilar stand types emerged from the two-way cluster analysis of stands by their floristic composition (Figure 12; see groups A, B, C and D). Stands dominated by *Oplopanax horridus* cover in combination with some *Thuja plicata* cover comprise one group (A), which includes site series vk2-01, wk3-05a and wk3-05b. Stands containing an intermediate level of *Oplopanax* in combination with higher proportions of other shrub species (*Rubus idaeus*, *Sambucus racemosa* and *Rubus parviflorus*), as well as some understory *Thuja plicata*, *Tsuga heterophylla* and *Abies lasiocarpa*, comprise another group (B), and almost all belong to the wk3-05a and wk3-05b site series. A third group (C) contains little shrub cover, little *Thuja* regeneration, but ample *Tsuga* regeneration and some *Abies* and *Picea* cover. This grouping is made up primarily of wk3-01a, wk3-01b, and vk2-06 site series. Finally, wk3-07 stands dominated by *Hylocomium splendens* form a distinct cluster (D).

Figure 13 shows site series groupings visible in biplots of RDA plant community ordination. Stands were coloured according to their site series to see if they formed clusters based on their post-defoliation composition. This output revealed definite grouping among some site series in ordination space. Site series vk2-01 and wk3-07 occupy dissimilar parts of the RDA biplot; vk2-01 stands have high *Oplopanax horridus* cover and wk3-07 sites have minimal shrub cover and some regenerating *Abies lasiocarpa* and *Tsuga heterophylla*. Site series vk2-06 and wk3-05a and 05b stands overlap in ordination space and may be indistinguishable in terms of their recovery response, which appears to include higher shrub cover of all the four competitive species and some *Thuja plicata*, *Picea engelmanii x glauca* and *Betula papyrifera* regeneration.

If site vectors from the correlation biplot in Figure 11a are overlaid on Figure 13, the environmental variables contributing to the way stands are grouped can be visualized. In particular, wk3-07 stands appear to be warmer (have a higher MAT), vk2-01 stands are wetter, and the remaining stands in site series vk2-6, wk3-01a and b and wk3-05a and b do not appear to cluster based on an ecological gradient.



Figure 12. Two-way similarity analysis of defoliated stands in the ITR, using a flexible beta linkage method and Sorenson dissimilarity coefficient with PC-ORD. Samples (stands) are arranged on the basis of species dendrogram sequences. Darker squares represent higher percent cover of a species. This diagram enables the relationship between samples (stands) and species groups to be more easily recognized (Kent 2012). The four groups of stands (A, B, C, D) are indicated by red boxes.



Figure 13. Plant community RDA showing the arrangement of understory shrubs and trees and plots in ordination space. Score scaling is focused on species scores. Stands, represented by circles, are colour-coded according to site series. The distance between the symbols approximates the dissimilarity of their species composition as measured by their Euclidean distance. 3.5.3.2 Plant community and outbreak severity

There was a significant association with RDA Axis-2 scores by cumulative damage class rating (Kruskal-Wallis $X^2=15.351$, df=3, P=0.0015), but no statistical difference was evident between RDA Axis-1 or Axis-3 and cumulative damage class rating (Axis-1: Kruskal-Wallis $X^2=2.967$, df=3, p=0.3967; Axis-2: $X^2=7.499$, df=3, p=0.0576). Multiple comparisons between cumulative damage class ratings revealed that against RDA Axis-2 scores, ratings "moderate" and "severe" (p<0.001), and "severe" and "severe" (p<0.001) were significantly different from each other.

3.5.4 Regeneration

There was a significant negative correlation between the total density of germinants, seedlings and saplings and both percent competitive shrub cover (r_s =-0.3883, p=0.0017) and percent tall shrub cover (r_s =-0.3979, p=0.0012). This relationship is shown in Figure 14, although the slope of the least squares regression line appears subtle because of the scale of the Y-axis. Similarly, there is a significant negative correlation between well-spaced stems/ha and both percent competitive shrub cover (r_s =-0.3685, p=0.003; Figure 15) and percent tall shrub cover (r_s =-0.3818, p=0.002). Only relationships with competitive shrub cover are displayed in figures.

Of total regeneration by size class, *Tsuga heterophylla* and *Abies lasiocarpa* had significant relationships with shrub cover (Table 14). *Tsuga* seedling density is negatively correlated

with competitive shrub cover (r_s =-0.52, p<0.001; Figure 16a) and tall shrub cover (r_s =-0.52, p<0.001). *Tsuga* sapling density is negatively correlated with competitive shrub cover (r_s =-0.51, p<0.001; Figure 16b) and tall shrub cover (r_s =-0.55, p<0.001). Analyzed as one group, *Tsuga* regeneration is negatively associated with competitive shrub cover (r_s =-0.38, p<0.0017; Figure 16c) and tall shrub cover (r_s =-0.41, p<0.001).

Total *Abies lasiocarpa* seedling density is negatively correlated with competitive shrub cover (r_s =-0.39, p<0.001; Figure 17a) and tall shrub cover (r_s =-0.36, p=0.002). *Abies* sapling density is negatively correlated with competitive shrub cover (r_s =-0.54, p<0.001; Figure 17b) and tall shrub cover (r_s =-0.49, p<0.001). Analyzed as one group, *Abies* regeneration is negatively correlated with both competitive shrub cover (r_s =-0.48, p<0.001; Figure 17c) and tall shrub cover (r_s =-0.44, p<0.001).

Analyzed as a cohort with all species included, total seedlings and saplings are both significantly negatively correlated with competitive and tall shrubs. Seedlings are negatively associated with competitive shrub cover (r_s =-0.53, p<0.001; Figure 18a) and tall shrub cover (r_s =-0.51, p<0.001). Saplings are also negatively associated with competitive shrub cover (r_s =-0.53, p<0.001, Figure 18b) and tall shrub cover (r_s =-0.54, p<0.001).

Of well-spaced regeneration by size class, only *Tsuga heterophylla* and *Abies lasiocarpa* had significant relationships with shrub cover (Table 15). *Tsuga* seedling density is negatively correlated with competitive shrub cover (r_s =-0.49, p<0.001; Figure 19a) and tall shrub cover (r_s =-0.46, p<0.001). *Tsuga* sapling density is negatively correlated with competitive shrub

cover (r_s =-0.55, p<0.001; Figure 19b) and tall shrub cover (r_s =-0.59, p<0.001). Analyzed as one group, *Tsuga* regeneration is negatively associated with competitive shrub cover (r_s =-0.44, p<0.001; Figure 19c) and tall shrub cover (r_s =-0.46, p<0.001).

Well-spaced *Abies lasiocarpa* seedling density is negatively correlated with competitive shrub cover (r_s =-0.43, p<0.001; Figure 20a) and tall shrub cover (r_s =-0.40, p=0.001). *Abies* sapling density is negatively correlated with competitive shrub cover (r_s =-0.48, p<0.001; Figure 20b) and tall shrub cover (r_s =-0.45, p<0.001). Analyzed as one group, *Abies* regeneration is negatively associated with competitive shrub cover (r_s =-0.55, p<0.001; Figure 20c) and tall shrub cover (r_s =-0.51, p<0.001).

Analyzed as a cohort with all species included, well-spaced seedlings and saplings are both significantly negatively correlated with competitive and tall shrubs. Seedlings are negatively associated with competitive shrub cover (r_s =-0.38, p<0.001; Figure 21a) and tall shrub cover (r_s =-0.35, p<0.0044). Saplings are also negatively associated with competitive shrub cover (r_s =-0.53, p<0.001; Figure 21b) and tall shrub cover (r_s =-0.53, p<0.001).



Figure 14. Scatterplots with linear least-squares regression lines for total regeneration density and percent competitive shrub cover. log y=-0.16(log x) + 3.51, R^2 =0.11, p=0.006. All zeros in this data were changed to '0.1' to accommodate a log transformation.



Figure 15. Scatterplots with linear least-squares regression lines for well-spaced regeneration density and percent competitive shrub cover. $\log y=-0.15(\log x) + 3.12$, $R^2=0.13$, p=0.002. All zeros in this data were changed to '0.1' to accommodate a log transformation.

| | | % Competitive shrub cover | | %Tall shrub cover | | |
|-------------|-----------|---------------------------|----------|-------------------|---------|--|
| Total reg | eneration | r | <u>р</u> | r _s | p | |
| Tsuga | Germ. | -0.1096 | 0.3925 | 0.5079 | 0.5079 | |
| | Seed. | -0.5272 | <0.001* | -0.5292 | <0.001* | |
| | Sap. | -0.5174 | <0.001* | -0.5562 | <0.001* | |
| All Tsuga | - | -0.3881 | 0.0017* | -0.4148 | <0.001* | |
| Thuja | Germ. | 0.0787 | 0.5397 | 0.0655 | 0.6100 | |
| | Seed. | -0.0727 | 0.5712 | -0.0827 | 0.5192 | |
| | Sap. | 0.1564 | 0.2209 | 0.1305 | 0.3082 | |
| All Thuja | - | 0.1093 | 0.3937 | 0.0716 | 0.5770 | |
| Abies | Germ. | 0.0730 | 0.5697 | 0.0643 | 0.6164 | |
| | Seed. | -0.3928 | 0.0015* | -0.3692 | 0.0029* | |
| | Sap. | -0.5487 | <0.001* | -0.4974 | <0.001* | |
| All Abies | | -0.4800 | <0.001* | -0.4463 | <0.001* | |
| Picea | Germ. | 0.1433 | 0.2625 | 0.1602 | 0.2098 | |
| | Seed. | -0.1986 | 0.1188 | -0.1184 | 0.3555 | |
| | Sap. | 0.0786 | 0.5402 | 0.1238 | 0.3338 | |
| All Picea | | -0.0470 | 0.7148 | 0.0304 | 0.8130 | |
| All species | Germ. | -0.0695 | 0.5885 | -0.0485 | 0.7056 | |
| - | Seed. | -0.5364 | <0.001* | -0.5144 | <0.001* | |
| | Sap. | -0.5332 | <0.001* | -0.5484 | <0.001* | |

Table 14. Spearman's correlations for the total number of total understory trees by size class and two classes of shrub cover.

*Correlation is significant at $\alpha = 0.05$.





Figure 16. Scatterplots with linear least-squares regression lines for associations between understory regeneration density and percent competitive shrub cover: a) total *Tsuga* seedlings; b) total *Tsuga* saplings; and c) total *Tsuga* (all size classes). a) y=-696.26(log x) + 1309.06, R²=0.22, p=<0.001; b) y=-409.48(log x) + 1049.96, R²=0.22, p=<0.001; c) log y=-0.28(log x) + 3.14, R²=0.06, p=0.03. All zeros in shrub cover data were changed to '0.1' to accommodate a log transformation, as were zeros in regeneration density data in c).





Figure 17. Scatterplots with linear least-squares regression lines for associations between understory regeneration density and percent competitive shrub cover: a) total *Abies* seedlings; b) total *Abies* saplings; and c) total *Abies* (all size classes). a) log y=-0.70(log x) + 1.64, R²=0.12, p=0.004; b) log y=-0.981(log x) + 1.81, R²=0.25, p=<0.001; c) log y=-0.81(log x) + 2.29, R²=0.17, p=<0.001. All zeros in this data were changed to '0.1' to accommodate a log transformation.



Figure 18. Scatterplots with linear least-squares regression lines for associations between understory regeneration density and percent competitive shrub cover: a) total seedlings (all species); and b) total saplings (all species). a) $y=-933.52(\log x) + 2149.77$, $R^2=0.28$, p=<0.001; b) y=-19.55 x + 1652.27, $R^2=0.22$, p=<0.001. Shrub cover values in a) that were zero were changed to '0.1' to accommodate a log transformation.

| | | % Competitiv | ve shrub cover | %Tall shrub cover | | |
|-------------|--------------|----------------|----------------|-------------------|---------|--|
| Well-spaced | regeneration | r _s | Р | rs | Р | |
| Tsuga | Germ. | -0.0481 | 0.7083 | -0.0601 | 0.6401 | |
| | Seed. | -0.4960 | <0.001* | -0.4642 | <0.001* | |
| | Sap. | -0.5596 | <0.001* | -0.5915 | <0.001* | |
| All Tsuga | | -0.4404 | <0.001* | -0.4689 | <0.001* | |
| Thuja | Germ. | 0.1533 | 0.2304 | 0.1306 | 0.3076 | |
| | Seed. | 0.0063 | 0.9611 | -0.0197 | 0.8780 | |
| | Sap. | 0.2197 | 0.0836 | 0.2098 | 0.0988 | |
| All Thuja | | 0.2040 | 0.1088 | 0.1714 | 0.1792 | |
| Abies | Germ. | 0.0299 | 0.8162 | 0.0398 | 0.7566 | |
| | Seed. | -0.4396 | <0.001* | -0.4037 | 0.001* | |
| | Sap. | -0.4839 | <0.001* | -0.4550 | <0.001* | |
| All Abies | | -0.5511 | <0.001* | -0.5118 | <0.001* | |
| Picea | Germ. | 0.1792 | 0.1598 | 0.1792 | 0.1599 | |
| | Seed. | -0.0319 | 0.8041 | 0.0345 | 0.7885 | |
| | Sap. | 0.0025 | 0.9844 | 0.0375 | 0.7705 | |
| All Picea | | 0.0543 | 0.6725 | 0.1119 | 0.3826 | |
| All species | Germ. | 0.0399 | 0.7562 | 0.0281 | 0.8267 | |
| | Seed. | -0.3877 | 0.0017* | -0.3545 | 0.0044* | |
| | Sap. | -0.5320 | <0.001* | -0.5309 | <0.001* | |

Table 15. Spearman's correlations between the number of well-spaced understory trees by size class and two classes of shrub cover.

*Correlation is significant at $\alpha = 0.05$.





Figure 19. Scatterplots with linear least-squares regression lines for associations between understory regeneration density and percent competitive shrub cover: a) well-spaced *Tsuga* seedlings; b) well-spaced *Tsuga* saplings; and c) well-spaced *Tsuga* (all size classes). a) y=-221.81(log x) + 388.55, R²=0.25, p=<0.001; b) y=-197.48(log x) + 515.53, R²=0.23, p=<0.001; c) log y = -0.015x + 2.76, R²=0.13, p=0.003. Shrub cover values in a) and b) that were zero were changed to '0.1' to accommodate a log transformation, as were regeneration density values in c).

b)



% Competititve shrub cover



a)



Figure 20. Scatterplots with linear least-squares regression lines for associations between understory regeneration density and percent competitive shrub cover: a) well-spaced *Abies* seedlings; b) well-spaced *Abies* saplings; and c) well-spaced *Abies* (all size classes). a) y=-89.11(log x) + 165.54, R²=0.55, p=<0.001; b) log y=-0.75(log x) + 1.41, R²=0.16, p=<0.001; c) log y = -0.27(log x) = 3.46, R²=0.17, p=<0.001. All shrub cover values that were zero were changed to '0.1' to accommodate a log transformation, as were regeneration density values in b) and c).



Figure 21. Scatterplots with linear least-squares regression lines for associations between understory regeneration density and percent competitive shrub cover: a) well-spaced seedlings (all species); and b) well-spaced saplings (all species). a) $y=-291.07(\log x) + 673.28$, $R^2=0.26$, p=<0.001; b) y=-8.85x + 839.59, $R^2=0.19$, p=<0.001. All shrub cover values in a) that were zero were changed to '0.1' to accommodate a log transformation.

3.5.4.1 Regeneration niche

I treated regeneration densities by tree species and size class as multivariate response variables in an RDA analysis. An overall test of significance showed that the canonical relationship between regeneration density by species and size class and the explanatory variables was highly significant (p = 0.001 after 999 permutations; pseudo-F = 2.4 on all axes), meaning that there was a meaningful association between the explanatory variables and regeneration densities. Total variation of the RDA model was 26%. The resulting explained variation (adj. R^2) of the global model (which included all the site variables) was 24%.

Table 16 shows the explanatory influence of each variable and its contribution to the model. The forward selection process identified four of the 14 predictors as a sufficient subset: site index, index of soil moisture, percent live stems and total live basal area (Table 17). I included these four variables in the final constrained RDA analysis (Table 18). The first two axes summarize approximately 18% of the variation in the regeneration density by species and size class data from defoliated stands. Only these two axes are represented in the scatterplot (Figure 22).

The four site variables accounted for 23.7% of the total variation in the regeneration attributes of defoliated stands. The explained variation (adj. R^2) of this model was 18.4% (pseudo-F=4.5, p=0.001).

A greater abundance of *Thuja plicata* of all size classes (germinants, seedlings and saplings) in high site index stands was also seen in the plant community RDA analysis. *Tsuga heterophylla* seedlings, *Picea engelmanii* x *glauca* and *Abies lasiocarpa* appear to tolerate lower-productivity sites. *Picea* and *Abies* seedlings and saplings occur in higher densities on sites with higher relative moisture. If a higher proportion of live stems is interpreted as an indicator of a lower-severity defoliation, then *Abies* seedling and sapling densities are higher in stands that experienced lower-severity outbreaks.

The regeneration niche RDA (Figure 23) shows that regenerating trees group themselves across site series by species, and that the site series wk3-07, vk2-01 and vk2-06 form distinct clusters, while the remaining site series are not as distinguishable from each other in their regeneration response to defoliation history. *Tsuga heterophylla* seedlings are concentrated in wk3-07 site series stands, *Abies lasiocarpa* seedlings and saplings occur mostly in vk2-06 site series stands, and *Thuja plicata* regeneration of all size classes is found in the vk2-01 and wk3-05. Site series wk3-01 stands contain regenerating trees of all species. *Picea engelmanii* x *glauca* regeneration is sparse but found primarily in the vk2 biogeoclimatic variant. The stands that do not cluster based on site series (wk3-01 (a and b) and wk3-05 (a and b)) appear to fall along a moisture gradient.

Table 16. a) Summary of the independent effects of all explanatory variables on overall regeneration density by species and size class; b) Summary of the conditional effect of each predictor, representing the variation and significance explained by a predictor after accounting for the effect of the predictors placed above it in the list. The predictors were chosen in the order of their decreasing explained variation.

| Variable | Explains % | pseudo-F | р |
|------------------------------|------------|----------|-------|
| site index | 9.8 | 6.6 | 0.001 |
| indexed soil moisture regime | 6.2 | 4 | 0.001 |
| canopy density | 6 | 3.9 | 0.001 |
| % live stems (all) | 5.7 | 3.7 | 0.002 |
| steepness | 4.7 | 3 | 0.006 |
| total live basal area | 4.7 | 3 | 0.006 |
| slope position | 4.3 | 2.7 | 0.012 |
| elevation | 3.9 | 2.5 | 0.022 |
| frost hazard | 3.6 | 2.3 | 0.021 |
| mean annual temperature | 2.9 | 1.8 | 0.091 |
| radiation | 2.2 | 1.4 | 0.195 |
| soil nutrient regime | 1.5 | 0.9 | 0.45 |
| annual heat:moisture index | 1.1 | 0.7 | 0.67 |
| mean annual precipitation | 0.8 | 0.5 | 0.868 |

| b) Conditional Term Effects: | | | |
|------------------------------|------------|----------|----------|
| Variable | Explains % | pseudo-F | <u>p</u> |
| site index | 9.8 | 6.6 | 0.001 |
| indexed soil moisture regime | 5.4 | 3.8 | 0.002 |
| % live stems (all) | 5.2 | 3.8 | 0.004 |
| total live basal area | 3.4 | 2.6 | 0.012 |
| mean annual temperature | 2.1 | 1.6 | 0.13 |
| elevation | 1.5 | 1.2 | 0.313 |
| slope position | 2 | 1.5 | 0.143 |
| mean annual precipitation | 1.9 | 1.5 | 0.18 |
| annual heat:moisture index | 5.5 | 4.6 | 0.001 |
| steepness | 1.2 | 1 | 0.38 |
| soil nutrient regime | 0.9 | 0.8 | 0.659 |
| frost hazard | 1 | 0.8 | 0.587 |
| radiation | 0.9 | 0.7 | 0.665 |
| canopy density | 0.5 | 0.4 | 0.903 |

Table 17. Summary of tree regeneration niche ordination results from forward selection. Variables are in selection order and the model adj. R^2 after inclusion of each successive variable is shown. Only significant predictors (p<0.05) were retained.

| Variable | Explains % | Contribution % | pseudo-F | р |
|------------------------------|------------|----------------|----------|-------|
| site index | 9.8 | 23.8 | 6.6 | 0.001 |
| indexed soil moisture regime | 5.4 | 13 | 3.8 | 0.002 |
| % live stems (all) | 5.2 | 12.5 | 3.8 | 0.001 |
| total live basal area | 3.4 | 8.3 | 2.6 | 0.019 |

Table 18. Summary of results from the final constrained RDA for tree regeneration niche.

| Statistic | Axis 1 | Axis 2 | Axis 3 | Axis 4 |
|---|--------|--------|--------|--------|
| Eigenvalues | 0.1064 | 0.0824 | 0.0339 | 0.0143 |
| Explained variation (cumulative) | 10.64 | 18.88 | 22.27 | 23.7 |
| Pseudo-canonical correlation | 0.7296 | 0.6243 | 0.4409 | 0.3217 |
| Explained fitted variation (cumulative) | 44.89 | 79.64 | 93.96 | 100 |



Figure 22. a) Redundancy analysis (RDA) correlation biplot for tree regeneration density by species and size class response variables and explanatory variables identified during forward selection. This figure shows the two first axes of a canonical ordination of 63 sites, 10 Hellinger-transformed regeneration densities by species and size class and four significant explanatory variables. Explanatory variables are shown as vectors and tree species names are coded. The longer the vector arrow, the stronger the inferred correlation between the explanatory variable and the species (ter Braak and Smilauer 2002). Tree species codes are based on the first two letters of the genus followed by the first letters of the size class. "thsap" represents the *Thuja plicata* saplings.



Figure 23. Total regeneration density RDA showing the arrangement of understory tree species by size class and plots in ordination space. Score scaling is focused on tree species scores. Stands, represented by circles, are colour-coded according to site series. The distance between the symbols approximates the dissimilarity of their regeneration composition as measured by their Euclidean distance.

3.5.4.2 Regeneration substrate

The availability of each substrate (forest floor, coarse woody debris and mineral soil) was not measured in this study, and so it is not possible to determine the relative importance of each substrate to regenerating trees in defoliated stands. In general, however, it was observed that forest floor was always more abundant than coarse woody debris (CWD), which was more abundant than exposed mineral soil. Across stands, CWD was the substrate with the highest number of regenerating trees (Figure 24a), with forest floor being the substrate type with the second highest number of regenerating trees, and mineral soil having the fewest germinants, seedlings or saplings using it. *Tsuga heterophylla*, as the most abundant regenerating species, was the most prolific user of CWD, and germinants were the size class most numerous on this substrate type (Figure 24b). Again, it is not always possible to correctly identify the establishment substrate for a sapling, and this should be considered in when interpreting the regeneration substrate results for this size class.

Analyzed as one cohort, *Tsuga heterophylla* regeneration on CWD is negatively correlated with competitive and tall shrub cover (r_s =-0.27, p<0.001; r_s =-0.27, p=0.030; Table 19). *Tsuga* seedlings and saplings analyzed separately are negatively correlated with competitive shrub cover (r_s =-0.38, p=0.001; r_s =-0.48, p<0.001) and tall shrub cover (r_s =-0.38, p=0.001; r_s =-0.51, p<0.001). All *Abies lasiocarpa* regeneration on CWD, as well as *Abies* saplings on CWD analyzed on their own, are also negatively correlated with competitive and tall shrub cover. Analyzed as a cohort with all species included, seedlings and saplings are both significantly correlated with competitive shrubs (r_s =-0.32, p=0.008; r_s =-0.43, p<0.001) and

tall shrubs (r_s =-0.28, p=0.022; r_s =-0.45, p=0.001), showing negative associations in both instances. The exception to this pattern is *Thuja plicata* regeneration, which has a positive association with both competitive and tall shrubs (r_s =0.31, p=0.0129; r_s =0.2940, p=0.0193).

There was no significant correlation between the proportion of total regeneration of all understory tree species on CWD and competitive shrub cover ($r_s = 0.1970$, p = 0.1218) or tall shrub cover ($r_s = 0.2105$, p = 0.0977). However, there was a positive association between the proportion of *Thuja plicata* saplings on CWD and both competitive shrub cover ($r_s = 0.30$, p = 0.014) and tall shrub cover ($r_s = 0.29$, p = 0.017; Table 20). Analyzed as one group (all size classes), *Thuja* regeneration on CWD is positively associated with competitive shrub cover ($r_s = -0.39$, p = 0.0017) and tall shrub cover ($r_s = -0.38$, p = 0.0019).



Figure 24. Mean tree regeneration density (\pm S.E.) by species, size class and substrate, grouped by substrate a) and by species b). CWD: coarse woody debris, FF: forest floor, MS: mineral soil.

| | | % Competitive shrub cover | | %Tall shrub cover | | |
|-------------|-------|---------------------------|---------|-------------------|---------|--|
| stems/ha on | CWD | r _s | р | r _s | р | |
| Tsuga | Germ. | -0.0984 | 0.4429 | -0.0669 | 0.6022 | |
| | Seed. | -0.3878 | 0.0017* | -0.3873 | 0.0017* | |
| | Sap. | -0.4846 | <0.001* | -0.5113 | <0.001* | |
| All Tsuga | | -0.2707 | 0.0319* | -0.2730 | 0.0304* | |
| Thuja | Germ. | 0.1707 | 0.1811 | 0.1825 | 0.1522 | |
| | Seed. | 0.0569 | 0.6576 | 0.0750 | 0.5592 | |
| | Sap. | 0.2350 | 0.0637 | 0.2130 | 0.0937 | |
| All Thuja | | 0.3118 | 0.0129* | 0.2940 | 0.0193* | |
| Abies | Germ. | 0.0838 | 0.5137 | 0.0559 | 0.6636 | |
| | Seed. | -0.1657 | 0.1943 | -0.1467 | 0.2512 | |
| | Sap. | -0.3418 | 0.0061* | -0.2981 | 0.0177* | |
| All Abies | | -0.2947 | 0.019* | -0.2654 | 0.0355* | |
| Picea | Germ. | 0.1433 | 0.2625 | 0.1602 | 0.2097 | |
| | Seed. | -0.0445 | 0.7290 | 0.0431 | 0.7372 | |
| | Sap. | 0.1108 | 0.3874 | 0.1509 | 0.2377 | |
| All Picea | | 0.0703 | 0.5840 | 0.1458 | 0.2542 | |
| All species | Germ. | -0.0603 | 0.6388 | -0.0280 | 0.8276 | |
| | Seed. | -0.3287 | 0.0085* | -0.2877 | 0.0222* | |
| _ | Sap. | -0.4380 | <0.001* | -0.4595 | <0.001* | |

Table 19. Spearman's correlations for regeneration density (stems/ha) on coarse woody debris by size class and two classes of shrub cover.

*Correlation is significant at $\alpha = 0.05$.

| | | % Competitiv | % Competitive shrub cover | | %Tall shrub cover | | |
|-------------|-------|----------------|---------------------------|----------------|-------------------|--|--|
| % on CWD | | ۲ _s | р | r _s | p | | |
| Tsuga | Germ. | -0.1531 | 0.2311 | -0.1162 | 0.3643 | | |
| | Seed. | -0.1074 | 0.4023 | -0.0862 | 0.5020 | | |
| | Sap. | -0.0725 | 0.5722 | -0.0763 | 0.5524 | | |
| All Tsuga | | 0.1128 | 0.3786 | 0.1371 | 0.2840 | | |
| Thuja | Germ. | 0.1701 | 0.1827 | 0.1825 | 0.1522 | | |
| | Seed. | 0.1613 | 0.2065 | 0.1827 | 0.1518 | | |
| | Sap. | 0.3057 | 0.0148* | 0.2996 | 0.0170* | | |
| All Thuja | | 0.3901 | 0.0017* | 0.3868 | 0.0019* | | |
| Abies | Germ. | 0.0838 | 0.5137 | 0.0559 | 0.6636 | | |
| | Seed. | -0.0727 | 0.5714 | -0.0707 | 0.5821 | | |
| | Sap. | -0.2125 | 0.0945 | -0.1865 | 0.1432 | | |
| All Abies | | -0.1066 | 0.4057 | -0.0927 | 0.4699 | | |
| Picea | Germ. | 0.1435 | 0.2620 | 0.1599 | 0.2108 | | |
| | Seed. | -0.0438 | 0.7329 | 0.0434 | 0.7354 | | |
| | Sap. | 0.0957 | 0.4557 | 0.1331 | 0.2984 | | |
| All Picea | | 0.0578 | 0.6525 | 0.1285 | 0.3156 | | |
| All species | Germ. | -0.1102 | 0.3901 | -0.0671 | 0.6013 | | |
| | Seed. | 0.0793 | 0.5367 | 0.1268 | 0.3219 | | |
| | Sap. | 0.0364 | 0.7773 | 0.0079 | 0.9512 | | |

Table 20. Spearman's correlations for the proportion of total stems on coarse woody debris by size class and two classes of shrub cover.

*Correlation is significant at $\alpha = 0.05$.

4.0 Discussion

4.1 Overstory recovery

4.1.1 Effect of outbreak severity and site variables

The effect of a defoliation event on overstory trees is a function of the interacting factors of severity, timing and duration of defoliation, site characteristics, the initial condition of trees and presence of secondary insects and disease organisms (Kulman 1971, Laursen 1977). In comparing the growth response effects of different severities of hemlock looper defoliation to those of other defoliators, such as the western spruce budworm (Iqbal 2011), researchers have found that it may be the stimulation of suppressed buds that greatly increases foliage regrowth and tree recovery from defoliation (Piene 1989, Piene and MacLean 1999, Iqbal 2011). Similarly to the spruce budworm, the hemlock looper consumes all age classes of foliage, including buds, which may contribute to the quicker observed recovery of hemlock looper defoliated trees when compared to trees defoliated by other species, such as the balsam fir sawfly (*Neodiprion abietis* Harris) (Iqbal 2011).

Aerial survey data of insect defoliation can be more economical than large-scale field surveys and provide greater spatial coverage of the symptoms caused by forest pests (Harris and Dawson 1979). They are known, however, for lacking the accuracy necessary for local or operational purposes (MacLean and MacKinnon 1996, Magnussen and Alfaro 2012). In this study, Forest Health Aerial Overview Survey data were used to create a Defoliation Severity Index (DSI), and were also used in combination with on-the-ground data of percentages of live stems at the stand level to derive the Overstory Recovery Index (ORI_{ave}). In other words, aerial survey data were relied upon in this study for information on defoliation history and hence the degree of contrast (recovery) of stand overstories.

To the extent that the Forest Health Aerial Overview Surveys from 1991 to 1994 can be relied upon, overstory recovery in the ITR has been greatest in stands with a more severe outbreak history, and in those with lower site productivity. One possible explanation is a greater probability of individual tree recovery and growth in stands that are sparsely stocked with mature, living trees (which therefore experience less competition). Another possibility is that there is higher nutrient availability (from frass) is more severely defoliated stands. Yet the poor resolution and reliability of the aerial surveys still makes these very tenuous relationships. It is also unclear why stands with a lower site index have greater recovery than stands with a higher site index, as one would expect higher-productivity sites to have more soil resources available for tree recovery.

The demographic response of trees – their survival and reproduction – only portrays one dimension of recovery after a WHL defoliation. There is likely a continuum of growth responses of trees, both in the surviving overstory and suppressed "pole-sized" trees. That growth response can be described with the analysis of tree ring increments. Follow-up dendrochronological research is recommended for a more accurate description of overstory recovery at the stand level.

96

One study examining *Tsuga heterophylla* recovery in managed stands following an outbreak of western blackheaded budworm (*Acleris gloverana* Walsingham), found that recovery was greatest in stands that had been spaced, even where the defoliation had been most severe (Nealis and Turnquist 2010). This may be due to greater resource availability for individual trees in stands that have been spaced. Other researchers suspect that greater resource availability in the form of nutrients, water and sunlight in higher productivity stands provide trees with the ability to produce foliage with greater resistance to defoliators (Day 2013). These researchers suggest that tree recovery following defoliation may be tied to stores of non-structural carbohydrates in sapwood that can be used to grow new foliage and produce compounds such as lignins and tannins (Day 2013).

4.2 Understory recovery

4.2.1 Effect of outbreak severity

Any influence of mapped outbreak severity on shrub cover and tree regeneration was not apparent in defoliated stands when evaluated in a correlation analysis using the Defoliation Severity Index as the independent variable. These results could also indicate that the cumulative damage class ratings and the DSI are too coarse to capture the variation in severity across landscapes aerially surveyed, or that a broader range of defoliation severities should have been included in this study.

The proportion of dead stems is a weaker representation of defoliation severity than the DSI, since this metric may be representing mortality due to other factors, and here we assume that

it is an adequate surrogate for the proportion of trees killed directly or indirectly by the WHL. Shrub cover has a distinctly positive association with the proportion of dead stems, and both regeneration types (total and well-spaced stem counts) have a slightly weaker negative association with this measure of defoliation severity. Tree regeneration appears to be suppressed by the growth of shrubs observed in high-severity outbreak areas.

Shrubs are presumably responding to an increase in light levels and/or a pulse in nutrients brought about by the return of frass to the forest floor (Reichle 1973). Although there is research showing that atmospheric nitrogen deposition of inorganic nitrogen leads to fertilization effects in terrestrial ecosystems (Throop and Lerdau 2004), and that frass deposited by defoliators contributes to forest floor nitrogen levels (Grace 1986, Hunter 2001, Lovett et al. 2002), there seems to be little published evidence demonstrating an increase in understory growth due to the influence of frass from other defoliating insects such as the gypsy moth (*Lymantria dispar* L.), western spruce budworm or forest tent caterpillar (*Malascosoma disstria* Hubner). In general, the long-term consequences of the transfer of foliage to insect biomass and then to the forest floor are not well understood (Russell et al. 2004).

Twenty years following a WHL outbreak, the influence of nutrient inputs to the forest floor may be less important than the effect of higher light levels in more severely defoliated stands. High precipitation could decrease the contact of nitrogen from frass with soil during or after a defoliation event, flushing this nutrient before it can be retained (Lovett et al. 2002), and this scenario seems plausible in a high-precipitation system such as the ITR. Defoliation increases light penetration to the forest floor (Collins 1961, Campbell and Sloan 1977) and even though tree growth rates can recover to pre-defoliation levels within five years of an outbreak (Iqbal 2011) it likely takes longer than that for a severely defoliated canopy to return to creating pre-disturbance light levels on the forest floor.

4.2.2 Effect of site variables

Shrub cover responded strongly to site index in defoliated stands, being greater in higherproductivity stands. Although site index is commonly used for silvicultural purposes and forest planning based on specified managed tree species (MoFR 2011), it was designed to reflect the net effects of climate, terrain and soil on tree growth, and so it is a suitable indicator of general plant productivity. The four competitive shrub species (analyzed together due to their similar functional effects on tree regeneration) are also all nitrophilous to varying degrees, and might also be reacting to higher soil nitrogen resulting from the WHL defoliation event while already exhibiting good productivity on high site index stands. In particular, *Rubus idaeus* tends to be profuse immediately after a nitrate-releasing disturbance event, before abating quickly after nutrients have subsided, unless the site is exceptionally rich (S. Haeussler, pers. comm.). *Sambucus racemosa* similarly establishes and grows immediately after a disturbance but persists longer than *Rubus idaeus* (Haeussler et al. 1990). *Rubus parviflorus* and *Oplopanax horridus* are longer lived and more tolerant of later seral conditions (S. Haeussler, pers. comm.). It is not known what the abundance of these species was in sampled stands before the defoliation event, but it is likely that the increased light
and/or nitrate inputs from defoliation encouraged their establishment or growth following the disturbance.

Shrub cover was higher on steeper slopes and lower in stands with a higher canopy density. A comparison of means between generally North-facing slopes and generally South-facing slopes found no significant difference between shrub cover based on aspect, indicating that higher shrub cover on steeper slopes may be a function of better water drainage in those stands rather than a function of radiation. *Oplopanax horridus* is said to require waterreceiving but well-drained sites (Klinka et al. 1989, Beaudry et al. 1999) and higher shrub cover on steeper sites may be reflecting this species primarily.

In general, shrub cover is largely a function of canopy openness in defoliated stands. The four competitive shrub species included in this analysis have different shade tolerances, however. *Rubus idaeus* is considered shade-intolerant (Beaudry et al. 1999) and requires canopy openings in order to establish and survive (Haeussler et al. 1990). *Sambucus racemosa, Rubus parviflorus* and *Oplopanax horridus* are all considered somewhat shade-tolerant (Beaudry et al. 1999). *Sambucus,* although tolerant of deep shade, grows best in forest openings (Harcombe et al. 1983). *Rubus parviflorus* grows under closed canopies and in open conditions, but has higher cover and greater vigour as understory light increases (Mueggler 1965, Irwin and Peak 1979). *Oplopanax horridus* will grow towards canopy gaps and sunflecks in low light conditions (Lantz and Antos 2002) and thereby maximizes light capture in forest understories (Roorbach 1999). *Oplopanax* dominates the shrub layer across most stands, and was absent from only three of the 63 plots included in this study.

The correlation analysis of relationships between regeneration densities and various site and stand factors suggests that perhaps regeneration might be responding to the abundance of competitive shrubs, and that the results are not necessarily a reflection of how regeneration directly responds to the site variables measured. That total regeneration increased with canopy cover and decreased with site index, while shrub cover did the opposite, probably indicates that shrubs were able to react sooner or more strongly to these site variables and flourish before regeneration was able to establish post-disturbance. Well-spaced regeneration appears to respond to sites that are warmer and drier, indicating that the most vigourous germinants, seedlings and saplings have somewhat more of a competitive advantage in stands on such sites.

4.2.3 Plant community

The multivariate plant community analysis revealed that competitive shrubs occupy a different portion of multivariate space than do most regenerating trees. With the exception of *Thuja plicata*, which appears to tolerate stands with more competitive shrub cover, regenerating tree cover of *Tsuga heterophylla*, *Abies lasiocarpa* and *Picea engelmannii* x *glauca* is higher in stands where there is less shrub cover. As in the exploration of associations through bivariate correlation analysis, site index is the strongest explanatory driver of competitive shrub cover. Regenerating tree species generally fell in different quadrats of the RDA output from each other, reflecting their relative abundance across plant community types in defoliated stands, the site variables that underpin that variation, and their inherent niche differentiation that facilitates their coexistence in the ITR.

When considered together, the site variables with the most explanatory influence on understory vegetation pattern are (in decreasing order): site index, total live basal area, soil moisture index, slope position, mean annual temperature, annual heat:moisture index, steepness, percent live stems and relative soil nutrients. Site index exerts a powerful positive influence on shrub cover, with steepness and relative soil nutrient regime influencing shrub cover to a lesser degree. Soil moisture index, annual heat:moisture index, mean annual temperature and the proportion of live stems in the overstory have a positive association with *Tsuga heterophylla*, *Abies lasiocarpa*, *Picea engelmanii* x glauca and Betula papyrifera. *Thuja plicata* appears to endure a shrub canopy and thrives under the same site characteristics exploited by competitive shrub species in this ecosystem.

4.2.3.1 Cluster analysis

The motivation for the cluster analysis was primarily to see whether plant communities could be objectively grouped twenty years following the WHL outbreak. Using arbitrary "stopping points," four reasonably dissimilar stand types emerged from the hierarchical cluster analysis. Figure 25 shows photographs of the site series that typify each of the four clusters (groups A to D) resulting from this analysis. The RDA cluster analysis was useful is visualizing how stands clustered by site series based on their plant community response to the defoliation event. There appears to be overlap among some site series, and clear clustering among others. The RDA cluster analysis also allowed us to see which site characteristics underpin those patterns, namely mean annual temperature and soil moisture availability.

102

I expected that some group structure (Kent 2012) was present in the data, and anticipated that similar stand types might group together according to site series in a hierarchical cluster analysis. The overlap in site series between clusters observed using both methods (hierarchical cluster analysis and the RDA cluster analysis) indicates that it might not be possible to create distinct categories that can be used to predict trajectories of understory development following a WHL outbreak. It also confirms that stands recovering from a WHL defoliation in the ITR are part of a continuous plant community, with stands distinguished by subtle site differences. This conclusion is in agreement with the interpretation of many scientists who believe that the classification of vegetation samples can produce artificial and misleading results, since plant communities exist as a continuum (McIntosh 1967, Kent 2012) and do not necessarily fall naturally into distinct groups. More study is needed to identify the other factors responsible for discriminating recovery patterns in defoliated stands.





Figure 25. Forest stand types representative of cluster analysis groupings: group A) an ICH vk2-01 stand with a prominent *Oplopanax horridus* understory; group B) an ICHwk3-05b stand with mixed shrub cover and mixed conifer regeneration; group C) an ICHwk3-01a stand with little shrub cover and mixed conifer regeneration; and group D) an ICH wk3-07 stand with few understory shrubs or large herbs.

4.2.3.2 Plant community and outbreak severity

Results of the Kruskal-Wallis test are taken to mean that the cumulative damage classification rating (i.e., local WHL outbreak severity) increased with RDA Axis-2 scores. In other words, the constrained community was related to cumulative damage classification. When this result is used to interpret the RDA biplot, the four competitive shrub species appear to be organized along a severity gradient, with Rubus idaeus having the highest relative abundance in stands that were most severely defoliated and Oplopanax horridus having the highest relative abundance in less severely defoliated stands. When this suggestion is subjected to an attendant correlation analysis, however, only non-significant relationships are found that mostly contradict the RDA axis scores. Rubus idaeus and R. parviflorus and Oplopanax horridus all show higher abundances in stands that were less severely defoliated (r_s =-0.04, p=0.715; r_s =-0.171, p=0.180; r_s =-0.01, p=0.902). Only Sambucus racemosa correlation results are more consistent with their arrangement in the RDA biplot; that is, *Sambucus* appears to increase with defoliation severity ($r_s=0.162$, p=0.203). There are two possible explanations for these results: the RDA Axis-2 is an imperfect proxy for defoliation severity or the cumulative damage classification ratings are too crude to detect subtle differences between plant community responses to defoliation severity.

4.2.4 Regeneration

Tree regeneration (both total and well-spaced) in defoliated stands is a negative function of

shrub cover. *Tsuga heterophylla* and *Abies lasiocarpa* have a particularly negative response to higher shrub cover, indicating lower shade tolerance or poorer competition tolerance than *Thuja plicata*. There also may be other elements of competition that these species are deficient in when compared to *Thuja*. *Picea engelmanii x glauca* is said to have lower shade tolerance than *Tsuga heterophylla* and *Abies lasiocarpa* (Klinka et al. 2000), so the reason for its placement with shade tolerant *Thuja plicata* is unclear. That larger size classes of all species (seedlings and saplings) respond negatively to higher shrub cover may indicate that there is enough light available for germination but not enough for newly established seedlings to grow well.

In general these findings confirm that twenty years following a WHL event, the patterns found by Hoggett and Negrave (2001) seven years after the outbreak continue to persist. Increased canopy mortality (lower canopy density) is associated with increasing cover of understory shrub species, which in turn was negatively correlated with tree regeneration density (Hoggett and Negrave 2001). The degree of canopy mortality is somewhat a function of tree layer composition, but also may reflect proximity to outbreak centers. The trajectory of forest recovery subsequently depends on terrain position and site variables in addition to the degree of canopy opening.

4.2.4.1 Regeneration niche

Autotrophic plants all need light, carbon dioxide, water and the same mineral nutrients (Grubb 1977) but differences in regenerating tree species composition and abundance among

defoliated stands suggest additional requirements for germination and establishment by different species. Species in a community often differ from one another during the regeneration phase of their life cycle (Silvertown 2004). These differences are described by the 'regeneration niche' of each species, which is the component of the niche that is concerned with processes such as seed production and germination and by which one mature individual is replaced by another (Grubb 1977).

The results of the regeneration niche RDA analysis suggest that site index and soil moisture regime are responsible for variation in the composition of the regenerating tree assemblage among defoliated stands of the ITR. There are likely other nuanced differences among stands that were not captured by this study but that matter to the germination, successful establishment, growth and survival of trees. Small-scale heterogeneity within stands affects patterns of regeneration (Harmon and Franklin 1989, Nakashizuka 1989, Hulme 1996). In particular, litter (forest floor) depth has been found to create differential effects on the regeneration success of tree species with different seed mass (Christie and Armesto 2003). Soil organisms are of special interest in stands that have been subject to foliar herbivory (Bardgett et al. 1998, Hunter 2001) and the presence of root mycorrhizae may influence the growth of seedlings (Wright 1963, Clark 1963, Wallander 1995). Herbivory from browsing ungulates may also create differential success of regenerating species in recovering stands (Hulme 1996).

108

4.2.4.2 Regeneration substrate

Conifer regeneration is rarely randomly distributed on the forest floor (Maguire and Forman 1983); young conifer seedlings are associated with particular microsites (Simard et al. 1998). In stands of the ITR that have not experienced a recent WHL outbreak, coarse woody debris (CWD) is common (Stevenson and Keisker 2002, Stevenson et al. 2006). In defoliated stands of the ITR, CWD is the most favourable substrate type. Coarse woody debris may be helping regenerating trees avoid competition with species on the forest floor (Harmon and Franklin 1989, Daniels and Gray 2006) and could also function to hide or block access to regenerating trees from browsing ungulates (Ripple and Larsen 2001).

Since the total availability of CWD was not measured, this study cannot conclude that this substrate is comparatively more important to regenerating trees than either forest floor or mineral soil. Although all regenerating tree species in the ITR use CWD as a substrate, *Thuja plicata* seems to increase its use of CWD as shrub cover increases, appearing to take advantage of this substrate in defoliated stands. This effect is consistent with the results of the plant community analysis showing *Thuja plicata* in stands with higher competitive shrub cover; the presence of CWD in these stands may have facilitated the germination and growth of this tree species. This substrate preference of *Thuja plicata* in shrubby stands has been seen in *Thuja occidentalis* L. as well (Simard et al. 1998).

5.0 Conclusions and synthesis

Forest response to western hemlock looper (WHL) outbreaks in the inland temperate rainforest (ITR) can be quite variable. Overstory recovery appears to be most pronounced on lower productivity sites and in stands with a more severe outbreak history. Forest regeneration is strongly constrained by shrub cover, which is promoted by canopy openness and soil nutrients, both of which can be accentuated by defoliators, as well as being more pronounced on steep slopes. Immediately post-disturbance, shrubs are likely able to react sooner or more strongly than trees to nutrient inputs to the forest floor, particularly in stands with a higher site index, and flourish before regeneration is able to establish or release from a seed bank. Twenty years following a WHL outbreak, the influence of nutrient inputs to the forest floor from the defoliation event may be less important than the effect of canopy openness and stand site index.

Regenerating *Tsuga heterophylla* and *Abies lasiocarpa* have a particularly negative response to higher shrub cover, indicating lower shade tolerance or poorer competition tolerance than *Thuja plicata*, which appears to tolerate stands with higher shrub cover. The reason for this species' apparent tolerance for stands with higher shrub cover might also be its proficient use of CWD, the substrate most commonly used in defoliated stands by all regenerating tree species. *Thuja plicata* appears to take advantage of CWD in order to escape competition with shrubs, but the relative importance of this substrate to *Thuja plicata* or to other species cannot be determined without considering the availability of CWD in all stands, which was not measured in this study. In terms of site characteristics, site index and soil moisture

110

availability are primarily responsible for the niche differentiation among regenerating tree species in defoliated stands of the ITR.

6.0 Management of defoliated stands

The WHL is a natural part of the ITR and plays a critical role in shaping the spatial patterns and functioning of this ecosystem (Rhemtulla et al. 2001, Stevenson et al. 2011). Any management that takes place in the ITR needs to consider maintaining ecological patterns and processes, including those created by this defoliating insect. In anticipation of more suitable conditions for outbreaking insects as climate change proceeds (Haughian et al. 2012), more old forest needs to be protected from harvest in order to mitigate the effects of the WHL. Sound landscape-level management decisions can enhance the resilience of the ITR to climate change (Stevenson et al. 2011), species loss and other human-created impacts.

In addition to landscape-level management, current industrial timber harvesting practices need to be reconsidered, as some studies suggest that they are contributing to an increase in the severity and extent of insect outbreaks (Rhemtulla et al. 2001). In eastern Canada and Oregon, fire suppression, clearcutting and the selective harvesting of non-susceptible species have been found to be primary contributors to an increase in the severity, frequency and area affected by the spruce budworm (Lewis and Lindgren 2000). In the ITR, it has been postulated that large clearcuts in the vicinity of a WHL infestation near Crescent Spur in 2000 may have helped to trigger an outbreak by creating drying winds that increased water stress in adjacent stands (Rhemtulla et al. 2001).

Stand-scale management of defoliated stands for tree production should consider differences in site index, site series, canopy density and annual heat:moisture index among stands.

112

Stands with a higher site index are likely to require much more shrub control than stands with a lower site index; it appears that a multi-species average site index of 16 m @ 50 yrs is optimal for tree regeneration, although this is a weak relationship. Stands with site indices greater than 16 would require silvicultural intervention to accelerate reforestation, although *Thuja plicata* would probably become established without treatment. Stands suitable for regeneration by natural ingress generally have canopy densities over 75%, while stands with an annual heat:moisture index 16 or greater have optimal warmth for the establishment and growth of young trees.

In this study, site series with the lowest site indices were ICHvk2-03, ICHvk2-06 and ICHwk3-07. Stands falling into these site series tended to have higher *Tsuga heterophylla* regeneration with some *Abies lasiocarpa* and *Picea engelmanii* x *glauca* cover and would likely require minimal shrub management. For *Thuja plicata* promotion, stands within the ICHwk3-05 site series are best, and should require little shrub management. In contrast, ICHvk2-01 site series stands also have high cover of *Thuja plicata* regeneration, but also have the highest site index (19.8), thereby making shrubs more abundant and their control more important where tree establishment is required.

The following management guidelines for stand types identified in the hierarchical cluster analysis (Figure 12) will encourage forest regeneration in the understory and recovery in the overstory. Stands found in Group A (Figure 12) will have the poorest overstory recovery potential, as they tend to have the highest site indices (19.8 for vk2-01 stands and 19.6 for wk3-05 stands). These stands have heavy *Oplopanax* cover but also tend to have robust

densities of *Thuja* in the understory. These stands should be left for natural recovery. Manual mechanical release around individual seedlings may accelerate redcedar vigour and growth.

Group B stands (Figure 12) are made up of stands that fall in to site series wk3-05, and so do not have the strongest overstory potential. They do, however, have mixed conifer regeneration, making them a more resilient stand type than Group A stands. B-type stands are likely able to recover naturally, and inherently have more flexibility (diversity) for coping with a changing climate than stands with fewer regenerating tree species.

Group C stands (Figure 12), made up mostly of wk3-01 and vk2-06 site series, have an intermediate level of overstory recovery potential, due to intermediate site indices (19.1 and 17.4 respectively) and mixed conifer regeneration (in particular *Tsuga*). One stand of the site series vk2-03, which has the lowest site index (12.6) and thus the highest overstory recovery potential, fell in the C-type stand grouping because of the similarity of its' understory to wk3-01 and vk2-06 stands. Little shrub cover in C-type stands makes them ideal for underplanting, with light unlikely to be a limiting factor in most stands of this type. C-type stands, like B-type stands appear to be resilient due to the presence of several regenerating tree species in the understory.

In Group D stands (Figure 12), overstory recovery potential is the greatest (save for vk2-03 stands), with wk3-07 stands having a relatively low site index (16). The understory of D-type stands is moss-dominated, with little tree regeneration or shrub cover, most likely because the thick moss carpet inhibits natural regeneration from seed. If the overstory is mostly alive,

it should be left to recover naturally by an infilling crown. If the overstory is mostly dead, Group D stands might benefit from underplanting and standard silvicultural stand renewal practices, which may include salvage logging, mechanical site preparation, and planting. Information about the environmental impacts, implications and limitations of salvage logging can be found in Lindenmayer et al. 2008.

In summary, management of WHL-affected stands in the ITR should be undertaken cautiously. A full range of responses to outbreak severity and site factors were found across stands, and subtle differences between stands classified as similar mean that it is difficult to predict with high precision the outcome of management activities. The ITR is much more robust and resilient to disturbances such as the WHL than expected, so management interventions should rarely be considered "necessary" and require careful planning and restraint where they are carried out.

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