RESPONSE OF SEEDLINGS AND SAPLINGS TO CANOPY GAPS IN COASTAL OLD-GROWTH FORESTS

by

Jennifer A. Passmore
Bachelor of Science (Biology), UBC 2001

PROJECT SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF RESOURCE MANAGEMENT

In the
School
of
Resource and Environmental Management

SIMON FRASER UNIVERSITY

Fall 2007

APPROVAL

Name: **Jennifer A. Passmore**

Degree: **Master of Resource Management**

Title of Project: **Response of Seedlings and Saplings to Canopy Gaps in Coastal Old-Growth Forests**

Report No.: **433**

Examining Committee:

Dr. K. Lertzman
Senior Supervisor
Professor in the School of Resource and Environmental Management, SFU

Dr. Lori Daniels
Supervisor
Assistant Professor in the Department of Geography, UBC

Date Defended/Approved: July 11, 2007

SFU SIMON FRASER UNIVERSITY
LIBRARY

Declaration of Partial Copyright Licence

The author, whose copyright is declared on the title page of this work, has granted to Simon Fraser University the right to lend this thesis, project or extended essay to users of the Simon Fraser University Library, and to make partial or single copies only for such users or in response to a request from the library of any other university, or other educational institution, on its own behalf or for one of its users.

The author has further granted permission to Simon Fraser University to keep or make a digital copy for use in its circulating collection (currently available to the public at the "Institutional Repository" link of the SFU Library website <www.lib.sfu.ca> at: <http://ir.lib.sfu.ca/handle/1892/112>) and, without changing the content, to translate the thesis/project or extended essays, if technically possible, to any medium or format for the purpose of preservation of the digital work.

The author has further agreed that permission for multiple copying of this work for scholarly purposes may be granted by either the author or the Dean of Graduate Studies.

It is understood that copying or publication of this work for financial gain shall not be allowed without the author's written permission.

Permission for public performance, or limited permission for private scholarly use, of any multimedia materials forming part of this work, may have been granted by the author. This information may be found on the separately catalogued multimedia material and in the signed Partial Copyright Licence.

While licensing SFU to permit the above uses, the author retains copyright in the thesis, project or extended essays, including the right to change the work for subsequent purposes, including editing and publishing the work in whole or in part, and licensing other parties, as the author may desire.

The original Partial Copyright Licence attesting to these terms, and signed by this author, may be found in the original bound copy of this work, retained in the Simon Fraser University Archive.

Simon Fraser University Library
Burnaby, BC, Canada

Revised: Fall 2007

ABSTRACT

Fine-scale disturbances involving the death of one to a few trees create gaps in the forest canopy and, where large-scale disturbances are rare, exert a dominant influence on community and population dynamics. I examine the natural regeneration and recruitment of seedlings and saplings following fine-scale, gap forming disturbances in old-growth stands within the Capilano, Seymour and Coquitlam River watersheds. I compared the abundance of western redcedar, western hemlock, and Pacific silver fir seedlings and saplings between plots located within and adjacent-to 20 gaps of known date of origin. I also destructively sampled seedlings and saplings of each species and applied dendroecological methods to determine the age of each sample, and to elucidate patterns of suppression and release in radial growth. My results support the paradigm of gap-scale canopy replacement. Seedlings and saplings were more abundant in gap versus forest environments, and exhibited increased rates of establishment and radial growth.

Keywords: canopy gap; temperate rainforest; *Tsuga heterophylla; Abies amabilis; Thuja plicata;* forest dynamics

ACKNOWLEDGEMENTS

I extend my sincere thanks to Amanda Stan, whose concurrent Ph.D. research provided much of the context, methods and analyses essential to this study. Many of the seedlings and saplings collected for my research were laboriously packed out of the forest on Amanda's shoulders. I also thank my supervisors, Ken Lertzman and Lori Daniels, for their extensive and helpful advice, expertise and support. In addition, I am indebted to my friends, classmates and family for their encouragement and good humour. And finally, I extend a special thanks to Erik for his patience and understanding.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

In forests where large, stand-replacing disturbances are rare, fine-scale disturbances forming small gaps in the canopy provide new opportunities for recruitment and regeneration and have a dominant influence on community and population dynamics (Lertzman et al. 1997, Spies and Franklin 1989, Spies et al. 1990). Fine-scale disturbances distributed over time and space influence structural attributes such as the range of tree sizes, the abundance of large snags and coarse woody debris, and the horizontal and vertical heterogeneity of the canopy (Franklin et al. 2002). These structural attributes influence resource availability, microclimate, ecosystem functions such as production and nutrient cycling, and community dynamics such as the recruitment and regeneration of canopy trees, and the abundance, composition, and diversity of shrubs, herbs, birds, insects, and small mammals (Coates and Burton 1997). The structural heterogeneity that results from fine-scale disturbance also characterizes and distinguishes old-growth forests from earlier seral stages (Wells et al. 1998).

In the coastal old-growth forests of British Columbia and the Pacific Northwest, large, stand-replacing disturbances are rare, and disturbances involving the death of one to a few canopy-class trees dominate ecosystem dynamics (Daniels 2003, Daniels and Gray 2006, Franklin et al. 2002, Lertzman and Krebs 1991, Lertzman et al. 1996, Spies and Franklin 1989, Wells et al. 1998). However, the characteristics and effects of fine-scale disturbances in this region have been investigated in only a limited subset of ecosystem types. Most interest has focused within the Douglas-fir and western hemlock dominated forests of coastal Washington and Oregon where extensive research has quantified historic fine-scale disturbance regimes (Spies et al. 1990, Winter et al. 2002), the effects of gaps on abiotic factors such as photosynthetically active radiation, soil moisture, and air temperature (Gray et al. 2002, Mariscal et al. 2004), and the effects of gaps on regeneration and recruitment (Christy 1986, Gray and Spies 1996, Gray and Spies 1997, Stewart 1986, Van Pelt and Franklin 1999). In coastal BC, gap-based research is considerably less extensive and has focused on quantifying gap-phase structure (Arsenault 1995, Daniels 1994, Lertzman and Krebs 1991, Lertzman et al 1996), and the effects of gaps on regeneration and recruitment (Brang and Lertzman unpublished manuscript, Daniels 1994, Daniels and Klinka 1996, Lertzman 1992) within higher elevation motane forests dominated by mountain hemlock and Alaska yellow-redcedar. Gap-based research in the mid-elevation coastal western hemlock forests of British Columbia is limited to investigations of the spatial distribution of fine-scale disturbances across stands, and the effects of gaps on the spatial distribution of seedlings and saplings (Arsenault 1995, Daniels 1994, Lertzman et al 1996). In these mid-elevation forests, it is assumed that gaps provide opportunities for canopy accession, but the responses of seedlings, saplings, and sub-canopy and canopy trees to gap-formation have not been quantified. The paucity of research regarding the characteristics and effects of fine-scale disturbances across the range of BC's coastal ecosystem types is particularly confounding given the global significance these forests. Coastal British Columbia boasts the largest tracts of undeveloped temperate rainforest in the world (MacKinnon 2003).

An understanding of the dynamics and effects of fine-scale disturbance regimes is increasingly relevant to forest management in British Columbia. Many contemporary forest conservation and management problems are attributed to differences between forest management practices and natural disturbance regimes (Lertzman et al. 1997). Increased appreciation for the resilience and sustainability of natural ecosystems has fostered support for the use of natural disturbance regimes as models for forest management, an idea consistent with the principles of ecosystem management (Grumbine 1994, Grumbine 1997, Holling and Meffe 1996, Landres et al. 1999). For example, an understanding of the historic spatial and temporal distribution of fine-scale disturbances in a particular forest type can be used to direct management actions such as the size and distribution of patch cuts (Coates and Burton 1997, Ott and Juday 2002). This information is particularly relevant to variable retention harvesting, which, only 11 years after its conception in 1995, is currently applied to between 50% and 60% of BC's coastal forest region (Swift, 2006). Although this method of harvest is more akin to patterns of natural disturbance (Beese et al. 2003, Mitchell and Beese 2002, Clayoquot Sound Scientific Panel 1995), the trade-offs associated with different types and levels of retention are not well understood, and retention levels based on natural fine-scale disturbance regimes are prudent management targets. Further, understanding the specific effects of gaps on ecosystem dynamics will enable forest managers to predict how human-made gaps might influence forest dynamics, and to assess how human-made gaps compare to natural gaps in form and function. Our limited understanding of gap-phase processes in BC's coastal old-growth forests hinders the application and evaluation of ecosystem-based management.

Knowledge of natural patterns of disturbance and recovery also contribute to our understanding of succession and co-existence in mixed-species stands. Competing ecological theories regarding the mechanisms responsible for co-existence within mixed stands has spurred considerable research concerning patterns of replacement in gaps (Brokaw and Busing 2000, Denslow 1980, Grey and Spies 1996, Lertzman 1992, Veblen 1986, Wright et al. 1998). Grubb (1977), hypothesized that the different establishment requirements (regeneration niches) of otherwise similar tree species may explain their ability to co-exist under niche theory. For example, in tropical forests, diversity in gap sizes may account for the co-existence of large- and small-gap specialists (Denslow, 1980). Conversely, Connell (1978) attributes the co-existence of forest species to the role of canopy gaps in maintaining non-equilibrium conditions, and preventing competitive exclusion. For example, in a tropical Panamanian forest, the stochastic distribution of fine-scale disturbances in space and time, coupled with the limited distribution of advanced regeneration, promotes species richness by sustaining high stem densities (Brokaw and Busing 2000). Competitive balances between species may also vary with disturbance history (Wright *et al.* 2000).

To better understand the response of seedlings and saplings to fine-scale disturbances in the Coastal Western Hemlock Zone of British Columbia, I examined patterns of regeneration and recruitment within and adjacent-to canopy gaps of known date of origin. I compared the abundance of Pacific silver fir (*Abies amabalis* (Dougl. Ex Loud.) Dougl. Ex J. Forbes), western redcedar (*Thuja plicata* Donn ex D. Donn), and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) seedlings and saplings within and between gap and closed-canopy environments, and between species. I applied dendroecological techniques to determine the ages of seedlings and saplings, and to ascertain patterns of suppression and radial-growth release over the duration of each chronology. I compared patterns of establishment and release between seedlings and saplings collected from gap and closed-canopy environments, and between species, with a particular focus on the time-period that brackets each gap-formation date. In addition, to investigate the influence of large-scale phenomena such as climate on patterns of radial growth, I compared patterns of release between gaps.

Based on my assumptions about light limitation in the understory, and the positive effects of gaps on light availability, I began this research with a number of expectations. First, I expected gaps to support higher densities of seedlings and saplings, and for these increases in abundance to be most pronounced in the northern and western portions of the gap (the sunniest portions). Second, I expected gap-formation to increase rates of establishment and/or survival in new recruits, and therefore, for a greater proportion of the seedlings and saplings in gap plots to have established around the dates of gap formation. Third, I expected gaps to increase rates of radial and vertical growth in seedlings and saplings, resulting in greater rates of initial growth in seedlings and saplings that established in gap plots around the dates of gap-formation, greater incidence of radial growth release for seedlings and saplings already existing in gap plots, larger magnitudes of release, and taller or younger populations of seedlings and saplings. Fourth, I expected fine-scale phenomena such as competition, rather than large-scale phenomena such as climate, to be the main factor limiting growth in seedlings and saplings. Therefore, I expected patterns of radial growth release to be asynchronous between gaps.

STUDY AREA

This research was conducted in the Coquitlam, Capilano and Seymour River watersheds in the Coast Mountains of southwestern British Columbia (Figure 1). The watersheds occupy 53,600 ha of area and, under the management of the Greater Vancouver Regional District (GVRD), supply Greater Vancouver's drinking water (Acres International 1999). Similar to other watersheds in the Pacific Ranges of the Coast Mountains, the Coquitlam, Capilano and Seymour River watersheds are characterized by rugged topography and steep slopes. The typical range of relief is between 900 and 1300 m (Acres International 1999). Steep slope, coarse-skeletal, Ferro-Humic Podzals are the dominant soil types. These soils lie atop a granite bedrock and derive from deposits of colluvium and glacial till following the last glacial maximum (Agricultural Canada Expert Committee on Soil Survey 1987). Most of the areas in the watersheds comprise ecosystems in the Coastal Western Hemlock (CWH) and Mountain Hemlock (MH) biogeoclimatic zones. A small proportion of the watersheds comprise the Alpine Tundra (AT) biogeoclimatic zone (Acres International 1999).

My study sites were located between 400m and 700m in elevation, within the Very Wet Maritime Coastal Western Hemlock (CWHvm) biogeoclimatic subzone. The CWHvm biogeoclimatic subzone is dominated by a very wet, cool, mesothermal climate (Klinka et al. 1991). Mean monthly temperatures range from 16.0 to 0.3 °C, with an annual mean temperature of 8.2 °C (Canadian Climate Program 1993). Mean annual precipitation is 2787 mm, of which 752 mm falls during the summer growing season

(Canadian Climate Program 1993). Dominant tree species within the CWHvm biogeoclimatic subzone of the GVRD watersheds are western hemlock, Pacific silver fir, and western redcedar (Acres International 1999). All three species are classified as very shade tolerant (Klinka et al. 1992a, Klinka et al. 1992b). We also occasionally observed remnant Douglas-fir in the canopy. Most un-logged stands in the GVRD watersheds are considered old-growth due to their structural complexity and the advanced age of canopy-class trees (Acres International 1999). In these particular stands, western hemlock, Pacific silver fir and western redcedar are known to reach diameters at breast height of 120cm, 100cm, and 250 cm, respectively, and ages of 450 yrs, 360 yrs and >1000 yrs, respectively (Daniels 1994). Further, age records from nearby stands show that pacific silver fir and western hemlock can reach much greater ages of 697 and 944 years, respectively (Lertzman 1989).

METHODS

Data Collection

This research was conducted in conjunction with a larger study undertaken by A. Stan (Stan, in progress). Over the course of three field seasons, Stan located stands of old-growth forest in the Coquitlam, Seymour, and Capilano River watersheds and identified canopy gaps formed by the uprooting of large, canopy-class trees (gap-makers). Gaps were selected based on a series of criteria including the approximate date of gap-maker death and fall, and the extent of closed-canopy forest surrounding each gap. Gap-makers lacking intact bark, gaps formed by multiple gap-makers, gaps existing adjacent to edaphic features such as streams or rocky outcrops, and gaps in close proximity to harvested areas and/or roads were avoided.

Stan estimated the dates of gap-formation using a combination of dendroecological techniques. To determine the year each gap-maker died, they cored the gap-makers and crossdated their outer-most rings. To determine the year each gap-maker fell, seedlings or saplings that were obviously injured when the gap-maker fell to the forest floor were collected, and their scars or reaction wood were crossdated. To provide a minimum estimate of the date of tree-fall, Stan also aged seedlings and saplings growing on the up-turned root-ball. These methods provided independent dates for gap-maker death and fall.

Although all of the canopy gaps I sampled within were formed by wind-throw, many of the gap-makers died before they fell (Stan in progress). More specifically, when both dates were available, outer-ring dates often preceded scars or reaction-wood dates, and it is likely that many gaps were not formed as a discreet event. Between 2002 and 2005, Stan identified and dated a total of 20 gaps. The dates of gap-formation ranged between 1965 and 2001, and the gaps ranged in size between 118 m^2 and 560 m^2 (expanded gap size) or 28m^2 and 157m^2 (canopy gap size). The expanded gap is defined by the boles of the trees whose canopies define the canopy gap. The canopy gap is defined by the vertical projection onto the ground of the opening in the forest canopy caused by the mortality of a tree (Lertzman and Krebs 1991).

At each of the 20 gaps, Stan identified and mapped boundary trees in relation to the top of the root-ball of the gap-maker. I subsequently established four two-by-two meter plots within the gap (gap plots), and four two-by-two meter plots in the surrounding closed-canopy forest (forest plots). I positioned plots along transects that ran in the four cardinal directions from the top of the root-ball. Gap plots were positioned along each transect halfway between the top of the root-ball and the boundary of the expanded gap (i.e. the opening in stems defined by the centres of the boles of the boundary trees). Forest plots were positioned 10m into the forest from the boundary of the expanded gap (Figure 2). If such a location for a forest plot landed in another gap (edaphic or developmental), I first attempted to shift the plot 5 meters to the right or left of the transect. If this shift failed to place the plot under closed-canopy forest, I extended the transect to the edge (expanded gap boundary) of the secondary gap and continued another 10 meters along the transect. One of these two steps usually sufficed for locating closed-canopy conditions. However, due to the prevalence of gaps in these forests, two of the 20 study sites provided only three suitable forest plots each.

Within each two-by-two meter plot, I measured the abundance of Pacific silver fir, western redcedar and western hemlock seedlings and saplings in five height classes. Height class 1 included seedlings less than 10 cm in height and greater than 1 year in age (i.e. new germinants with cotyledons but without true leaves were not included). Height class 2 included seedlings between 10 and 30 cm in height. Height class 3 included seedlings between 30 and 130 cm in height. Height class 4 included saplings between 130 and 300 cm in height. Height class 5 included saplings greater than 300 cm in height but less than 10 cm in diameter at breast height (130cm).

Within each of the three watersheds, I selected two nearby gaps for more intensive dendroecological investigation. These focal gaps were selected based on the degree of confidence in their dates of origin. The two gaps selected from the Capilano watershed (CAP-GA and CAP-GB) are estimated to have formed in 1995 and 1999, and were 351m^2 and 383m^2 in size (expanded gap), respectively; the two gaps from the Seymour watershed (SEY-GA and SEY-GB) are estimated to have formed in 1992 and 1998, and were 429m^2 and 381m^2 in size (expanded gap), respectively; the two gaps from the Coquitlam watershed (COQ-GA and COQ-GB) are estimated to have formed in 1986 and 1985, and were 359m^2 and 127m^2 in size (expanded gap), respectively. From this subset of 6 study sites, I destructively sampled Pacific silver fir, western redcedar and western hemlock seedlings (30-130cm in height) and saplings (>130cm in height but < 5cm dbh) by sawing or clipping the trees at the root collar. From the four, two-by-two meter plots located in each gap I randomly sampled up to 5 seedlings and 5 saplings of each species. This sampling strategy provided a total of six gap replicates (CAP-GA, CAP-GB, COQ-GA, COQ-GB, SEY-GA, SEY-GB) for each species and height class, with approximately 5 sub-samples in each grouping (Table 1). From the four forest plots surrounding each gap I randomly sampled up to 3 seedlings and 3 saplings per species. I collected fewer seedlings and saplings from the forest plots because tree regeneration tended to be scarce there. Because the two gaps selected in each watershed were in close proximity to each other, I pooled the seedling and sapling subsamples collected from forest plots. This sampling strategy provided a total of three forest replicates (CAP-F, COQ-F, SEY-F) for each species and height class, with approximately six seedling and sapling sub-samples in each species and height class. When seedlings and sapling densities in the two-by-two meter plots were insufficient for a balanced study design, I sampled the nearest individuals growing adjacent to the plots. Nevertheless, I was not always successful in obtaining complete sets of sub-samples and, in particular, western redcedar saplings were so rare, I excluded them from further analyses (Table 1).

I measured the height of each seedling and sapling by measuring the distance between the root collar and the tip of the longest leader. In the lab, I used a chop-saw to remove basal discs from the seedlings and saplings and calculated the basal diameter of each sample by taking the average of the widest and narrowest diameter of the disks. To determine ages and growth rates, I processed the basal disks from seedlings and saplings according to standard dendroecological techniques (Stokes and Smiley 1968). I sanded the basal disks using sandpaper of increasingly finer grit to expose the annual rings. I dated the annual growth rings along two perpendicular radii for each disk and attempted to visually cross-date the radii within and between samples of the same species using marker-rings (Yamaguchi 1991). I measured ring-widths to the nearest 0.001 mm along one or two radii of each disk using a Velmex bench interfaced with a computer. Due to the prevalence of asymmetric radial growth and incomplete rings, I was not able to measure all samples along two radii.

Visual cross-dating of ages was statistically verified using the program COFECHA (Grissino-Mayer 2001). Independent analyses were conducted for each species and size class (seedlings and saplings). Due to the limited length of some chronologies, I set COFECHA to conduct analyses using segment lengths of 30 years and lags of 10 years. Nevertheless, chronologies for most seedlings and some saplings were too short to cross-date with meaningful statistical power. Radii with crossdating errors were re-examined under the microscope and compared with other radii around the circumference of the disk to identify incomplete rings. I corrected measurement files by inserting zero values for the incomplete rings and verified the corrections by reassessing the series in another iteration of COFECHA analyses. Several iterations of COFECHA correctly identified numerous missing rings that I subsequently located upon repeated observation of the samples. I did not modify the measured ring-width series for the cases in which COFECHA indicated that at least 1 ring was missing, but for which I was not able to locate any incomplete rings.

For samples with one crossdated radius, I calculated the average ring width to estimate mean growth rate over the lifespan of the individual. For samples with two crossdated radii, I averaged the two series to represent growth rates through time and then calculated the average ring width to estimate mean growth rate over the lifespan. The calendar year of the pith estimated the date of establishment for each seedling and sapling. Therefore, the age of each sample was determined by subtracting the year attributed to the pith from the year the sample was harvested. Because I harvested seedlings and saplings at the root collar and all samples included the pith, no age-corrections were required.

Data Analyses

Abundance

For the 20 gaps, I compared the abundance of seedlings and saplings between species (Pacific silver fir/western redcedar/western hemlock), height classes (1-5), locations (gap/forest) and directions (plot position relative to gap centre: N-S-E-W). I evaluated the effects of each variable on mean abundance using a randomized complete block design in JMP version 5.0.1. I analyzed two different combinations of variables:

1. Location (gap versus forest), direction (plot position relative to gap-centre) and height class, assessed independently for each species.
2. Location (gap versus forest), direction (plot position relative to gap centre) and species, assessed independently for each height class.

In each analysis, the study site was a random variable (block) and I tested for interactions between the effects of each variable on abundance. Due to the prevalence of zero-counts, I transformed the data using a square-root function prior to analysis.

Size, Age and Growth

All other analyses were based on the sizes, ages and growth rates of the seedlings and saplings destructively sampled at the subset of six focal gaps. I examined the effect of gap-formation on tree regeneration by comparing the mean height, basal diameter, age and average radial growth of Pacific silver fir and western hemlock saplings, and Pacific silver fir, western redcedar, and western hemlock seedlings in the gap versus forest plots. For each size class (saplings and seedlings), I conducted statistical comparisons between species and locations using a randomized complete block design in JMP version 5.0.1. In each analysis, the watershed was a random variable (block) and I tested for interactions between the effects of location and species on mean height, basal diameter, age and radial growth. I also examined relationships between age and height, and age and diameter using regression analyses in JMP version 5.0.1.

Establishment

To test the effects of gap-formation on patterns of establishment, I compared the proportions of seedlings and saplings that established within 10 years of the gap-formation date between gap and forest sites. This analysis was conducted at two spatial scales. First, to investigate the effects of gap-formation on the overall frequency of establishment across gaps, I compared the total proportion of samples that established within 10 years of the gap-formation dates between gap and forest plots. Second, to investigate the effects of gap-formation at the scale of individual gaps, I conducted separate analyses that compared the samples from each gap with their corresponding forest sample. In the latter analyses, each forest sample was compared to two gap samples. Statistical comparisons were made using Fisher's exact test of proportions in Sigma Stat version 2.03. I selected Fisher's exact test of proportions over a chi-squared test because, when the analyses were divided into separate watersheds, average expected frequencies were less than 6.0 (Zar 1996).

I examined the effects of gaps on recruitment by comparing the initial growth rates of seedlings and saplings that established within 10 years of the gap-formation date between gap and forest sites. I approximated rates of initial growth by averaging ring widths over the first five and 10 rings closest to the pith, and conducted separate comparisons using each measure. Although I pooled data for the seedling and sapling size classes, replication was insufficient and limited the analyses to graphical comparisons between the gap and forest sub-samples.

I examined the effects of gaps on tree establishment and growth by comparing the initial growth rates of seedlings and saplings that established in gap plots within 10 years of gap-formation (gap-regeneration)) to those that established at least 10 years prior to gap-formation (pre-gap regeneration). Due to the limited amount of gap-regeneration, I pooled the seedling and sapling size classes. Statistical comparisons between species, and between the growth rates of gap-regeneration and pre-gap regeneration, were conducted using a completely randomized block design in JMP version 5.0.1. I performed separate analyses for 5-year and 10-year measures of initial growth. Each comparison tested for interactions between the effects of species and the timing of regeneration and indicated the watershed as a random variable (block).

Radial Growth Releases

I interpreted patterns of radial growth to identify and quantify releases within the ring-width series representing the lifespan of each sample. I identified radial-growth releases based on the relative growth criteria outlined by Nowaki and Abrams (1997), as follows. Increases and decreases in radial growth were quantified by calculating a running mean of percent-growth-change (%GC) over a 5-year window (Figure 3). A release occurred when %GC exceeded the threshold value of +100%. The precise year each release began was defined as the year following the maximum %GC within 5-years of exceeding the 100% GC threshold (Nowaki and Abrams 1997) (Figures 3 and 4).

I calculated the duration of each release by subtracting the year a release began from the year it ended. The year a release ended was determined using a novel "frozen running-mean" technique. This technique compares average ring width during the five-year period immediately prior to a release (*e.g.*, a 5-year window "frozen" in time) to a running mean of ring widths following the release (Figure 3). The frozen running mean technique results in a measure of frozen-%GC (F%GC). When the F%GC decreased and remained below the 100% threshold for ≥ 2 consecutive years, I considered the release terminated (Figures 3 and 4). Similar to the beginning of a release, I designated the precise year of termination as the year following the minimum %GC within 5-years of the F%GC decreasing below 100%. When the F%GC did not decrease below 100% following a release, the release was classified as a "sustained" and no end date was assigned.

I attributed all releases which began within ±10-years of the gap-formation dates determined by Stan (in progress) to gap-formation. I quantified and analyzed the growth history of individuals prior to the period bracketing gap-formation and during the period bracketing gap-formation in two sets of independent analyses.

To investigate patterns of release that were independent of the dated gaps, I excluded releases attributed to gap-formation by truncating each ring-width series 10-years prior to the year of gap formation. From this remaining (pre-gap) portion of each ring-width series, I calculated the proportion of samples in each species and size class showing at least one release. I also identified all pre-gap releases in each sample and quantified four attributes of release: the total number of releases, the release rate per century, the mean duration of release, and the proportion of lifespan spent in release. For each species and size class, I compared these four release attributes using a completely randomized block design in JMP version 5.0.1. Each analysis indicated the watershed as a random variable (block).

I visually assessed the synchrony of releases among gaps by plotting patterns of release over time. For each gap I plotted years in which at least 2 samples initiated release. I also calculated the number of years in which various numbers of gaps (ranging from zero gaps to all six gaps) concurrently initiated at least two releases.

For the releases resulting from the formation of gaps of known date (i.e. releases occurring within 10 years of the date of gap-formation), I compared the proportions of seedlings and saplings that released between gap and forest sites. I conducted statistical comparisons between gap and forest plots at two spatial scales using Fisher's exact test of proportions in Sigma Stat version 2.03. To investigate the effects of gap-formation on the overall frequency of release among gaps, I compared the total proportion of sub-samples releasing in gap versus forest plots. To investigate the effects of gap-formation at the scale of individual gaps, I compared each gap sample with its corresponding forest sample.

To understand how gap-formation affected patterns of radial growth within the expanded gap relative to the surrounding closed-canopy forest I compared observed and expected numbers of release for the 21-year periods bracketing each date of gap-formation between gap and forest sites. I estimated the expected frequencies of release using the release rate per century, calculated from the ring-width series of each sample and summarized for each species, size class and site. Because the SEY-GA, CAP-GA and CAP-GB gaps were formed fewer than 10 years ago, I calculated their expected frequencies using a reduced (<21-year) time-period. Further, expected frequencies for the SEY-F and CAP-F sites were calculated according to the average of the time periods used to calculate expected frequencies in the corresponding gap sites. Comparisons between observed and expected frequencies of release were conducted at two spatial scales using Fisher's exact test of proportions in Sigma Stat version 2.03. Among watersheds, I compared the total proportions of sub-samples observed and expected to release in gap versus forest plots. At the scale of individual gaps, I compared the proportions of observed and expected releases between each gap sample and its corresponding forest sample. At each scale of analysis, I conducted separate comparisons for each species and size class.

For seedlings and saplings that released within 10 years of gap-formation, I compared the lag between disturbance and release, the duration of release, and the magnitude of release between species and locations. I calculated lag as the difference in years between the date of gap-formation and the year the each release began; duration as the difference (in years) between the beginning and end of release; and magnitude as the maximum %GC observed in the five-year running mean. I tested for the effects of species and plot location using a completely randomized block design in JMP version 5.0.1. Separate analyses were conducted for each attribute and size class. In each analysis the watershed was a random variable (block) and I tested for interactions between the effects of location (gap versus forest) and species on mean lag, duration, and magnitude of release. I also investigated the relationship between release magnitude and age using regression.

In a final set of tests, I calculated differences in growth rates before and after gap formation for all seedlings and saplings using 5-yr and 10-yr windows. For each size class and time-window I compared mean %GC between gap and forest sites and among species using a completely randomized block design in JMP version 5.0.1. In each analysis the watershed was a random variable (block) and I tested for interactions between the effects of location and species on mean %GC. These analyses allowed a more complete evaluation of disturbance-induced growth changes because they included the full range of changes in radial growth following gap formation. Similar to release magnitude, I also investigated the relationship between age and %GC using regression.

RESULTS

Abundance

Effect of location (gap versus forest), direction (plot position relative to gap centre) and height class, assessed independently for each species

The abundance of Pacific silver fir increased between height classes 1 and 3 and decreased between height classes 3 and 5 (Figure 5). Differences were significant between all non-adjacent height classes, except classes 1 and 4. Differences between classes 1 and 2 and classes 3 and 4 were also significant ($P<0.001$). On average, and for height classes 1 to 4, Pacific silver fir was more abundant in gap (0.64 ± 0.14 stems) (mean +/- SD) than forest (0.49 ± 0.14 stems) plots; however, this difference was not significant ($P=0.11$). Pacific silver fir abundance did not vary significantly with direction ($P=0.58$), nor were there any significant interactions between location and height class ($P=0.38$), direction and height class ($P=0.86$), or direction and location ($P=0.11$).

The abundance of western hemlock varied inversely and significantly with height class ($P<0.001$), and significantly with location ($P=0.001$). Differences in western hemlock abundance between gap and forest plots were not similar between height classes and there was a significant interaction between the effects of height class and location on western hemlock abundance ($P=0.001$). Although western hemlocks were more abundant in gap versus forest plots across height classes 1 to 4, seedlings in height class 1 exhibited the greatest difference in abundance between gap (10.97 ± 1.15 stems) and forest (2.75 ± 1.15 stems) plots, while saplings in height class 5 exhibited a greater abundance in forest versus gap plots (Figure 5). Western hemlock abundance did not vary significantly with direction (P=0.46); nor were there any significant interactions between direction and height class (P=0.97), or direction and location (P=0.80).

The abundance of western redcedar varied inversely and significantly height class (P<0.001), and significantly with location (P<0.001). Further, differences in the abundance of western redcedar between gap and forest plots were not similar between height classes and there was a significant interaction between the effects of height class and location on western redcedar abundance (P<0.001). Although western redcedar was more abundant in gap versus forest plots across height classes 1 to 4, those in height class 1 exhibited the greatest difference in abundance between gap (1.65 ± 0.17) and forest (0.19 ± 0.17) plots (Figure 5). Western redcedar in height class 5 were not observed in either location. The abundance of western redcedar did not vary significantly with direction (P=0.91); nor were there any significant interactions between direction and height class (P=0.96) or direction and location (P=0.80).

Effect of location (gap versus forest), direction (position relative to gap centre) and species, assessed independently for each height class

The abundances of seedlings and saplings varied significantly with species and/or location in all height classes. Only the abundance of western hemlock saplings in height class 5 varied significantly with direction (orientation from plot centre: N, S, E, W).

The abundance of seedlings in height class1 varied significantly with species (P<0.001) and location (P<0.001). The abundance of western hemlock (6.86 ± 0.95) was much greater than that of Pacific silver fir (0.55 ± 0.95) and western redcedar (0.92 ± 0.95), and together, all three species were more abundant in gap (4.45 ± 0.83) versus forest (1.12 ± 0.82) plots (Figure 6). Further, because the difference in mean abundance between gap and forest plots was greatest for western hemlock and smallest for Pacific silver fir, there was a significant interaction between the effects of species and location on abundance (P=0.002). The abundance of seedlings in height class 1 did not vary significantly with direction (P=0.93), nor were there any significant interactions between the effects of direction and species (P=0.89), or direction and location (P=0.32).

The abundance of seedlings in height class 2 varied significantly with species (P<0.001) and location (P=0.04). The abundance of western hemlock (3.82 ± 0.59) was significantly higher than that of Pacific silver fir (0.95 ± 0.59) and western redcedar (0.21 ± 0.59), and together, all three species were more abundant in gap (1.87 ± 0.50) versus forest plots (1.46 ± 0.50) (Figure 6). The abundance of seedlings in height class 2 did not vary significantly with direction (P=0.58), nor were there any significant interactions between the effects of species and location (P=0.63), direction and species (P=0.90), or direction and location (P=0.2527).

The abundance of seedlings in height class 3 varied significantly with species (P<0.001) but not location (P=0.17). The abundances of western hemlock (2.05 ± 0.27) and Pacific silver fir (1.06 ± 0.27) were each significantly greater than that of western redcedar (0.13 ± 0.27) (Figure 6). However, abundances in gap plots (1.13 ± 0.23) were only marginally greater than those in forest plots (1.03 ± 0.23). The abundance of seedlings in height class 3 did not vary significantly with direction (P=0.49), nor were there any significant interactions between the effects of species and location (P=0.86), direction and species (P=0.79), or direction and location (P=0.90).

The abundance of saplings in height class 4 varied significantly with species ($P<0.001$) and location ($P=0.05$). The abundances of western hemlock (0.33 ± 0.05) and Pacific silver fir (0.19 ± 0.05) were significantly higher than that of western redcedar (0.01 ± 0.05), and together, all three species were more abundant in gap (0.22 ± 0.04) versus forest (0.13 ± 0.04) plots (Figure 6). The abundance of saplings in height class 4 did not vary significantly with direction ($P=0.42$), nor were there any significant interactions between the effects of species and location ($P=0.43$), direction and species ($P=0.79$), or direction and location ($P=0.83$).

The abundance of saplings in height class 5 varied significantly with species ($P<0.001$) and location ($P=0.05$). The abundance of western hemlock (0.19 ± 0.02) was significantly greater than that of Pacific silver fir (0.07 ± 0.02) and western redcedar (0.00 ± 0.02). In contrast to height classes 1 to 4, all three species were more abundant in forest (0.11 ± 0.02) versus gap (0.06 ± 0.02) plots (Figure 6), and the abundance of saplings in height class 5 varied considerably (though not significantly) with direction ($P=0.07$). The majority of the difference in abundance between directions was due to variations in the abundance of western hemlock, and there was a significant interaction between the effects of species and direction on abundance ($P=0.004$). A significantly greater number of western hemlocks in size class 5 were observed in north (0.20 ± 0.05) and east (0.40 ± 0.05) plots than in south (0.08 ± 0.05) and west (0.10 ± 0.05) plots (Tukey HSD). There were no significant interactions between the effects of species and location ($P=0.35$), or direction and location ($P=0.82$).

Growth and Age

Mean heights of seedlings and saplings varied significantly with species but not location (Table 2). Western hemlock saplings were significantly taller than Pacific silver fir saplings. Similarly, western hemlock seedlings were significantly taller than western redcedar seedlings, and both were significantly taller than Pacific silver fir seedlings. Saplings from forest plots were marginally taller than saplings from gap plots. Seedlings from gap and forest plots were remarkably similar in height. For both saplings and seedlings there were no significant interactions between the effects of species and location on mean height.

Mean basal diameters of saplings varied significantly with species and location, while mean basal diameters of seedlings varied significantly with species only (Table 2). Pacific silver fir saplings were significantly larger in basal diameter than western hemlock saplings, and Pacific silver fir seedlings were significantly larger in basal diameter than western redcedar and western hemlock seedlings. Saplings from forest plots were significantly larger in basal diameter than those collected from gap plots. In contrast, seedlings from forest plots were marginally smaller in basal diameter than those collected from gap plots. For both seedlings and saplings there were no significant interactions between the effects of species and location on mean basal diameter.

Mean ages of saplings varied significantly with location and species, while mean ages of seedlings varied with species only (Table 2). Saplings collected from forest plots were significantly older than those from gap plots, while seedlings collected from forest plots were only marginally older than those from gap plots. Pacific silver fir saplings were significantly older than western hemlock saplings, and Pacific silver fir seedlings were significantly older than both western redcedar and western hemlock seedlings. For both saplings and seedlings, there were no significant interactions between the effects of species and location on mean age.

The mean overall growth rates of saplings and seedlings did not vary significantly with location or species (Table 2). Although saplings and seedlings collected from forest plots grew at marginally lower rates of mean radial growth than saplings and seedlings collected from gap plots, these differences were not significant. Similarly, although mean radial growth in western hemlock saplings was marginally higher than that in Pacific silver fir saplings, and mean radial growth in western redcedar seedlings was marginally higher than those in Pacific silver fir and western hemlock seedlings, there were no significant differences between species. For both seedlings and saplings there were no significant interactions between the effects of species and location on mean radial growth. Though no formal statistical comparisons were made between size classes, mean growth rates in saplings were substantially greater than those in seedlings.

The height of seedlings and saplings was not strongly correlated with age (adjusted $r^2 = 0.25$) (Figure 7). Instead, average basal diameter was a better predictor of seedling and sapling age (adjusted $r^2 = 0.56$) (Figure 8). Separate analyses of seedlings and saplings sampled from forest and gap plots yielded lower values of adjusted r^2.

Establishment

For each of the three species, a greater proportion of seedlings and saplings established within 10 years of the gap formation dates in gap versus forest plots (Figure 9a). These differences were significant for Pacific silver fir (P=0.04) and western hemlock (P=0.01), but not for western redcedar (P=0.08). Differences between gap and forest plots were more complex when considered at the scale of individual gaps (Figures 9b-9d). For example, for Pacific silver fir seedlings and saplings, differences in establishment between gap and forest plots were significant only for the comparison between the COQ-F and COQ-GA sites (P=0.03). In fact, four of the seven Pacific silver fir samples estimated to have established within 10-years of the gap-formation date occurred in the COQ-GA sample. Similarly, for western hemlock seedlings and saplings, differences were significant for the COQ-GB versus COQ-F (P=0.005) and SEY-GA versus SEY-F (P=0.002) comparisons only. All other sites exhibited similar proportions of western hemlock establishment between gap and forest plots. Moreover, western redcedars in the COQ watershed exhibited an opposite trend; a marginally greater proportion of western redcedars were estimated to have established within 10 years of the gap-formation date in the forest site than in either of the gap sites.

Seedlings and saplings that established within 10-years of the gap-formation dates exhibited higher rates of average initial growth (ring widths) in gap versus forest plots. Average initial growth rates over the first 10 years of growth for all seedlings and saplings that germinated in gap plots within 10 years of the dates of gap formation (0.31 mm/yr) were nearly two times greater than those of seedlings and saplings that germinated in forest plots (0.17 mm/yr) during the corresponding time-periods (Figure 10). Average initial growth rates based on the first 5 years of growth yielded similar, but less pronounced results. Namely, mean initial growth rates in gap sites were lower and more similar to average initial growth rates in forest sites using a 5 yr, rather than a 10 yr, time window. Due to the limited number of sites with recent germinants in forest plots, I did not conduct statistical comparisons between the means. Graphical comparisons of average initial growth were limited only to western redcedar and western hemlock seedlings and saplings because too few Pacific silver fir germinated within ± 10 years of the gap-formation date in forest plots.

Seedlings and saplings that established in gap plots within ± 10 years of the gap formation dates (gap-regeneration) exhibited higher rates of average initial growth (ring widths) than seedlings and saplings that established in gap and forest plots at least 10 years prior to gap formation (pre-gap regeneration) (Figure 11). The mean initial growth rate over the first 5 years of growth in gap-regeneration (0.26 ± 0.02 mm/yr) was significantly greater than that of pre-gap regeneration (0.17 ± 0.02 mm/yr) (P=0.005). Comparisons based on mean initial growth rates during the first 10 years of growth yielded similar results; the mean rate of initial growth in gap-regeneration (0.29 ± 0.03 mm/yr) was significantly higher than that in pre-gap regeneration (0.19 ± 0.03 mm/yr) (P=0.02).

Mean initial growth rates over the first 5 years of growth also varied significantly with species (Figure 11). Mean initial growth rates in Pacific silver fir (0.22 ± 0.02 mm/yr) and western redcedar (0.28 ± 0.02 mm/yr) seedlings and saplings were significantly greater than those observed in western hemlock (0.14 ± 0.02 mm/yr) seedlings and saplings (P=0.002). However, differences between species were not significant when comparisons were based on the first 10 years of growth (P=0.18). Although the mean initial growth rates of western redcedar (0.29 ± 0.04 mm/yr) and Pacific silver fir (0.21 ± 0.04 mm/yr) remained similar to those calculated with the 5-year period, the mean initial growth rate of western hemlock (0.21 ± 0.03 mm/yr) was higher and more closely approximated those of Pacific silver fir and western redcedar. Differences between initial growth rates in gap-regeneration and pre-gap regeneration were similar between species and there were no significant interactions between the effects of species and the timing and location of establishment in either the 5-year (P=0.34) or the 10-year (P=0.75) comparisons.

Radial Growth Releases

Attributes of releases were variable, but no significant differences between species were detected in either saplings or seedlings (Table 3). Releases were observed in approximately 50% of saplings and 25% of seedlings, but the percentage of saplings and seedlings experiencing at least 1 release did not vary significantly between species. Pacific silver fir saplings experienced nearly twice the number of releases as western hemlock saplings, and Pacific silver fir and western hemlock seedlings experienced nearly a third more releases than western redcedar seedlings, however, these differences were also not statistically significant. The mean durations of releases were also similar between species in both saplings and seedlings. Releases in saplings were approximately seven years in duration, and releases in seedlings were approximately two years in duration. In addition, the estimated release rate per century did not differ significantly between species. Saplings released an average of 2.5 times per century, and seedlings released an average of once per century. Overall, approximately 30% of each sapling's life and 10% of each seedling's life was spent in release. For both seedlings and saplings, differences in the proportion of life spent in release between species were marginal and insignificant.

Releases were not strongly synchronous between gaps. Rather, patterns of release over time reveal clustering in time within gaps rather than between gaps (Figure 12). The number of years in which gaps initiated at least two simultaneous releases varied inversely with the number of gaps considered (Figure 13). The most frequent occurrences were years in which zero, one, or two gaps experienced at least two releases.

Release Attributed to Gap Formation

A greater proportion of western hemlock and Pacific silver fir saplings and seedlings released in gap plots compared to forest plots (Figures 14a and 15a); however, the difference was significant only for Pacific silver fir saplings (P=0.007). Twenty-two of 25 Pacific silver fir saplings in gap plots versus nine of 19 Pacific silver fir saplings in forest plots released within 10 years of the gap-formation dates. However at the scale of individual gaps, this result was largely driven by the response of Pacific silver fir saplings in the Seymour River watershed (Figure 14b). A significantly greater proportion of Pacific silver fir saplings released within 10 years of gap formation in the SEY-GB sample relative to the SEY-F sample (P=0.002). Similarly, a substantially greater proportion of Pacific silver fir saplings released within 10 years of gap formation in the SEY-GA sample relative to the SEY-F sample, but this difference was only marginally significant (P=0.06). Within the Capilano and Coquitlam River watersheds, variability among plots was not significant, but, in contrast to the Seymour River watershed, comparison of the COQ-F and COQ-GB samples revealed a greater proportion of Pacific silver fir saplings released in the forest compared to the gap. Similarly, although overall, a marginally greater proportion of western hemlock saplings released in gap versus forest plots, analysis at the scale of individual gaps revealed the opposite trend for the comparison between COQ-F and COQ-GB (Figure 14c).

Similar to saplings, differences between gap and forest plots with respect to the proportion of seedlings releasing within 10 years of the gap formation date are more variable at the scale of individual gaps (Figures 15b-15d). Across watersheds, Pacific silver fir seedlings exhibited marginally higher proportions of release in gap versus forest plots. However, this trend was not consistent between gaps. A significantly smaller proportion of Pacific silver fir seedlings exhibited release in the SEY-F sample compared to the SEY-GA (P=0.02) and SEY-GB (P=0.002) samples. However, for one of the comparisons in the Capilano watershed and both of the comparisons in the Coquitlam watershed, the proportions of Pacific silver fir seedlings releasing within 10 years of the gap formation date were marginally greater in forest versus gap plots. Likewise, with the exception of the comparison between the SEY-F and the SEY-GB samples, western redcedar seedlings showed marginally greater proportions of releases in forest as opposed to gap plots. Consistent with the trend across watersheds, western hemlock seedlings from the two gap sites in the Seymour watershed, and from one of the gap sites in the Coquitlam watershed exhibited marginally greater proportions of release than those observed in the corresponding forest sites. However, western hemlock seedlings from both gap sites in the Capilano watershed and one gap site in the Coquitlam watershed exhibited marginally lower proportions of release than those observed in the corresponding forest sites. Within watersheds, none of the comparisons involving western redcedar or western hemlock seedlings were significant.

Frequencies of release in Pacific silver fir and western hemlock saplings were higher than those expected based on historic rates of release in gap plots, and similar to those expected based on historic rates of release in forest plots (Figure 16a). However, the overall proportion of samples observed and expected to release did not differ significantly between gap and forest plots for either Pacific silver fir (P=0.40) or western hemlock (P=0.57). At the scale of individual sites, differences between observed and expected release frequencies in saplings were more variable; however their remained no significant differences between the proportions of saplings observed and expected to release in individual gap versus forest sites (Figures 16b and 16c). With the exception of COQ-GB sample, Pacific silver fir saplings from gap sites exhibited higher numbers of release than those expected based on historic rates of release. However, a similar trend was observed in the CAP-F and COQ-F sites. Of the three forest sites, only Pacific silver fir saplings from the SEY-F site exhibited fewer numbers of release than expected based on historic rates of release. Similarly, western hemlock saplings in gap sites exhibited consistently higher numbers of release than expected based on historic rates of release. Although this trend was reversed in the SEY-F and CAP-F sites, the COQ-F site also exhibited higher numbers of release than expected based on historic rates of release.

Frequencies of release in Pacific silver fir, western hemlock, and western redcedar seedlings were greater than or equal to those expected based on historic rates of release in both gap and forest plots (Figure 17a), and the overall proportion of samples observed and expected to release did not differ significantly between gap and forest plots for either Pacific silver fir (P=0.66), western hemlock (P=1.00), or western redcedar (P=0.59). At the scale of individual sites, differences between observed and expected release frequencies were more variable, but their remained no significant differences between the proportions of seedlings observed and expected to release in individual gap versus forest sites (Figures 17b-17d). Pacific silver fir seedlings in all six gap-sites exhibited higher numbers of release than expected based on historic rates of release. However, the same trend was observed in the CAP-F and COQ-F sites, and only the SEY-F site exhibited fewer releases than expected. Western hemlock seedlings in all six gap sites and all three forest sites exhibited higher numbers of release than expected based on historic frequencies of release. Western redcedar seedlings exhibited higher numbers of release than expected based on historic rates of release in all three sites in the SEY watershed (F, GA, GB), and in the CAP-F and CAP-GA sites. No western redcedar seedlings were sampled from the CAP-GB site. Moreover, more western redcedar seedlings than expected were observed to have released in the COQ-F site, and fewer western redcedar seedlings than expected were observed to have released in the COQ-GA and COQ-GB sites.

For all releases that initiated within 10 years of gap formation, in both gap and forest plots, the mean lag between the date of gap-formation and the start of release was similar between locations and between species in both saplings and seedlings (Figures 18a and 18b). The mean lag for Pacific silver fir and western hemlock saplings in gap plots (-0.41 ± 1.81 yrs) did not differ significantly from the mean lag in forest plots (-0.58 ± 1.59 yrs) (P=0.75); Nor did mean lag in Pacific silver fir saplings (-1.0 ± 1.73 yrs) differ significantly from that in western hemlock saplings (-0.05 ± 1.67 yrs) (P=0.26). The mean lag for Pacific silver fir, western hemlock, and western redcedar seedlings in gap plots (-0.62 ± 1.03 yrs) did not differ significantly from the mean lag in forest plots (-

0.74 ± 1.19 yrs) (P=0.89); Nor were there any significant differences in mean lag between Pacific silver fir (-0.11 ± 1.26 yrs), western hemlock (-2.43 ± 1.26 yrs) and western redcedar (0.88 ± 1.54 yrs) seedlings (P=0.25). There were also no significant interactions between the effects of species and location on mean lag in saplings (P=0.25) or seedlings (P=0.93).

The mean duration of releases that initiated within 10 years of the gap-formation date were similar between locations and species in both saplings and seedlings (Figures 19a and 19b). The mean duration of releases in Pacific silver fir and western hemlock saplings did not differ significantly between gap (11.15 ± 3.74 yrs) and forest (10.38 ± 3.99 yrs) plots (P=0.51); nor were there any significant differences in mean release duration between Pacific silver fir (11.86 ± 3.82 yrs) and western hemlock (10.10 ± 3.82 yrs) saplings (P=0.73). Similarly, the mean duration of releases in Pacific silver fir, western hemlock, and western redcedar seedlings did not differ significantly between gap (7.42 ± 0.77 yrs) and forest (6.62 ± 0.85 yrs) plots (P=0.20); Nor were their any significant differences in mean release duration between Pacific silver fir (7.86 ± 0.90 yrs), western hemlock (7.10 ± 0.84 yrs), and western redcedar (6.25 ± 0.90 yrs) seedlings (P=0.37). There was not a significant interaction between the effects of species and location on mean release duration in saplings (P=0.57). In seedlings, however, differences between locations were greatest in western redcedar, and lowest in Pacific silver fir, and, although there were no significant differences between any combination of species and location (Tukey HSD), there was a significant interaction between the effects of species and location on mean release duration (P=0.02).

The mean magnitudes (maximum % growth change) of releases occurring within 10 years of the gap-formation date differed substantially with location, but not with species, in both saplings and seedlings (Figures 20a and 20b). Differences between locations were marginally insignificant in both seedlings and saplings. The mean magnitude of releases in Pacific silver fir and western hemlock saplings was considerably greater in gap (260.22 ± 37.36%) versus forest (158.99 ± 48.93%) plots (P=0.09); and the mean magnitude of releases in Pacific silver fir, western hemlock, and western redcedar seedlings was considerably higher in gap (267.36 ± 34.31%) versus forest (149.92 ± 43.69%) plots (P=0.06). Release magnitudes were marginally, but not significantly higher in western hemlock saplings (266.76 ± 43.53%) than in Pacific silver fir saplings (186.19 ± 43.53%) (P=0.25). Release magnitudes in seedlings were similar between Pacific silver fir (234.16 ± 46.34%) and western hemlock (243.27 ± 47.86%), but marginally lower in western redcedar (186.57 ± 50.05%) (P=0.79). There were no significant interactions between the effects of species and location on the magnitude of releases in saplings (P=0.43) or seedlings (P=0.89). In addition, I found no relationship between release magnitude and the ages of seedlings and saplings.

The mean change in rates of radial growth (%GC) between the periods 10 years preceding and subsequent to the dates of gap formation varied significantly with location, but not with species, in both saplings and seedlings (Figure 21a and 21b). Mean %GC in Pacific silver fir and western hemlock saplings was significantly higher in gap (168.85 ± 30.93%) versus forest (38.03 ± 43.74%) plots (P=0.03). Similarly, mean %GC in Pacific silver fir, western hemlock, and western redcedar seedlings was significantly higher in gap (122.22 ± 21.06%) versus forest (30.55 ± 26.82%) plots (P=0.01). Changes in rates of radial growth following the date of gap-formation did not differ significantly between Pacific silver fir (130.17 ± 37.88%) and western hemlock (120.31 ± 37.88%) saplings (P=0.82). Further, although changes in radial growth were slightly lower in Pacific silver fir seedlings (63.87 ± 28.44%) relative to western hemlock (101.16 ± 29.38%) and western redcedar (103.44 ± 30.72%) seedlings, there were no significant differences between species with respect to %GC in seedlings (P=0.54). There were also no significant interactions between the effects of species and location on %GC in saplings (P=0.89), or seedlings (P=0.50). Similar to release magnitude, I found no relationship between %GC and the ages of seedlings and saplings.

Comparisons between locations and species with respect to changes in radial growth following the date of gap formation were similar but less pronounced using a 5-year, rather than a 10-year window. However, because some gaps occurred fewer than 10-years prior to sampling, not all comparisons were based on a complete 10-year post-gap window.

DISCUSSION

Comparisons between gap and forest sites

There were many comparisons that I expected to produce meaningful differences between gap and forest locations. These expectations were based on my assumptions that the growth and abundance of vegetation in the understory is limited by competition with the overstory, and that fine-scale disturbances affecting canopy-class trees liberate resources for vegetation in the understory. I expected gaps to increase rates of establishment and to reduce rates of mortality in new recruits, resulting in greater abundances of seedlings and saplings, in greater rates of initial radial growth, and in increased incidence of establishment around the dates of gap formation. I also expected gaps to increase rates of radial and vertical growth in pre-existing seedlings and saplings, resulting in increased incidence of radial growth release around the dates of gap formation, greater magnitudes of radial growth release, and younger populations of seedlings and saplings.

Interestingly, my results did not always conform to these expectations. Although gaps supported greater densities of western hemlock and western redcedar seedlings less than 10cm in height, abundances of these species in gap and forest plots were similar for larger height classes, and abundances of Pacific silver fir were similar across all height classes. Similarly, although the proportions of seedlings and saplings having germinated around the dates of gap formation were higher in gap versus forest plots, suggesting that gaps increase rates of establishment and/or survival in new recruits, the differences were significant only for western hemlock and Pacific silver fir, and were inconsistent at the scale of individual gaps. Moreover, only pacific silver fir saplings experienced significantly greater rates of radial growth release following gap formation in gap versus forest plots, and even this pattern was inconsistent at the scale of individual gaps. However, consistent with my expectations, gaps supported younger populations of Pacific silver fir and western hemlock saplings. And, for seedlings and saplings of each species, changes in radial growth following the dates of gap formation, and in magnitudes of releases occurring around the dates of gap-formation, were larger in gap versus forest plots.

Despite these ambiguities, my results lend support to the paradigm of gap-phase replacement and suggest that gaps have an important influence on the dynamics of understory seedlings and saplings. Many of my results suggest that gaps improve conditions for the establishment and/or survival of new recruits. For example, western hemlock and western redcedar seedlings were more abundant in gap versus forest plots, greater proportions of western hemlock and Pacific silver fir seedlings and saplings established around the dates of gap formation in gap versus forest plots, and seedlings and saplings that established in gap plots around the dates of gap formation exhibited greater rates of initial radial growth that seedlings and saplings that established prior to gap formation or in forest plots during the corresponding time periods. Further, many of my results suggest that gaps improve conditions for growth in pre-established seedlings and saplings. For example, a greater proportion of Pacific silver fir saplings released around the dates of gap formation in gap versus forest plots, saplings from gap plots were younger than saplings from forest plots, and releases that occurred in seedlings and saplings from gap plots around the dates of gap formation were larger in magnitude than releases that occurred in seedlings and saplings from forest plots during the corresponding time periods.

Abundance, establishment, and patterns of radial growth

Gaps increase the recruitment and/or survival of newly established seedlings, and to a lesser degree, larger seedlings and saplings. Relative to the forest, gap sites supported higher densities of seedlings and saplings in all but the largest height class. However, differences in abundances between gap and forest sites were most dramatic in the smallest height class (height class 1). Though largely driven by the response of western hemlock, the relative abundance of seedlings in height class 1 in gap versus forest sites suggests that fine-scale disturbances increase rates of recruitment into height class 1 (regeneration) and/or reduce rates of mortality within height class 1. Given the corresponding increase in the abundance of larger height classes in gap versus forest sites, it is very unlikely that increases in abundance reflect reduced rates of recruitment out of height class 1. Further, estimates of the date of establishment for each seedling and sapling suggest that gaps increase rates of establishment and/or decrease rates of mortality in new recruits. For both Pacific silver fir and western hemlock, a greater proportion of seedlings and saplings estimated to have established within 10 years of the gap-formation date were observed in gap versus forest sites.

Although differences in abundance and dates of establishment do not discern between increases in rates of establishment and reductions in rates of mortality, it is clear that gaps improved conditions for growth in new recruits. Initial rates of radial growth in seedlings and saplings that established in gap sites within 10-years of the date of gap-formation were higher than those of seedlings and saplings that established in forest sites during the corresponding time periods, and higher than those of seedlings and saplings that established in gap and forest sites at least 10-years prior to the gap-formation dates. Although the former difference is based on comparisons between sub-samples and may not reflect the true variability in response across gaps, the latter comparison lends support to this finding and suggests that, on average, older seedlings and saplings did not establish under conditions as favourable as the gaps we sampled in.

Though less dramatic than seedlings in height class 1, the abundances of seedlings and saplings in larger height classes (height classes 2-4) remained higher in gap versus forest sites. This result suggests that fine-scale disturbances also increase recruitment and/or reduce mortality in larger height classes. However, in contrast to all other height classes, the finding that saplings in the largest height class (height class 5) were more abundant in forest versus gap sites is unexpected and difficult to interpret. The trend suggests that gaps increase recruitment out of height class 5 and into the sub-canopy, reduce recruitment into height class 5, or increase mortality in height class 5. Increased recruitment out of the sapling layer and into the sub-canopy is consistent with our understanding of the effects of gaps on resource availability, but is not supported by the finding that saplings collected from gap sites were considerably shorter than saplings collected from forest sites. However, the finding that saplings collected from gap sites were significantly younger and smaller in basal diameter than saplings collected from forest sites suggests that gaps increase rates of vertical growth in saplings and larger seedlings and, therefore, increase the recruitment rate into and/or out of the sapling layer (lowering the mean age and basal diameter of saplings). Increased mortality in gap sites is unlikely because Pacific silver fir and western hemlock tolerate and grow vigorously in full sunlight (Klinka et al. 1992, Carter and Klinka 1992).

In addition to the abundance and the general physical attributes of seedlings and saplings, radial growth releases around the dates of gap-formation were more prevalent in gap versus forest sites. Although this trend was significant only for Pacific silver fir saplings, (and reversed in western redcedar seedlings), it suggests that gaps reduce competition and improve conditions for growth in seedlings and saplings. However, the effects of location on the incidence of radial growth release were highly variable between sites and, at the scale of individual gaps, differences between gap and forest samples were inconsistent and contradictory. Overall differences between gap and forest sites were mostly driven by differences in the Seymour watershed. The variability in response among sites suggests that environmental conditions and/or stochastic events in addition to fine-scale disturbance affect the incidence of radial growth releases.

Independence of Gap and Forest Plots

It is possible that similarities between gap and forest sites with respect to the abundance and physical characteristics of seedlings and saplings result from forest sites not being fully independent from the gaps. Forest plots were located 10 meters from the boundary of the expanded gap. This distance was chosen because it seemed reasonable and convenient, but without prior knowledge of the degree to which canopy gaps influence the surrounding closed canopy forest. Increases in the availability of above and below-ground resources following the death of canopy-class trees may extend beyond the confines of the expanded gap. An apparent lack of difference between gap and forest sites implies that gaps have not greatly influenced the variable in question, or, paradoxically, that gaps have influenced the variable in question to such a degree that the effects are measured in the surrounding closed canopy forest. For example, the marginal differences between gap and forest sites with respect to the proportion of seedlings and saplings releasing within 10 years of the gap-formation date may reflect the limited ability of fine-scale disturbances to promote release, or the capacity of fine-scale disturbances to induce releases in seedlings and saplings within and beyond the boundary of the expanded gap.

Comparisons of observed and expected frequencies of release in gap and forest sites provide some insight into the effect of gaps on seedlings and saplings in forest sites. Although comparisons between observed and expected frequencies of release assume that rates of release remain relatively constant over time, they suggest that gaps did initiate releases in both gap and forest sites for some species and size classes, in some watersheds. In saplings, observed frequencies of release across watersheds were marginally higher than expected based on historic rates of release in gap sites, and similar to those expected based on historic rates of release in forest sites. This finding suggests that gaps increase the frequency of release in gap sites, but not in forest sites, and that forest sites were independent from the gaps. Conversely, for seedlings, observed frequencies of release across watersheds were similar to or greater than expected frequencies of release in both gap and forest sites. This finding suggests that forest sites were not fully independent of the gap, and that fine-scale disturbances increase frequencies of release in both gap and forest sites. However, for both seedlings and saplings, differences between observed and expected release frequencies at the scale of individual gaps were variable and contradictory. For some species and size classes in some watersheds, releases were less frequent than expected in forest sites, and more frequent than expected in gap sites. However, for other species and size classes, in other watersheds, frequencies of release in gap and forest sites exceeded the number of releases expected based on historic rates of release. Despite these ambiguous results, releases in gap sites were substantially (though insignificantly) larger in magnitude than releases in forest sites, and changes in rates of radial growth (%GC) following the date of gap formation were significantly greater in gap versus forest sites. Together, these trends suggest that gaps improve conditions for seedlings and saplings growing within the expanded gap, relative to the surrounding closed-canopy forest.

Sample Size

In addition to issues of independence, my ability to discern differences between gap and forest sites was also restricted by the limited sample size. I measured the abundance of seedlings and saplings in twenty sites. However, the more labour-intensive dendroecological analyses were limited to a subset of only six sites; comparisons between gap and forest sites with respect to age, height, diameter, and various measures of radial growth are based on a limited sample size of only six replicates. In many cases differences were large enough to detect statistically significant results. However, some important comparisons were inconclusive. For example, differences in the mean magnitude of releases between gap and forest sites were substantial but marginally insignificant in both saplings and seedlings. To investigate patterns of gap-phase replacement with meaningful levels of statistical power requires either much larger sample sizes (more sites), or the use of individual tree samples as replicates rather than sub-samples.

Gap Size and Age

Similarities between the abundance and physical characteristics of larger seedlings and saplings growing in gap versus forest sites may also result from the limited size and age of the gaps in question. Because we sought simple gaps formed by discrete, datable disturbance events, we limited our investigations to gaps that were formed by 1 dominant gap-maker, and that were young enough for the outer rings of the gap-makers to be crossdated with certainty (limited rot with intact bark). Therefore, the gaps represent the smaller and younger end of the existing distribution in gap size and age.

Gap size directly affects climatic conditions within the gap such as moisture, temperature, humidity, wind, snow-pack, and solar insolation (Coates and Burton 1997, Denslow 1980). Consequently, across a wide variety of ecosystem types, variations in gap size have been linked to differences in population and community dynamics such as germination success, survival, growth, and species composition (Coates and Burton 1997). Our gaps ranged in size between 127m^2 and 429m^2 (expanded gap size) and 35m^2 and 107m^2 (canopy gap size), and were similar in size to those presented in other gap-based research in coastal forests (Lertzman 1992, Lertzman and Krebs 1991, Ott and Juday 2001). However, changes in the growth rates of understory seedlings and saplings, and variations in patterns of recruitment with orientation inside gaps, have been shown to be marginal for gaps less than 300m^2 (canopy gap size) (Coates 2000, Coates 2002, Spies et al. 1990). Moreover, our gaps were generally much smaller than those presented in more conclusive gap-based research. For example, research in the interior cedar-hemlock forests of British Columbia shows that seedling emergence is affected by gaps larger than 600m^2 (canopy gap size) (Wright et al. 1998). It is possible that our bias toward simple gaps formed by discrete mortality events resulted in gaps that were too small to produce biologically relevant and/or measurable responses in understory seedlings and saplings.

In addition to gap size, the relatively young age of our gaps may have limited my ability to detect significant differences between gap and forest plots. Because most seedlings and saplings established prior to gap formation and were much older than the gap in question, the effects of gaps on attributes that have been shaped over the entire lifespan of seedlings and saplings are limited. For example, although gaps were shown to increase rates of radial growth, average rates of radial growth did not differ significantly between gap and forest sites. Rather than reflecting the minor effect of gaps on radial growth, this trend reflects the relatively limited time period during which gaps had the potential to influence average radial growth. Similarly, the finding that abundance remained higher in gap versus forest sites for all but the largest height-class, but that differences in abundance were most extreme in the smallest height class, may reflect the bias of this study to relatively recent gaps because there has not been sufficient time for new seedlings to recruit into taller height classes. Our understanding of gap-phase processes in these stands would benefit from the additional study of gap-phase dynamics across a range of gap sizes, ages and levels of complexity.

Above and Below-Ground Resources

The findings that abundance did not vary significantly with direction (orientation from the gap-centre) and that some forest sites were not independent of the gap suggest that increases in below-ground rather than above-ground resources following gap-formation may be responsible for differences between gap and forest sites. Levels of incident light vary relatively predictably within gaps and between gaps and the surrounding closed canopy forest (Canham et al. 1990, Poulson and Platt 1989). For example, relative to gaps near the equator, gaps in the northern hemisphere experience higher levels of incident light at the northern and western ends of the gap, and light penetrates further into the forest in these directions. Below-ground resources, in contrast, are not known to vary consistently with orientation from gap-centre. The fine-scale geographic distribution of increases in below-ground resources following the death of canopy-class trees varies with the individual branching patterns of gap-maker roots, and the degree of soil disturbance caused by uprooting. Further, because the lateral spread of a tree's roots can be greater than the height of the tree (Vogt et al. 1991), the below-ground effects of gap-formation are likely to extend in area well beyond the above-ground effects. If light were the most limiting resource in these stands, plots located in the northern and western ends of the gap should function differently from plots located in the southern and eastern ends of the gap, and forest plots located to the north and west of the gaps should show stronger responses to gap-formation than forest plots located to the south and east of the gap. However, no such evidence was found.

In addition to the explanation that the establishment and/or survival of seedlings and saplings is more limited by below-ground resources than above ground resources, the absence of a clear relationship between orientation from gap-centre and the abundance of seedlings and saplings may also result from the relatively small size of the gaps under study. Attributes of seedling establishment and growth are known to vary with orientation in larger (canopy gap size 300-1000m^2), but not smaller (canopy gap size <300m^2) gaps (Coates 1999). Nevertheless, competition for below-ground resources is known to limit the growth of seedlings and saplings under closed canopy conditions

(Christy 1986), and is consistent with the finding of no significant relationship between orientation from gap-centre and the abundance of seedlings and saplings. Our understanding of the effects of fine-scale disturbance on community and population dynamics would benefit greatly from future research that quantifies changes in the availability of above and below-ground resources following gap-formation, and that investigates the relative effects of increases in above- and below-ground resources on regeneration and recruitment.

Indicators of Seedling and Sapling Vigour

A final consideration relevant to quantifying the effects of gaps on the regeneration and recruitment of seedlings and saplings is that increases in radial growth represent a conservative measure of response. Suppressed seedlings and saplings, when provided with increased levels of limiting resources, respond first by devoting energy toward the production of new shoots, roots, and leaves (Waring et al. 1989). Radial growth, being of little direct and immediate value, is one of the last traits that seedlings and saplings devote energy toward. It is an imperfect but relatively convenient proxy for changes in the overall vigour of seedlings and saplings. A lack of difference between gap and forest sites with respect to patterns of radial growth does not imply a complete lack of response to gap-formation because is possible that seedlings and saplings have allocated energy toward other traits such as leaf and root area.

Comparisons between species

Although I did not have clear expectations for how species may differ in their responses to gap-formation, western hemlock, western redcedar and Pacific silver fir seedlings and saplings did vary with respect to patterns of recruitment and regeneration in gap and forest environments. Species-specific responses to fine-scale disturbance indicate the potential for fine-scale disturbances to affect community dynamics and/or to promote co-existence in mixed species stands. For example, differences in abundance reflect variability between species with respect to life-history strategies and patterns of recruitment and regeneration following fine-scale disturbance. Further, differences in patterns of lifetime release, and in patterns of release following the dates of gap-formation, reflect variability between species with respect to shade-tolerance, and to the effects of fine-scale disturbance on radial-growth. This variation, in turn, may explain how otherwise similar tree species may co-exist under niche theory.

Abundance Between Height Classes.

Pacific silver fir, western redcedar, and western hemlock seedlings and saplings exhibit unique patterns of abundance between height classes. Abundance in any particular height class is a function of vertical growth and survival. It reflects the rate of recruitment into and out of each height class, and the rate of mortality within each height class. Both western redcedar and western hemlock exhibit an inverse relationship between height class and abundance. This pattern implies that western redcedar and western hemlock are not persisting in larger height classes, and that each height class experiences some mortality. Although height is an imprecise predictor of age, the relative abundance of western hemlock seedlings in the smallest height class (height class 1) suggests that western hemlock experience higher rates of reproduction but lower rates of juvenile survival. The similar but more gradual decline in the abundance of western redcedar as height class increases suggests that redcedar exhibit more moderate rates of reproduction and relatively consistent mortality over time.

The increased abundance of Pacific silver fir between small and medium height classes (height classes 1 and 3), and decreased abundance of Pacific silver fir between medium and large height classes (height classes 3 and 5), suggests that Pacific silver fir experience lower rates of reproduction and higher rates of recruitment into larger height classes. More specifically, the increased abundance of Pacific silver fir between height classes 1 and 3 suggests lower rates of mortality in height classes 1 and 2 (many Pacific silver fir are recruiting into height classes 2 and 3), and/or that seedlings in height classes 2 and 3 are relatively persistent. The decreased abundance of Pacific silver fir between height classes 3 and 5 suggests that saplings in height classes 4 and 5 are either dying or recruiting to the sub-canopy relatively quickly. The interpretation that Pacific silver firs experience lower rates of recruitment (i.e. slower rates of vertical growth) and higher rates of survival during the seedling and sapling stages is also supported by the finding that Pacific silver fir seedlings and saplings were significantly older than western hemlock and western redcedar seedlings and saplings.

In addition to differences in relative abundances between size classes, western hemlock seedlings and saplings were more abundant than western redcedar and Pacific silver fir seedlings and saplings. However, this result must be interpreted cautiously. To suggest that, in the absence of large-scale disturbances, more western hemlock will recruit to the canopy than will western redcedar or Pacific silver fir, or that western redcedar and Pacific silver fir will not maintain their status in the canopy, assumes that rates recruitment into the canopy do not vary inversely with abundance in the understory.

I did not collect any information on the survival rates of saplings or subcanopy trees. It is possible that western hemlock experience higher rates of mortality in larger height classes than do Pacific silver fir or western redcedar. Moreover, I did not collect data on the current composition of the canopy, without which it is very difficult to estimate changes in the future composition of the canopy. Although traditional theories of succession in this forest type suggest that western redcedar is replaced by western hemlock and Pacific silver fir, there is ample evidence to the contrary. For centuries, and in the absence of large-scale disturbance, western redcedar has successfully existed and regenerated in these stands (Daniels, 2003).

Unfortunately, my ability to interpret differences in abundance and age between species is limited because this study was not designed to sample populations of seedlings and saplings at the scale of forest stands. I targeted my sampling to small canopy gaps, and the surrounding closed-canopy forest; sites were not a random sample of each stand. It is possible that processes in addition to fine-scale disturbances influence patterns recruitment and regeneration in these stands. Therefore, the results of this study should not be applied to estimate patterns of regeneration and recruitment in the matrix between gaps or to the larger spatial scales of stands and landscapes.

Abundance Between Gap and Forest Plots

In addition to differences in general patterns of abundance between height classes, Pacific silver fir, western redcedar, and western hemlock seedlings and saplings also exhibited unique patterns of abundance between gap and forest plots. For all but the largest height class (height class 5), the abundance of Pacific silver fir was marginally greater in gap versus forest sites. Although these increases in abundance were not significant, they were similar between height classes. This trend suggests that gap-formation reduces the mortality of Pacific silver fir seedlings and saplings equally across height classes and without greatly affecting the establishment of new Pacific silver fir seedlings. For western redcedar and western hemlock, in contrast, differences in abundance between gap and forest sites were greatest in the smallest height class (height class 1). This trend suggest that gap-formation increases rates of establishment in western redcedar and western hemlock seedlings, many of which remain in height class 1, and/or reduces the mortality rate of western redcedar and western hemlock seedlings in height class 1. These interpretations of the effects of gaps on abundance in each height class are also supported by patterns of actual establishment in gap versus forest sites. Although a significantly greater proportion of Pacific silver fir seedlings and saplings established within 10-years of gap-formation in gap versus forest sites, the overall proportion of Pacific silver fir establishing within 10-years of gap-formation was lower than that observed in western hemlock and western redcedar seedlings and saplings.

Radial Growth Release

Species also varied with respect to patterns of radial-growth release in gap versus forest sites. Although the trend was consistent across all species and size classes except western redcedar seedlings, only Pacific silver fir saplings experienced a significantly greater proportion of samples releasing in gap versus forest sites. Further, the proportion of Pacific silver fir saplings that released within 10 years of the gap-formation dates was higher than any other species or size class. The distinct response of Pacific silver fir saplings suggests that they are more responsive to fine-scale disturbances than other species and size classes. Although it is possible that similarities between the proportions of samples that released in gap and forest sites reflect the sensitivity of western hemlock and western redcedar seedlings and saplings in forest sites to gap-formation, this interpretation is not supported by patterns of release in forest sites, or by patterns of lifetime release. The proportions of western hemlock and Pacific silver fir saplings releasing in forest sites were equal, suggesting that western hemlocks in forest sites are no more responsive to gap-formation than Pacific silver fir. Further, differences between species with respect to patterns of lifetime release support the interpretation that Pacific silver fir saplings are more responsive to fine-scale disturbance than other species and size classes; relative to other species and size classes, releases in Pacific silver fir saplings were marginally longer in duration, more frequent over time, and occupied a marginally greater proportion of each sample's life. A marginally greater proportion of Pacific silver fir saplings also experienced at least one release over their lifetime.

Implications For Shade Tolerance

Although all three species are classified as very shade tolerant (Carter and Klinka 1992, Klinka et al. 1992), the distinct response of Pacific silver fir saplings to gap-formation suggests variations in strategies of shade tolerance between species. Shade tolerance is identified by a species' ability to germinate and persist under closed canopies (Whitmore 1989), and is conceptualized as a continuum, defined by the degree to which different species respond to increased light availability (Canham 1989). At one extreme of shade-tolerance, juveniles grow slowly and consistently under closed-canopy conditions and do not respond greatly to canopy gaps (though they may require a gap to eventually recruit to the canopy). At the other extreme of shade-tolerance, juveniles persist in the understory, but rely on disturbances for any appreciable net growth. This continuum is likely observed because the traits required to maximize growth following canopy disturbance are different from those required to persist beneath an undisturbed canopy. The distinct response of Pacific silver fir saplings to gap-formation suggest that this species, though persistent in the understory, relies more heavily on canopy gaps for appreciable net growth. The more subtle responses of western redcedar and western hemlock suggests that these species may rely less on canopy gaps and more on their ability to function under the normal closed-canopy conditions. The finding that Pacific silver fir seedlings and saplings exhibit marginally slower rates of average radial growth than western hemlock and western redcedar seedlings and western hemlock saplings, respectively, also supports the above interpretation of each species' strategy for shade tolerance.

Differences in strategies of shade tolerance between species are, however, complicated by variation among species with respect to the attributes of releases that occurred within 10-years of the gap formation dates. If Pacific silver fir specialize in persisting under closed-canopy conditions and releasing following disturbance, while western hemlock and western redcedar specialize in moderate but consistent growth under both closed-canopy and gap-environments, then releases in Pacific silver fir should be not only more frequent than releases in western hemlock and western redcedar, but also larger in magnitude. However, western hemlock saplings and western redcedar seedlings from gap sites exhibited releases of marginally larger magnitudes than Pacific silver fir saplings and Pacific silver fir seedlings from gap sites, respectively. Furthermore, average changes in radial growth immediately following the dates of gap-formation were very similar between Pacific silver fir and western hemlock saplings, and were larger in western hemlock and western redcedar seedlings relative to Pacific silver fir seedlings. These results suggest that although Pacific silver fir saplings are more likely to release following gap-formation, western hemlock and western redcedar seedlings and saplings are also capable of experiencing dramatic increases in radial growth following gap-formation.

The relative success of shade-tolerant species differentiated along the gradient described above is likely to depend strongly on the frequency and spatial distribution of gap formation (Canham 1989). Species adapted to persist under closed-canopy conditions, but to release following gap-formation, are likely to be favoured in stands characterized by larger or more frequent disturbance events. In contrast, forests in which fine-scale disturbances are infrequent are likely to favour species adapted to grow modestly but consistently under both closed-canopy and gap conditions. My results suggest that western hemlock and western redcedar seedlings and saplings are less likely to release than Pacific silver fir saplings, but that releases in western redcedar and western hemlock seedlings and saplings are larger in magnitude than releases in Pacific silver fir. These scenarios do not fit either extreme of the shade-tolerance continuum, and suggest non-linear relationships between resource availability and releases in western redcedar and western hemlock. For example, the finding that releases in western hemlock saplings are less common, but larger in magnitude than releases in Pacific silver fir saplings, suggests that western hemlock saplings must experience a threshold level of resource availability in order to release, and that this threshold is higher than the threshold for Pacific silver fir.

Although we did not conduct formal statistical tests of differences between size classes, saplings consistently and dramatically surpassed seedlings with respect to patterns of lifetime release. Most notably, releases were longer and more frequent in saplings than seedlings. These differences suggest that releases are increasingly common as seedlings recruit to the sapling layer. It is likely that differences between seedlings and saplings with respect to responses to fine-scale disturbance result from seedlings being in more direct competition with shrubs. Competition with shrubs is known to affect rates of recruitment and regeneration in coastal forests of the Pacific Northwest, and is the main justification for the use of herbicides as a silvicultural treatment (Harrington 2006, Wagner et al. 2004).

Release criteria

Identifying releases is a fundamental approach for estimating disturbance history (Lorimer 1985, Lorimer and Frelich 1989). Knowledge of the timing and magnitude of releases provides insight into disturbance history at various spatial scales with exceptional temporal resolution (Black and Abrams, 2003). Most often, patterns of release are used to infer historic patterns of disturbance. I have identified radial growth releases as a means to assess the responses of seedlings and saplings to fine-scale disturbances of known magnitude and date of origin.

Radial-growth averaging techniques are an effective means of identifying releases because they are designed to discriminate against temporary increases in radial growth that may be attributed to annual variations in climate (Abrams and Orwig 1995, Black and Abrams 2003, Lorimer 1985, Lorimer and Frelich 1989, Nowacki and Abrams 1997, Rench *et al.* 2002). Rather, these methods estimate percent-growth-change (%GC) by comparing mean ring-widths over adjacent time-intervals sufficiently longer than most climate cycles. Because the length of the time interval affects how much of the beginning and end of each chronology is rendered irrelevant, and because we used relatively recent gaps whose signals were expected to emerge at the end of some chronologies, we opted for a 5-year time interval. Compared to the more common 10-year interval, the 5-year interval is more sensitive to annual variations in climate. However, it is also more sensitive to any short-term changes in radial growth that may result from disturbance.

A major challenge of applying radial growth release criteria based on relative growth is that the magnitude of any individual tree's response to disturbance will vary with disturbance intensity, the factors limiting growth, the rate of previous growth, and the maximum potential growth rate for each particular tree in each particular place (Fraver and White, 2005). Different species and populations are likely to exhibit distinctive responses to climate variation, and variable release potential at different crown, age, and radius classes (Lorimer and Frelich 1989; Nowacki and Abrams 1997; Black and Abrams 2003). Further, physiological constraints, not associated with age, radius, or crown-class *per se*, may also affect the magnitude of response to canopy disturbance as individual trees approach maximum growth rates (Fraver and White, 2005; Black and Abrams, 2003). Similar to other studies of radial growth release in seedlings and saplings (Abrams and Orwig 1995, Abrams and Orwig 1996, Abrams *et al.* 1998, Antos and Parish 2002, Cao and Ohkubo 1999, Copenheaver and Abrams 2003, Lorimer and Frelich 1989, Orwig and Abrams 1994, Pollmann 2002), we applied a radial growth release threshold of 100%. We chose this relatively conservative threshold because, compared to trees in the canopy, understory seedlings and saplings are often suppressed, and therefore respond with great magnitude to fine-scale disturbances (Abrams and Orwig 1995, Abrams and Orwig 1996, Abrams *et al.* 1998, Lorimer and Frelich 1989, Parshall 1995, Zeigler 2002). However, our release threshold of 100% may be too high to capture the more subtle releases of seedlings and saplings that were not suppressed prior to gap-formation.

Other options for identifying radial growth releases include criteria based on thresholds in absolute growth (Fraver and White 2005) and the boundary-line release criteria developed by Black and Abrams (2003). Release thresholds based on absolute growth identify releases as periods of growth, or increases in growth that exceed a certain threshold value. Release thresholds based on absolute growth rates are often based on prior knowledge of growth rates following disturbance. For example, to assess patterns of release and suppression in understory trees, absolute-growth release criteria are often set somewhere in between the contemporary growth rates of understory and open-grown seedlings and saplings (Canham 1985, Canham 1990, Cho and Boerner 1995, Wright *et al.* 2000, Wu *et al.* 1999). Release criteria based on changes in absolute growth were not considered appropriate for this study because prior information about absolute growth rates of western hemlock, western redcedar and Pacific silver fir in comparable understory and open-grown conditions were not available. To set absolute growth release criteria based on the growth rates we observed in seedlings and saplings growing in gap versus forest sites, and to then use these criteria to assess patterns of disturbance constitutes an illogical, circular argument. However, the results of this study could be used to derive empirical criteria for future studies that assess radial growth release using thresholds of absolute growth.

Boundary-line release criteria are based on relative growth release thresholds, but express %GC values as a fraction of their maximum potential value based on rates of prior growth (Black and Abrams, 2003). Boundary-line release criteria are calculated by constructing a scatter plot of %GC over prior growth, where each point on the plot represents one comparison in each running mean used to calculate %GC. The boundary line is then calculated by dividing the data into segments of prior growth, averaging the top 10 data points in each segment, and fitting the best of linear, power, logarithmic or exponential curves to the average %GC values calculated in each segment of prior growth. Unfortunately, boundary-line release criteria have only been applied in an old-growth eastern hemlock, white pine, and chestnut oak stands, and the general applicability of this method is unknown (Black and Abrams 2003). Future studies of release in mid-elevation coastal old growth forests would benefit from the application and comparison of multiple radial-growth release criteria, including boundary-line release criteria. Boundary-line release criteria are likely to be particularly useful in coastal old growth forests where gaps often represent the combined effects of distinct mortality events over time (Lertzman and Krebs 1991, Stan in progress). Individuals experiencing increases in radial growth following the primary disturbance episode may exhibit only slight responses to subsequent mortality events that broaden the canopy gap.

Releases and Climate

Patterns of lifetime release did not appear synchronous between gaps. This asynchrony suggests that releases are not directly driven by large-scale fluctuations in environmental conditions such as climate. Increases and decreases in radial growth in response to fluctuations in climate are usually observed across regional spatial scales (Fritts 1976). The three watersheds in which we sampled are in close proximity to one another and experience similar annual and inter-annual variations in climate. Therefore, if climate were responsible for radial growth releases, I would expect patterns of release to be synchronous between gaps. In contrast to climate, increases and decreases in radial growth in response to independent disturbance events are usually observed at spatial scales consistent with the extent of disturbance. The asynchrony of release events between gaps, particularly between gaps located in the same watershed, suggests that releases are induced by factors acting at much finer spatial scales. Increases and decreases in resource availability following independent fine-scale disturbances are the most likely explanation for the majority of releases I identified.

Difficulties in cross-dating the annual growth rings of seedlings and saplings also suggest that patterns of radial growth are more limited by processes acting at fine rather than broad spatial scales. Cross-dating is a common approach used to increase our degree of confidence in the years associated with different radial growth rings by helping to ensure that missing and/or false rings are not overlooked or misinterpreted (Fritts 1976, Stokes and Smiley 1968). The method is based on identifying and matching common patterns in radial growth, under the assumption that patterns of radial growth will be affected by fluctuations in climate and, therefore, will vary similarly across broad spatial scales. The difficulty I experienced in attempting to visually and statistically cross-date the samples suggests that rates of radial growth in seedlings and saplings from these stands were not limited by climate. Rather, it indicates that seedlings and saplings are growing in response to factors that operate at much finer spatial scales. Although a variety of abiotic (e.g. microclimate) and biotic (e.g. herbivores, parasites, disease, symbionts) factors may affect the growth of seedlings and saplings at fine spatial scales, competition for above and below-ground resources is considered the most important constraint on growth in understory seedlings and saplings of the Pacific northwest (Antos et al. 2005, Parish and Antos 2004).

Reconstruction of Historic Patterns of Fine-Scale Disturbance

Historic patterns of radial growth release are often used to infer historic patterns of disturbance in forest ecosystems (Cho and Boerner 1995, Copenheaver and Abrams 2003, Lorimer and Frelich 1989, Nowacki and Abrams 1997, Parshall 1995, Winter *et al.* 2002). The strength of these inferences depends on how well the processes contributing to patterns of radial growth are modelled and understood (Swetnam *et al.* 1999). I measured the response of seedlings and saplings to fine-scale disturbances of known magnitude and date of origin. This information is necessary to develop and calibrate predictive criteria for estimating historic patterns of fine-scale disturbance from patterns of radial growth release. Although it is unclear if all of the releases I identified owe to fine-scale disturbance affecting the forest canopy, my results suggest that the creation of canopy gaps initiate releases in nearby seedlings and saplings. Historic fine-scale disturbances of equal or greater magnitude are, therefore, likely to have similarly affected the radial growth of seedlings and saplings, and to be recorded in patterns of radial growth release.

The temporal distribution of releases in response to the gaps of known date of origin suggests that it is not possible to estimate historic fine-scale disturbance regimes by equating all years with release to years of disturbance. This distinguishes reconstructions of fine-scale disturbance history from reconstructions of fire-history. Unlike studies of fire-history, where each fire scar represents a distinct fire event, my results suggest that the initiation of radial growth releases can occur before, at, or after the fine-scale disturbance event. This might arise from a tree dying before it falls to the forest floor, gradually allowing more resources to pass through to the understory. The response of seedlings and saplings to gaps of known date of origin suggests that historic fine-scale disturbances can be approximated at a 5-10 year temporal scale, and that annual resolution is unlikely. The temporal distribution in release response is likely observed because standing death can initiate gap-formation prior to the gap-maker falling to the forest floor, and because of lags in the response of seedlings and saplings to gap-formation. Estimating historic disturbance events in these and similar forests will, therefore, rely on spatially explicit data that identify 5- to 10-year periods of time during which releases were more prevalent.

Most of the seedlings and saplings collected for this study were part of a seedling bank (i.e. established prior to gap-formation) and show evidence of radial growth releases that are not temporally associated with the known dates of gap-formation. These releases provide indirect evidence of historic fine-scale disturbances. At most sites, there were periods of time prior to gap-formation in which at least two samples released in any given year. The clumped distributions of releases in time mirror the response of seedlings and saplings to the gaps of known date of origin and suggest previous fine-scale disturbances. These patterns of release suggest that fine-scale disturbances are prevalent and occur roughly every 30-40 years. They also suggest that many seedlings and saplings survive multiple disturbance events before recruiting out of the seedling and saplings layers.

MANAGEMENT IMPLICATIONS

The maintenance of natural ecosystem structures and dynamics is considered the most reliable method of protecting biodiversity and ecological integrity (Holling and Meffe 1996, Landres et al. 1999, Lertzman et al. 1997, Swetnam et al. 1999). Consequently, in addition to other socioeconomic considerations, ecosystem-based management requires that ecosystem dynamics are understood and incorporated into management practices (Lertzman et al 1997). I investigated the effects of fine-scale disturbances on the composition, abundance, establishment and growth of seedlings and saplings across three watersheds. Although this research reflects a limited range of gap sizes and ages, and was conducted in a relatively restricted range of coastal old-growth forests, it increases our understanding of stand dynamics in these and similar forests and can be used to assess and direct forest management. Knowledge of patterns of regeneration and recruitment in natural gaps can be used to predict future growth and forest composition following the creation of human-made gaps. Further, an understanding of how natural gaps affect the abundance, composition, establishment and growth of seedlings and saplings enables future studies to compare the effects of natural versus human-made gaps.

My results indicate significant increases in rates of radial growth following gap-formation across all species and size classes. Although differences between gap and forest sites with respect to the incidence of radial growth release were significant only for saplings of Pacific silver fir, seedlings and saplings of each species experienced significant and substantial increases in radial growth following gap-formation. These findings suggest that advanced regeneration in human-made gaps is likely to experience increased rates of radial growth following harvesting. Coupled with future research that more thoroughly investigates the duration of such increases in growth, and the effects of gaps on the growth of larger sub-canopy and canopy-class trees, this information allows forest managers to better predict future growth and yield.

My results also indicate that planting within small patch cuts may be unnecessary. Although advanced regeneration was most common, rates of establishment and/or survival were greater within gaps than within the closed-canopy forest. Therefore, forest managers can expect larger and younger populations of seedlings and saplings to establish following harvest. In addition, my results indicate that the responses of advanced regeneration (seedlings and saplings that existed prior to gap-formation) to gap-formation do not vary significantly with age. I observed no relationships between the ages of seedlings and saplings and release magnitude or changes in radial growth (%GC) following gap-formation. Although I did not compare rates of absolute radial growth between younger and older seedlings and saplings, or between natural regeneration and transplanted seedlings, this result suggests that even relatively aged, long-suppressed seedlings and saplings can efficiently fill human-made gaps and negate the need to replant following harvesting. Future research that compares absolute values of radial and vertical growth between natural regeneration and transplanted seedlings will provide further insight into the potential benefits of planting within small patch-cuts.

In addition to predicting the effects of small human-made gaps, this research can also be used to assess the degree to which human-made gaps emulate natural disturbances. This study provides valuable baseline ecological information that can be compared with future research that investigates the effects of small-human made gaps, such as those formed following single-tree selection or high-retention variable retention harvests. For example, the abundance, composition and radial growth of natural regeneration in human-made gaps can be compared to the corresponding values observed in this study. However, because natural ecosystems are dynamic across a range of spatial and temporal scales, resource managers interested in practicing ecosystem-based management should focus on approximating the apparent range of natural variability (ARV) rather than static ecosystem targets (Wong and Iverson, 2004). My results contribute to our understanding of the range of natural variability in response to fine-scale disturbance. They quantify the effects of natural gaps on regeneration and recruitment, at particular moments in time, and within a relatively restricted sample of old-growth forest in the CWH zone. Further research that investigates the effects of larger and older gaps across a range of ecosystems types will help forest managers to more accurately estimate the true range of natural variability in response to fine-scale disturbance, and to determine how well various shapes, sizes, and distributions of human-made gaps emulate natural gaps.

My results can also be used to direct the development of strategies for active adaptive management. Uncertainties associated with our understanding of the range of natural variability in response to fine-scale disturbance, and with the potential effects of different management techniques on ecosystem function, necessitate the widespread application of active adaptive management (Walters and Holling 1990). For example, my results suggest that natural advanced regeneration will fill human-made canopy gaps.

However, this hypothesis could be more thoroughly tested using adaptive management techniques. Forest managers could compare the effects of human-made gaps on natural and transplanted seedlings and saplings, and adjust future management actions (e.g. plant or not plant) based on the results. Similarly, my results show that western hemlock is the most abundant species in the understory, and western redcedar is the least abundant species in the understory. However, it is unclear whether variations in gap-size, shape, or aspect favour the regeneration and recruitment of different species, or whether less abundant species such as western redcedar are limited by dispersal, the availability of safe-sites for germination, competition for above and below-ground resources, or other abiotic and biotic factors. Adaptive management strategies could more thoroughly investigate these questions, while at the same time meeting other management objectives. For example, forest managers could design harvesting strategies that create gaps of various sizes, shapes and aspects to determine the effects of these attributes on the composition and abundance of natural regeneration. Further, various experimental treatments such as seeding, weeding and trenching could be applied to determine why some species are less abundant than others, and to determine how to manage future forest composition.

In addition to providing direct applications to forest management and to guiding adaptive management, this research also draws attention to differences between traditional forest management practices and natural disturbance regimes. I collected seedlings and saplings that ranged in age between less than 10 years, and greater than 190 years. Although forest managers would, understandably, prefer much faster rates of growth and recruitment for seedlings and saplings in human-made gaps, it is unclear how the age structures of seedling and sapling populations affect ecosystem functions in these and similar stands. For example, it is likely that natural, uneven-aged populations of seedlings and saplings exhibit very high levels of genetic diversity.

CONCLUSIONS

My results support the application of the paradigm of gap-scale canopy replacement to the coastal western hemlock forests of coastal British Columbia. They demonstrate that fine-scale disturbances involving the death of one to a few canopy-class trees exert a substantial influence on patterns of recruitment and regeneration. Gaps affected the growth, establishment and/or mortality of Pacific silver fir, western hemlock, and western redcedar seedlings and saplings. All three species were more abundant in gap versus forest sites, and exhibited increases in rates of radial growth and in incidents of radial growth release around the time of gap formation. However, differences between gap and forest sites varied within and between watersheds. For example, differences in the number of radial growth releases between gap and forest sites were more apparent in the Seymour river watershed relative to the Capilano or Coquitlam river watersheds. This variability raises new questions about factors in addition to gap formation that may enhance or inhibit the response of seedlings and saplings to fine-scale disturbance.

My results also demonstrate that Pacific silver fir, western hemlock and western redcedar seedlings and saplings differ in their abundance and in their responses to fine-scale disturbance. Western hemlock seedlings and saplings were more abundant than Pacific silver fir or western redcedar seedlings and saplings, particularly in height class 1 (<10cm in height); and relative to Pacific silver fir and western redcedar, western hemlock seedlings in height class 1 exhibited dramatically greater abundances in gap versus forest sites. Despite the numerical dominance of western hemlock, differences between gap and forest plots with respect to the number of releases occurring in association with the dates of gap-formation were greatest in Pacific silver fir.

The disparate responses of Pacific silver fir, western hemlock and western redcedar seedlings and saplings to gaps of known date of origin suggest variability in strategies of shade tolerance between species. More specifically, my results suggest that Pacific silver fir seedlings and saplings persist in the understory, but rely on canopy gaps for any appreciable net growth. Western redcedar and western hemlock seedlings and saplings, in contrast, respond less frequently to canopy gaps but maintain higher growth rates under closed-canopy conditions. Interestingly, however, releases in western hemlock and western redcedar were larger in magnitude than releases Pacific silver fir. This finding suggests that Pacific silver fir require a lower threshold level of resource availability to release.

Although this study was not designed to determine the effects of gaps on canopy composition, variations between species with respect to responses to fine-scale disturbance suggests that species richness in these stands may be maintained because species occupy different regeneration niches (Grubb 1977). Additional research is required to determine whether these differences are enough to support partitioning within or between gaps, and, if so, whether partitioning does occur (Brokaw and Busing 2000). In addition to niche partitioning, it is also possible that species co-existence is supported by the interaction between climate change and the long-lived nature of these trees. This non-equilibrium "gradual change" hypothesis was proposed to explain co-existence in a nearby montane forest ecosystem (Lertzman 1992, Lertzman 1995), and suggests that changes in climate favour different species at different times, but that no species has the time to exclude others before their temporary competitive edge has ended (Connell 1978).

Despite the new answers and, more importantly, the new questions generated by this study, the knowledge required to practice forest management that incorporates aspects of fine-scale disturbances has existed for decades. Although forest ecologists have tended to occupy themselves with the study of large-scale disturbances, interest in fine-scale disturbances flourished in the early 1980's (Veblen 1989). Since then, forest ecologists have been calling for the integration of natural fine-scale disturbance processes into forest management (Clayoquot Sound Scientific Panel 1995, Coates 2000, Coates and Burton 1997, Lertzman et al. 1996, Lertzman et al. 2002, Ott and Juday 2002, Rench et al. 2002, Winter et al. 2002). The constraints on the widespread application of gap-based management arise more from social, political, and economic feasibility than scientific understanding (Lertzman et al. 1997). Nevertheless, this research contributes new information applicable to forest management in coastal British Columbia and abroad. Continued interest and research in natural gap dynamics will aid decision-makers who are attempting to balance the diverse costs and benefits of various management options.

Uncertainty regarding the effects of gap-based management, coupled with known differences between natural small-scale disturbances and human-made gaps, continue to stress the importance of adequate old-growth reserves. Patch-cuts, for example, will always differ from natural gaps due to the removal of coarse woody debris. The brief duration of harvesting events also differs temporally from many natural disturbance processes associated with standing death. Moreover, due to socioeconomic constraints, the frequency and/or distribution of patch-cuts applied within forests managed for timber are likely to surpass those observed within natural stands, particularly in high elevation forests (Brang and Lertzman, unpublished manuscript). The cumulative effects of natural and anthropogenic disturbances further enhance this reality. Though gap-based systems of forest management may contribute immensely to the hospitality of the forest matrix, reserves of old-growth forest are still required to provide important habitat types (Lertzman et al. 1997).

LITERATURE CITED

Abrams, M.D. and Orwig, D.A. 1995. Structure, radial growth dynamics and recent climate variations of a 320-year-old *Pinus rigida* rock outcrop community. Oecologia, 101: 353-360.

Abrams, M.D. and Orwig, D.A. 1996. A 300-year history of disturbance and canopy recruitment for a co-occurring white pine and hemlock on the Allegheny Plateau, USA. Journal of Ecology, 84: 353-363.

Abrams, M.D., Ruffner, C.M. and DeMeo, T.E. 1998. Dendroecology and species co-existence in an old-growth *Quercus-Acer-Tilia* talus slope forest in the central Appalachians, USA. Forest Ecology and Management, 106: 9-18.

Acres International. 1999. Annex to the Analysis Report Watershed Management Plan #5, Volume 1. GVRD Watershed Ecological Inventory Program, Burnaby, B.C.

Agricultural Canada Expert Committee on Soils Survey. 1987. The Canadian system of soil classification. 2nd edition Agriculture Canada Publication, 1646, 164 p.

Antos, J.A., Guest, H.J., Parish, R. 2005. The tree seedlings bank in an ancient montane forest: stress tolerators in a productive habitat. Journal of Ecology, 93: 536-543.

Antos, J.A. and Parish, R. 2002. Dynamics of an old-growth, fire-initiated, subalpine forest in southern interior British Columbia: tree size, age, and spatial structure. Canadian Journal of Forest Research, 32: 1935-1946.

Arsenault, A. 1995. Pattern and process in old-growth temperate rainforests of southern British Columbia. Ph.D. Thesis. University of British Columbia, Canada.

Beese W.J., Dunsworth, B.G., Zielke, K. and Bancroft, B. 2003. Maintaining attributes of old-growth forests in coastal B.C. through variable retention. The Forestry Chronicle, 79(3): 570-578

Black, B.A. and Abrams, M.D. 2003. Use of boundary-line growth patterns as a basis for dendroecological release criteria. Ecological Applications, 13(6): 1733-1749.

Brang, P. and Lertzman, K. Competition and demography of tree seedlings in a montane temperate rainforest. Unpublished manuscript.

Brokaw, N. and Busing, R.T. 2000. Niche versus change and three diversity in forest gaps. Trends in Ecology and Evolution, 15(5): 183-188.

Canham, C.D. 1985. Suppression and release during canopy recruitment in *Acer saccharum*. Bulletin of the Torrey Botanical Club, 112(2): 134-145.

Canham, C.D. 1989. Different responses to gaps among shade-tolerant tree species. Ecology, 70(3): 548-550.

Canham, C.D. 1990. Suppression and release during canopy recruitment in *Fagus granifolia*. Bulletin of the Torrey Botanical Club, 171(1): 1-7.

Canham, C.D., Denslow, J.S., Platt, W.J., Runkle, J.R., Spies, T.A. and White, P.S. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. Canadian Journal of Forest Research, 20: 620-631.

Canadian Climate Program. 1993. Canadian climate normals 1961-1990, British Columbia. Ministry of Supplies and Services of Canada. Ottawa, Ontario, 134 p.

Carter, R.E. and Klinka, K. 1992. Variation in shade tolerance of Douglas-fir, western hemlock, and western red cedar in coastal British Columbia. Forest Ecology and Management, 55: 87-105.

Cao, K.F. and Ohkubo, T. 1999. Suppression and release during canopy recruitment in *Fagus crenata* and *Acer mono* in old-growth beech forests in Japan. Forest Ecology, 145: 281-290.

Cho, D.S. and Boerner, R.E.J. 1995. Dendroecological analysis of the canopy history of two Ohio old-growth forests. Vegetatio, 120: 173-183.

Christy, J.E. 1986. Effect of root competition and shading on growth of suppressed western hemlock (*Tsuga heterophylla).* Vegetatio, 65: 21-28.

Clayoquot Sound Scientific Panel (CSSP). 1995. Scientific Panel for Sustainable Forest Practices in Clayoquot Sound, Report 5, Sustainable ecosystem management in Clayoquot Sound: planning and practices, Victoria, B.C. 296 p.

Coates, K.D. 2000. Conifer seedlings response to northern temperate forest gaps. Forest Ecology and Management, 127: 249-269.

Coates, K.D. and Burton, P.J. 1997. A gap-based approach for development of silvicultural systems to address ecosystem management objectives. Forest Ecology and Management, 99: 337-354.

Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs – high diversity of trees and corals is maintained only in a non-equilibrium state. Science, 199(4335): 1302-1310.

Copenheaver, C.A. and Abrams, M.D. 2003. Dendroecology in young stands: case studies from jack pine in northern lower Michigan. Forest Ecology and Management, 182: 247-257.

Daniels, L.D. 1994. Structure and regeneration of old-growth *Thuja plicata* stands near Vancouver, British Columbia. Master's Thesis. University of British Columbia, Department of Forestry (Forest Sciences).

Daniels, L.D. 2003. Western redcedar population dynamics in old-growth forests: contrasting ecological paradigms using tree-rings. The Forestry Chronicle, 79(3): 517-529.

Daniels, L.D. and Grey, A.N. 2006. Disturbance regimes in coastal British Columbia. Journal of Ecosystems and Management, 7(2): 44-56.

Daniels, L.D. and Klinka, K. 1996. The dynamics of old-growth *Thuja plicata* forests near Vancouver, British Columbia. Tree Rings, Environment and Humanity, eds. J.S. Dean, D.M. Meko and T.W. Swetnam. Radiocarbon 1996, pp. 379-393.

Denslow, J.S. 1980. Gap partitioning among tropical rainforest trees. Tropical Succession, 47-55.

Franklin, J.F., Spies, T.A., Van Pelt, R., Carey, A.B. et al. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir as an example. Forest Ecology and Management, 155: 399-432.

Fraver, S. and White, A.S. 2005. Identifying growth releases in dendrochronological studies of forest disturbance. Canadian Journal of Forest Research, 35: 1648-1656.

Fritts, H.C. 1976. Tree Rings and Climate. Academic Press, New York. 565 p.

Grey, A.N. and Spies, T.A. 1996. Gap size, within-gap position and canopy structure effects on conifer seedling establishment. The Journal of Ecology, 84(5): 635-645.

Grey, A.N. and Spies, T.A. 1997. Microsite controls on tree seedling establishment in conifer forest canopy gaps. Ecology, 78(8): 2458-2473.

Grissino-Mayer, H.D. 2001. Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. Tree Ring Research, 57(2): 205-221.

Grubb 1977. Grubb, P.J. 1977. Maintenance of species-richness in plant communities – importance of regeneration niche. Biological Reviews of the Cambridge Philosophical Society, 52(1): 107-145.

Grumbine, R.E. 1994. What is Ecosystem Management? Conservation Biology, 8(1): 27-38.

Grumbine, R.E. 1997. Reflections on "What is Ecosystem Management". Conservation Biology, 11(1): 41-47.

Harrington, T.B. 2006. Five-year growth responses of Douglas-fir, western hemlock, and western redcedar seedlings to manipulated levels of overstory and understory competition. Canadian Journal of Forest Research, 36(10): 2439-2453.

Holling, C.S. and G.K. Meffe. 1996. Command and control and the Pathology of Natural Resource Management. Conservation Biology, 10(2): 328-337.

Klinka, K., Pojar, J. and Meidinger, D.V. 1991. Revision of the biogeoclimatic units of coastal British Columbia. Northwest Science, 65: 32-47.

Klinka, K. Wang, Q., Kayahara, G.J., Carter, R.E. and Blackwell, B.A. 1992. Light-growth response relationships in Pacific silver fir (*Abies amabilis)* and sub-alpine fir (*Abies lasiocarpa).* Canadian Journal of Botany, 70(10): 1919-1930.

Landres, P.B., Morgan, P. and Swanson, F.J. 1999. Overview of the use of natural variability concepts in managing ecological systems. Ecological Applications, 9(4): 1179-1188.

Lertzman, K.P. 1989. Gap phase community dynamics in a sub-alpine old growth forest. Ph.D. thesis, University of British Columbia.

Lertzman, K.P. 1992. Patterns of gap-phase replacement in a subalpine old-growth forest. Ecology, 73(2): 657-669.

Lertzman, K.P. 1995. Forest dynamics, differential mortality and variable recruitment probabilities. Journal of Vegetation Science, 6(2): 191-204.

Lertzman, K.P. and Krebs, C.J. 1991. Gap-phase structure of a subalpine old-growth forest. Canadian Journal of Forest Research, 21: 1730-1741.

Lertzman, K.P., Gavin, D., Hallett, D., Brubaker, L., Lepofsky, D. and Mathewes, R. 2002. Long-term fire regime estimated from soil charcoal in coastal temperate rainforests. Conservation Ecology, 6(2): 5

Lertzman, K.P., Spies, T. and Swanson, F. 1997. From ecosystem dynamics to ecosystem management. Pgs. 361-382 *in* Schoonmaker, P., B. von Hagen, and E. Wolf, (eds.), The rainforests of home: Profile of a North American Bioregion. Island Press, Washington, D.C.

Lertzman, K.P., Sutherland, G.D., Inselberg, A. and Saunders, S.C. 1996. Canopy gaps and the landscape mosaic in a coastal temperate rain forest. Ecology, 77(4): 1254-1270.

Lorimer, C.G. 1985. Methodological considerations in the analysis of forest disturbance history. Canadian Journal of Forest Research, 15: 200-213.

Lorimer, C.G. and Frelich, L.E. 1989. A methodology for estimating canopy disturbance frequency and intensity in dense temperate forests. Canadian Journal of Forest Research, 19: 651-663.

MacKinnon, A. 2003. West coast, temperate, old-growth forests. The Forestry Chronicle, 79: 475-484.

Mitchell, S.J. and Beese, W.J. 2002. The retention system: reconciling variable retention with the principles of silvicultural systems. The Forestry Chronicle, 78(3): 397-403.

Nowacki, G.J. and Abrams, M.D. 1997. Radial-growth averaging criteria for reconstructing disturbance histories from presettlement-origin oaks. Ecological Monographs, 67(2): 225-249.

Orwig, D.A. and Abrams, M.D. 1994. Contrasting radial growth and canopy recruitment patterns in *Lindrodendron tulipifera* and *Nyssa sylvatica*: gap-obligate versus gap-facultative tree species. Canadian Journal of Forest Research, 24: 2141-2149.

Ott, R. and Juday, G.P. 2002. Canopy gap characteristics and their implications for management in the temperate rainforests of southeast Alaska. Forest Ecology and Management, 159: 271-291.

Parish, R. and Antos, J.A. 2004. Structure and dynamics of an ancient montane forest in coastal British Columbia. Oecologia, 141(4): 562-576.

Parshall, T. 1995. Canopy mortality and stand-scale change in a northern hemlock-hardwood forest. Canadian Journal of Forest Research, 25: 1466-1478.

Pollmann, W. 2003. Stand structure and dendroecology of an old-growth *Nothofacgus* forest in Conguillio National Park, south Chile. Forest Ecology and Management, 176: 87-103.

Poulson, T.L. and Platt, W.J. 1989. Gap light regimes influence canopy tree diversity. Ecology, 70(3): 553-555.

Rench, J.S., Desta, F. and Miller, G.W. 2002. Climate, canopy disturbance, and radial growth averaging in a second-growth mixed-oak forest in West Virginia, U.S.A. Canadian Journal of Forest Research, 32: 915-927.

Spies, T.A. and Franklin, J.F. 1989. Gap characteristics and vegetation response in coniferous forests of the Pacific Northwest. Ecology, 70(3): 543-545.

Spies, T.A., Franklin, J.F. and Klopsch, M. 1990. Canopy gaps in Douglas-fir forests of the Cascade Mountains. Canadian Journal of Forest Research, 20: 649-658.

Stan, A. Ph.D. Thesis (in progress), University of British Columbia.

Stewart, G.H. 1986. Forest development in canopy openings in old-growth Pseudotsuga forests of the western Cascade Range, Oregon. Canadian Journal of Forest Research, 16: 558-568.

Stokes, M.A. and Smiley, T.L. 1968. An introduction to tree-ring dating. University of Arizona Press, Tucson Arizona, 73 p.

Swetnam, T.W., Allen, C.D. and Betancourt, J.L. 1999. Applied historical ecology: Using the past to manage for the future. Ecological Applications, 9(4): 1189-1206.

Swift, K. 2006. Variable Retention Forestry Science Forum: Overview and key messages, April 21-22, 2004. Journal of Ecosystems and Management, 7(1): 3-8.

Van Pelt, R. and Franklin, J.F. 1999. Response of understory trees to experimental gaps in old-growth Douglas-fir forests. Ecological Applications, 9(2): 504-512.

Veblen, T.T. 1986. Treefalls and the coexistence of conifers in subalpine forests of the central Rockies. Ecology, 63(7): 644-649.

Veblen, T.T. 1989. Tree regeneration responses to gaps along a transandean gradient. Ecology, 70(3): 541-543.

Vogt, K.A., Vogt, D.J., Asbjornsen, H. and Dahlgren, R.A. 1991. Roots, nutrients and their relationship to spatial patterns. Plant and Soil, 168-169: 113-123.

Wagner, R.G., Newton, M., Cole E.C., Miller, J.H. and Shiver, B.D. 2004. The role of herbicides for enhancing forest productivity and conserving land for biodiversity in North America. Wildlife Society Bulletin, 32 (4): 1028-1041.

Walters, C.J. and Holling, C.S. 1990. Large-scale management experiments and learning by doing. Ecology, 71(6): 2060-2068.

Waring, R.H., Thies, W.G. and Muscato, D. 1980. Stem growth per unit of leaf area: a measure of tree vigour. Forest Science, 26(1): 112-117.

Wells, R.W., Lertzman, K.P. and Saunders, S.C. 1998. Old-growth definitions for the forests of British Columbia, Canada. Natural Areas Journal, 18(4): 279-292.

Whitmore, T.C. 1989. Canopy gaps and the two major groups of trees. Ecology, 70(3): 536-538.

Winter, L.E., Brubaker, L.B., Franklin, J.F., Miller, E.A. and DeWitt, D.Q. 2002. Canopy disturbances over the five-century lifetime of an old-growth Douglas-fir stand in the Pacific Northwest. Canadian Journal of Forest Research, 32: 1057-1070.

Wong, C. and Iverson, K. 2004. Range of Natural Variability: Applying the concept to forest management in central British Columbia. BC Journal of Ecosystems and Management, 4(1): 1-14.

Wright, E.F., Canham, C.D. and Coates, K.D. 2000. Effects of suppression and release on sapling growth for 11 tree species of northern, interior British Columbia. Canadian Journal of Forest Research, 30: 1571-1580.

Wright, E.F., Coates, K.D. and Bartemucci, P. 1998. Regeneration from seed of six tree species in the interior cedar-hemlock forests of British Columbia as affected by substrate and canopy gap position. Canadian Journal of Forest Research, 28: 1352-1364.

Wu, X., McCormick, J.F. and Busing, R.T. 1999. Growth patterns of *Picea rubens* prior to canopy recruitment. Plant Ecology, 140: 245-253.

Yamaguchi, D.K. 1991. A simple method for cross-dating increment cores from living trees. Canadian Journal of Forest Research, 21: 414-416.

Zar, J.H. 1996. Biostatistical Analysis, Third Edition. Prentice Hall Inc., Upper Saddle River, New Jersey 07458.

Ziegler, S.S. 2002. Disturbance regimes of hemlock-dominated old-growth forests in northern New York, USA. Canadian Journal of Forest Research, 32: 2106-2115.

TABLES

Table 1 Numbers of seedlings and saplings destructively sampled from the six focal gap and forest sites for dendroecological analyses.

	Capilano			Coquitlam			Seymour			Total
	Forest	Gap-A	Gap-B	Forest	Gap-A	Gap-B	Forest	Gap-A	Gap-B	
Ba-Sapling	6	2	5	7	6	2	5	6	5	44
Hw-Sapling	6	3	5	6	6	5	7	6	5	49
Cw-Sapling	1	0	0	1	2	0	1	0	0	5
Ba-Seedling	7	5	4	6	5	5	6	5	5	48
Hw-Seedling	7	5	5	6	5	5	6	4	6	49
Cw-Seedling	2	3	7	6	4	5	5	5	2	39

Table 2 **Mean heights, basal diameters, ages, and overall growth rates of Pacific silver fir and western hemlock saplings, and Pacific silver fir, western hemlock, and western redcedar seedlings.**

Mean values (+/- standard errors) are shown for individual species in gap and forest sites, for each site (species combined), and for each species (gap and forest sites combined). Significant differences are marked with asterisks. Significance values for comparisons between each species and site, and for the interaction between species and site are shown below the associated means.

Saplings:	Height (cm)	Basal Diameter (mm)	Age (Years)	Radial Growth (mm)
Ba Gap	202.8 +/- 18.2	42.8 +/- 3.1	74.8 +/- 19.2	0.40 +/- 0.09
Ba Forest	218.5 +/- 24.2	54.0 +/- 4.4	102.2 +/- 20.0	0.34 +/- 0.10
Hw Gap	225.8 +/- 18.2	35.4 +/- 3.1	66.8 +/- 19.2	0.43 +/- 0.09
Hw Forest	283.3 +/- 24.2	39.4 +/- 4.4	72.3 +/- 20.0	0.39 +/- 0.10
Gap (Ba+Hw)	214.3 +/- 14.2	39.1 +/- 2.2	70.8 +/- 18.8	0.41 +/- 0.09
Forest (Ba+Hw)	250.9 +/- 18.2	46.7 +/- 3.1	87.3 +/- 19.2	0.37 +/- 0.09
P-Value	0.086	0.066	0.034	0.235
Ba (Gap+Forest)	208.0 +/- 16.3	46.5 +/- 2.7	83.9 +/- 19.0	0.38 +/- 0.09
Hw (Gap+Forest)	245.0 +/- 16.3	36.7 +/- 2.7	68.7 +/- 19.0	0.41 +/- 0.09
P-Value	0.044	0.013	0.018	0.34
Interaction P-Value	0.306	0.357	0.137	0.869

Seedlings:	Height (cm)	Basal Diameter (mm)	Age (Years)	Radial Growth (mm)
Ba Gap	68.1 +/- 4.1	15.3 +/- 0.8	47.0 +/- 6.2	0.20 +/- 0.04
Ba Forest	58.9 +/- 5.7	13.1 +/- 1.2	48.2 +/- 7.0	0.21 +/- 0.05
Hw Gap	75.2 +/- 4.1	8.2 +/- 0.8	23.8 +/- 6.2	0.18 +/- 0.04
Hw Forest	78.5 +/- 5.7	8.0 +/- 1.2	25.7 +/- 7.0	0.27 +/- 0.05
Cw Gap	70.1 +/- 4.4	7.8 +/- 0.9	17.8 +/- 6.4	0.24 +/- 0.04
Cw Forest	70.9 +/- 5.7	6.3 +/- 1.2	19.4 +/- 7.0	0.22 +/- 0.05
Gap (Ba+Hw+Cw)	71.2 +/- 2.4	10.6 +/- 0.5	29.6 +/- 5.7	0.21 +/- 0.03
Forest (Ba+Hw+Cw)	69.4 +/- 3.3	9.1 +/- 0.7	31.1 +/- 5.9	0.24 +/- 0.03
P-Value	0.681	0.138	0.627	0.311
Ba (Gap+Forest)	65.0 +/- 3.5*	14.6 +/- 0.7*	47.4 +/- 6.0*	0.20 +/- 0.03
Hw (Gap+Forest)	76.3 +/- 3.5*	8.1 +/- 0.7	24.5 +/- 6.0	0.21 +/- 0.03
Cw (Gap+Forest)	70.4 +/- 3.6*	7.2 +/- 0.7	17.1 +/- 6.0	0.24 +/- 0.04
P-Value	0.048	<0.0001	<0.0001	0.716
Interaction P-Value	0.432	0.612	0.996	0.34

Table 3 **Mean values (+/- SE) describing the history and attributes of radial growth release in Pacific silver fir and western hemlock saplings, and Pacific silver fir, western hemlock and western redcedar seedlings.**

To ensure that these values of release history and attributes were independent of the current gaps, all calculations exclude the 20-year periods bracketing the gap-formation dates. Significance values for comparisons between species in each size class are shown below the associated means.

	Prop. Exp. At Least One Release	# Releases Per Lifetime	Release Rate Per Century	Proportion of Life in Release	Duration of Releases
Ba Saplings	0.54 +/- 0.13	2.01 +/- 0.62	2.60 +/- 0.57	0.34 +/- 0.09	7.75 +/- 2.06
Hw Saplings	0.46 +/- 0.13	1.08 +/- 0.62	2.29 +/- 0.57	0.28 +/- 0.09	5.83 +/- 2.06
P-Value	0.636	0.222	0.702	0.642	0.495
Ba Seedlings	0.24 +/- 0.12	0.36 +/- 0.18	0.67 +/- 0.62	0.08 +/- 0.06	3.33 +/- 1.32
Hw Seedlings	0.22 +/- 0.12	0.34 +/- 0.18	1.59 +/- 0.62	0.15 +/- 0.06	1.70 +/- 1.32
Cw Seedlings	0.21 +/- 0.12	0.22 +/- 0.18	0.75 +/- 0.62	0.06 +/- 0.06	1.16 +/- 1.32
P-Value	0.948	0.747	0.207	0.44	0.343

FIGURES

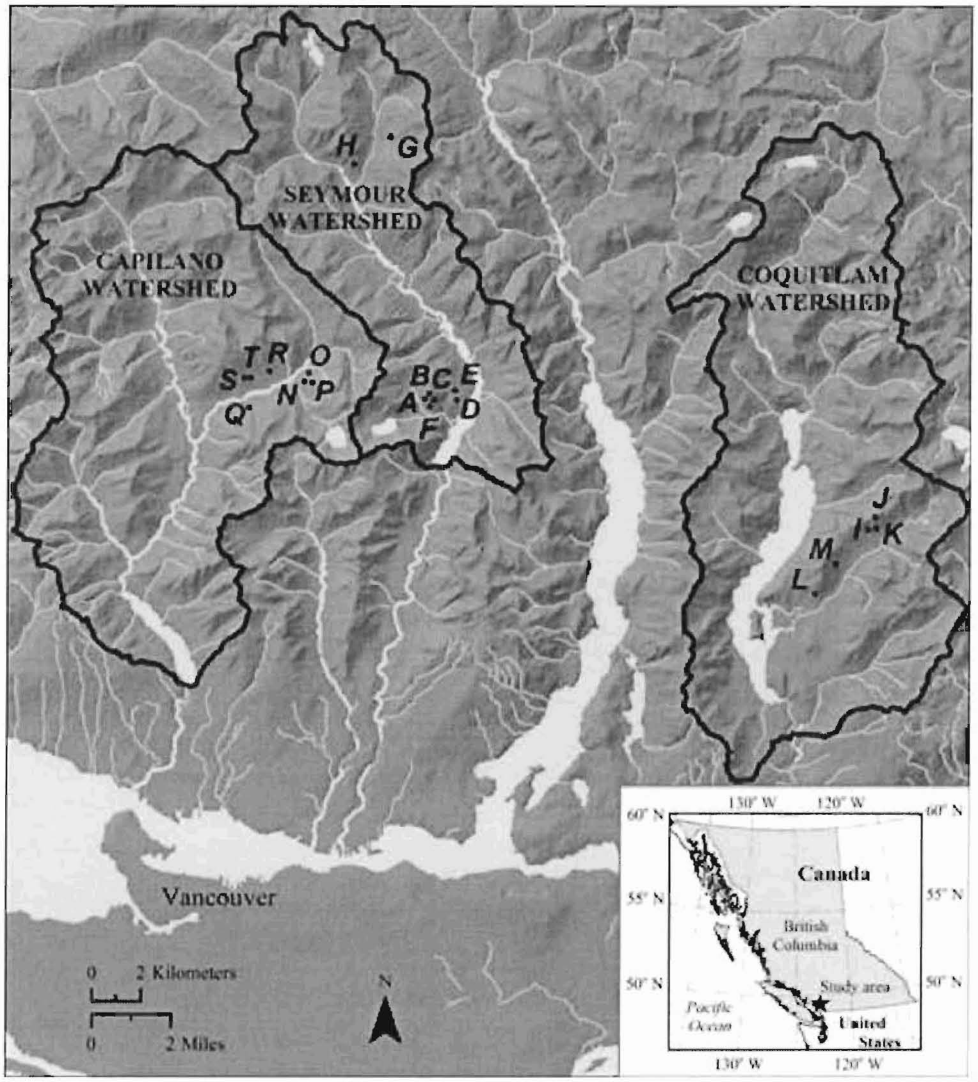


Figure 1 Diagram of the Capilano, Seymour, and Coquitlam River watersheds located north of the city of Vancouver, British Columbia.
The diagram also shows the locations of the 20 study sites. The six sites selected for more intensive, destructive sampling are sites "N" and "O" in the Capilano Watershed, sites "B" and "C" in the Seymour Watershed, and sites "J" and "K" in the Coquitlam Watershed.

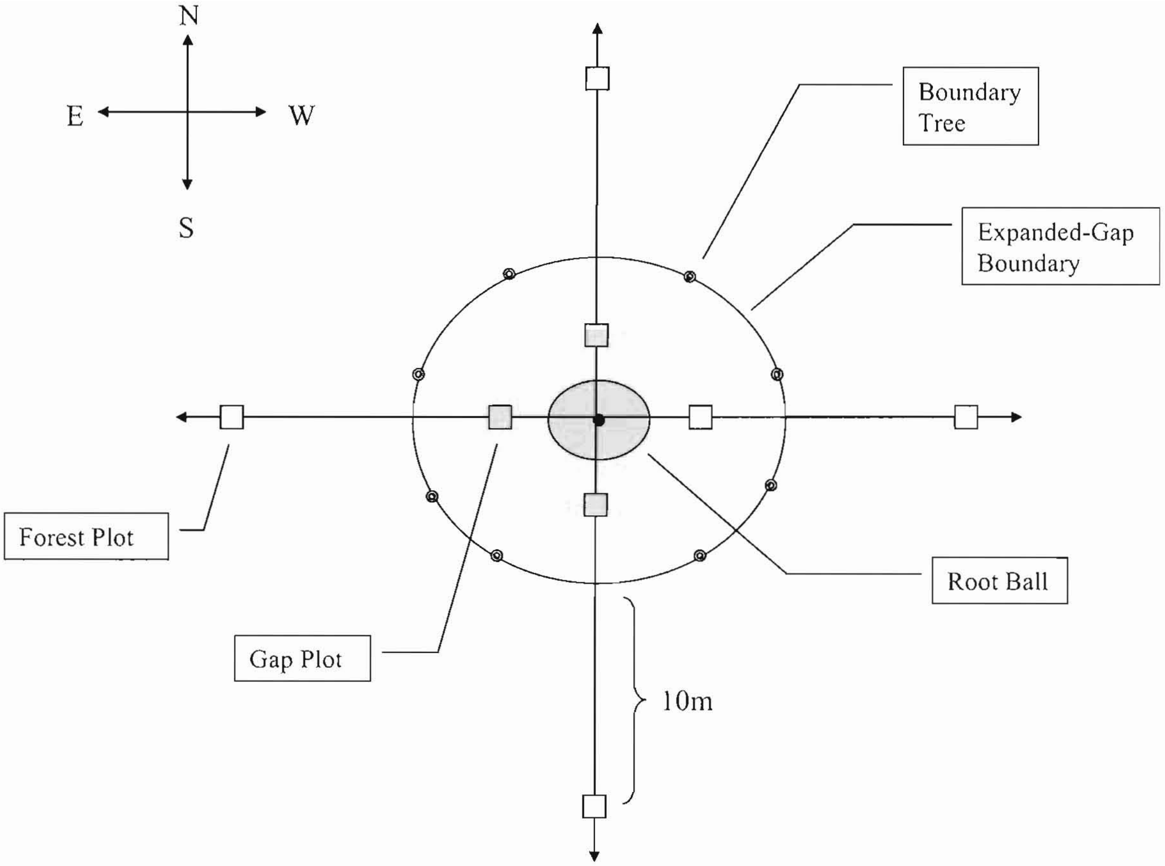
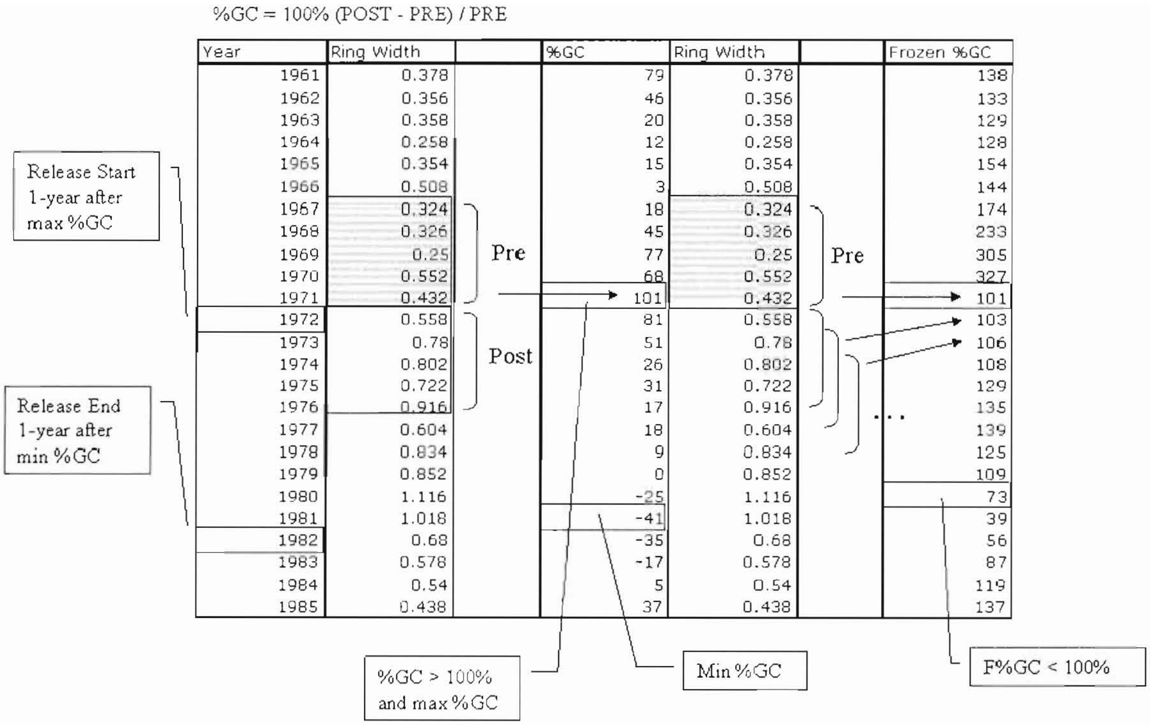


Figure 2 **Diagram of the sampling design showing the location of gap and forest plots at each site.**
All plots were 2m by 2m in area. Gap plots were located halfway between the centre of the root ball of the gap-maker (inner circle) and the boundary of the expanded gap (outer circle). Forest plots were located 10 meters from the boundary of the expanded gap in the surrounding closed-canopy forest.



%GC = 100% (POST - PRE) / PRE

Year	Ring Width		%GC	Ring Width		Frozen %GC
1961	0.378		79	0.378		138
1962	0.356		46	0.356		133
1963	0.358		20	0.358		129
1964	0.258		12	0.258		128
1965	0.354		15	0.354		154
1966	0.508		3	0.508		144
1967	0.324		18	0.324		174
1968	0.326		45	0.326		233
1969	0.25	Pre	77	0.25	Pre	305
1970	0.552		68	0.552		327
1971	0.432		101	0.432		101
1972	0.558		81	0.558		103
1973	0.78		51	0.78		106
1974	0.802	Post	26	0.802		108
1975	0.722		31	0.722		129
1976	0.916		17	0.916		135
1977	0.604		18	0.604		139
1978	0.834		9	0.834		125
1979	0.852		0	0.852		109
1980	1.116		-25	1.116		73
1981	1.018		-41	1.018		39
1982	0.68		-35	0.68		56
1983	0.578		-17	0.578		87
1984	0.54		5	0.54		119
1985	0.438		37	0.438		137

Release Start 1-year after max %GC

Release End 1-year after min %GC

%GC > 100% and max %GC

Min %GC

F%GC < 100%

Figure 3 Tabular example of how to identify a release, and how to determine the years a release started and ended, based on patterns of ring-width over time. The example details how to calculate percent growth-change (%GC) and frozen percent growth-change (F%GC) from ring-width series, how to determine release start dates based on patterns of %GC, and how to determine release end dates based on patterns of F%GC and %GC. Comparison of average ring widths for the period 1967-1971 (PRE) and the period 1972-1976 (POST), according to the %GC formula, shows a 101% increase in average radial growth. This value surpasses the growth change threshold of 100% and, therefore, qualifies as a radial growth release. The precise year the release started is then determined as the year following the maximum %GC value within 5 years of the %GC value exceeding 100%. In this case 101% is the maximum %GC value, and therefore 1972 is designated as the year the release began. Comparisons of average ring widths for the period 1967-1971(PRE) and subsequent 5-year periods (e.g. 1972-1976, 1973-1977... 1981-1985), show that the average change in radial growth drops below the 100% threshold in 1980 (F%GC=73%). The precise year the release ended is then determined as the year following the lowest %GC value (Min %GC) within 5 years of the F%GC value dropping below the threshold of 100%. In this case -41% is the minimum %GC value within 5 years of the F%GC value dropping below the threshold of 100%. Therefore 1982 is designated as the year the release ended.

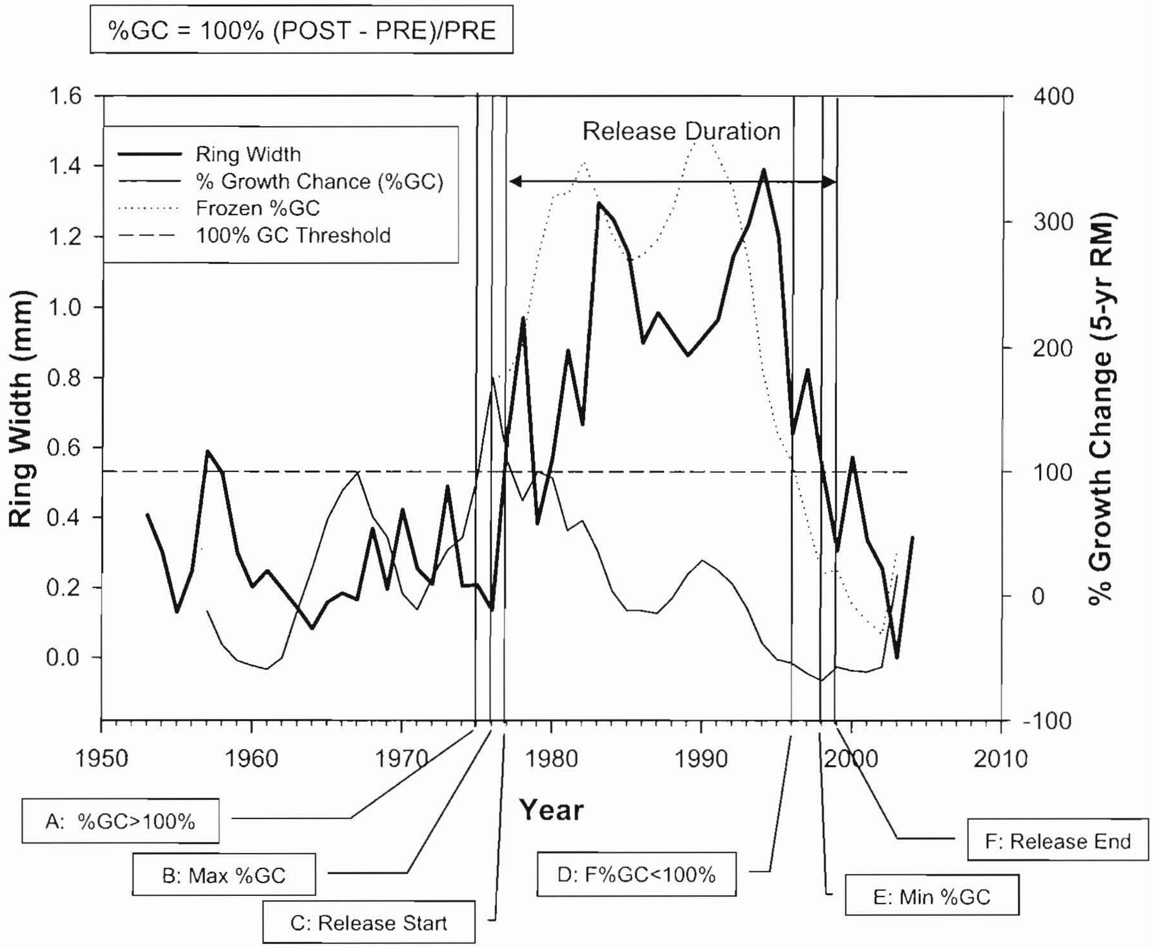


Figure 4 Graphical example of how to identify a release, and how to determine the years a release started and ended, based on patterns of ring-width over time.
The example indicates: A) the year percent growth-change (%GC) exceeds the release threshold of 100%, B) the maximum %GC within 5-years of %GC exceeding the 100% threshold, C) the designated year of release initiation at 1 year following the maximum %GC, D) the year frozen percent growth-change (F%GC) depreciates below the threshold value of 100%, E) the minimum %GC within 5-years of the F%GC depreciating below the 100% threshold, and F) the designated year of release termination at 1 year following the minimum %GC. The dashed horizontal line represents the release threshold of a 100% increase in average radial growth.

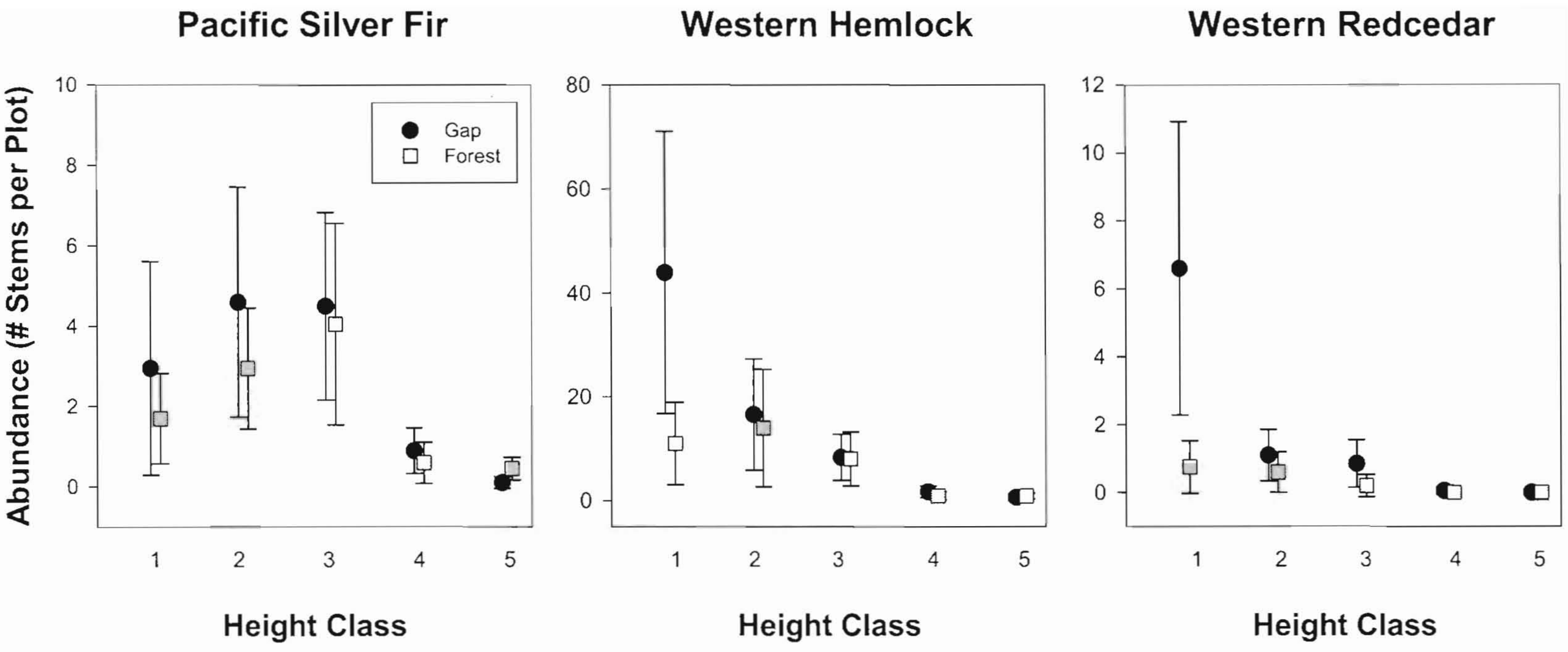


Figure 5 Abundances (+/- 95% CI's) of Pacific silver fir, western hemlock, and western redcedar regeneration in gap (circle) and forest (square) sites, separated by species.

Height Class 1 includes seedlings less than 10 cm tall, but greater than one-year in age; Height Class 2 includes seedlings between 10 and 30 cm tall; Height Class 3 includes seedlings between 30 and 130 cm tall; Height Class 4 includes saplings between 130 and 300 cm tall; and Height Class 5 includes saplings greater than 300 cm tall, but less than 10 cm in diameter at breast height.

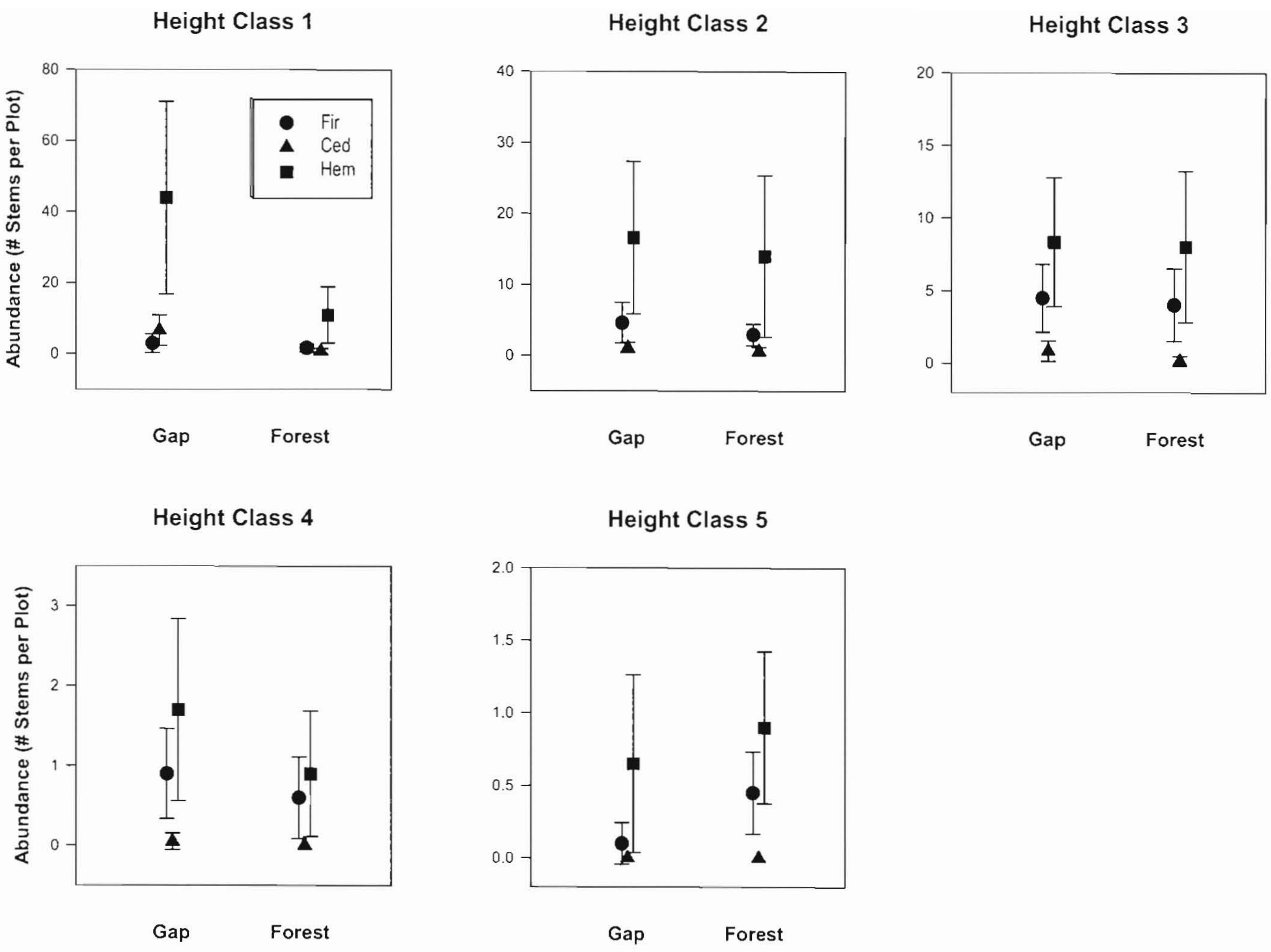


Figure 6 Abundances (+/- 95% CI's) of Pacific silver fir (circles), western redcedar (triangle) and western hemlock (squares) regeneration in gap and forest sites, separated by height class.
See Figure 5 for a description of the height classes.

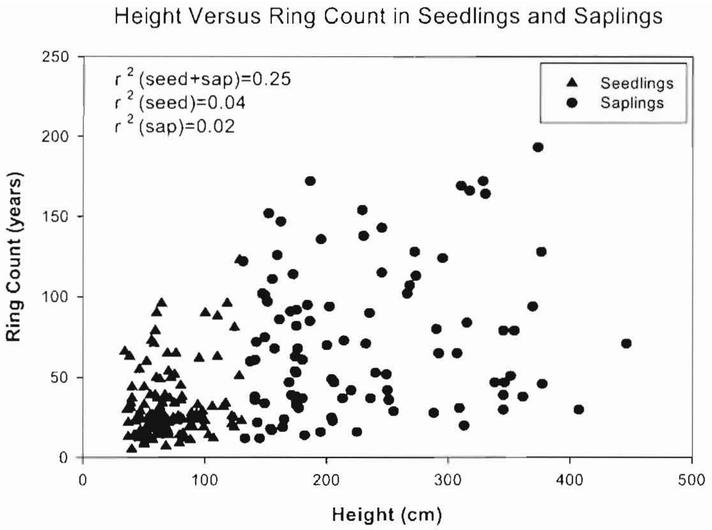


Figure 7 Relationship between Ring Count (age in years) and Height (cm) in saplings (circles) and seedlings (triangles) collected from both gap and forest sites. Correlation co-efficients (r^2) are shown for saplings and seedlings combined and separate.

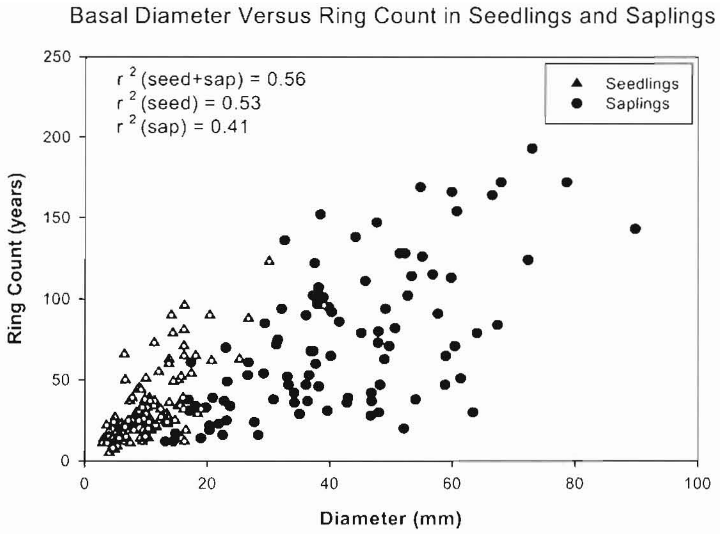


Figure 8 **Relationship between Ring Count (age in years) and Average Basal Diameter (mm) in saplings (circles) and seedlings (triangles) collected from both gap and forest sites. Correlation co-efficients (r^2) are shown for saplings and seedlings combined and separate.**

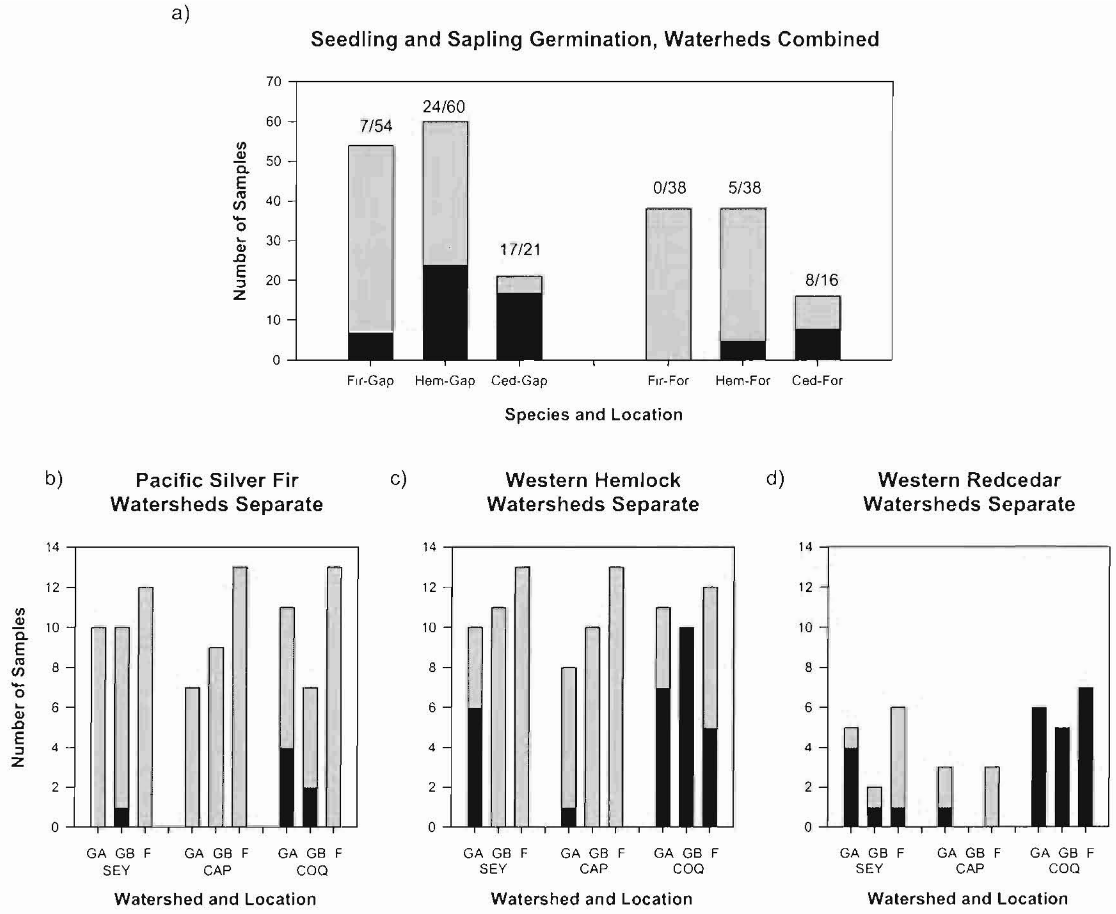


Figure 9 Number of seedlings and saplings that did and did not germinate within 10-years of the gap-formation dates, separated by species, location, and watershed.
a) Number of seedlings and saplings that did (black bar) and did not (grey bar) establish within 10-years of the gap-formation dates, separated by species (Pacific silver fir = Fir, western hemlock = Hem, and western redcedar = Ced) and location (gap and forest sites). The fractions of samples that germinated within 10-years of the gap-formation dates across all three watersheds are shown above each bar. b-d) Number of Pacific silver fir, western hemlock, and western redcedar seedlings and saplings that did (black bar) and did not (grey bar) establish within 10-years of the gap-formation dates separated by species, watershed (Seymour = SEY, Capilano = CAP, and Coquitlam =COQ River) and sites within each watershed (Gap-A, Gap-B, and Forest).

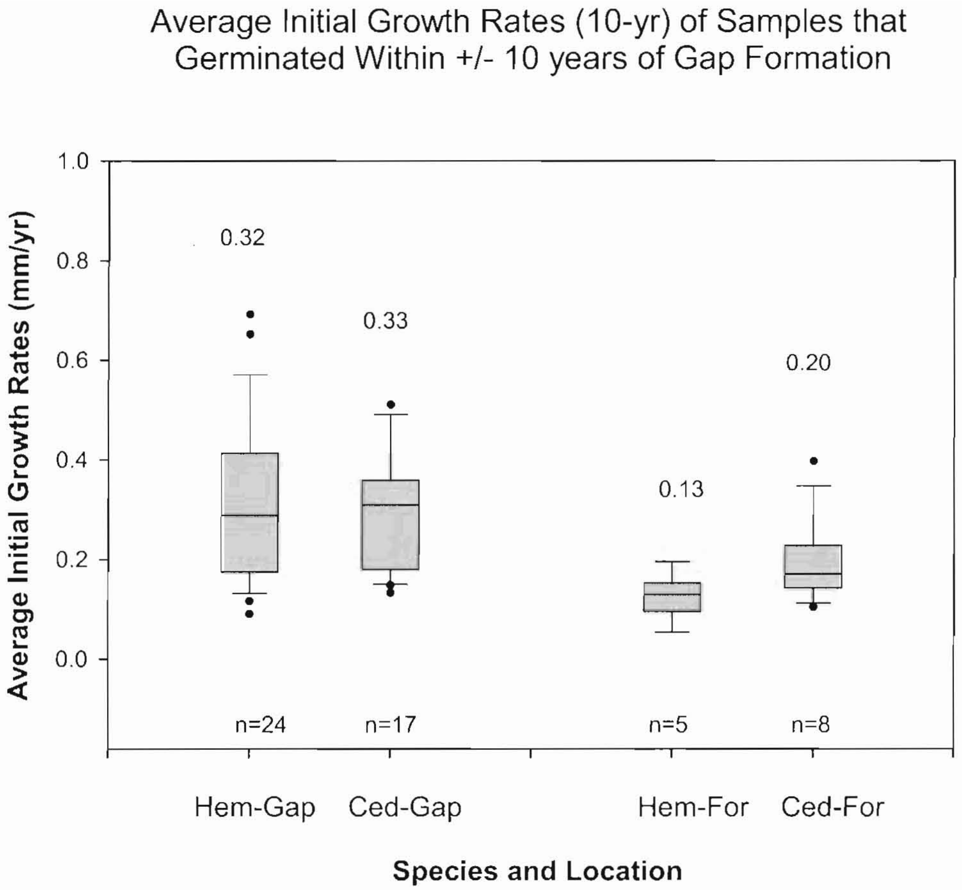


Figure 10 Average initial growth rates of western hemlock (Hem) and western redcedar (Ced) seedlings and saplings that established within 10-years of the gap formation dates in gap and forest sites.
Average initial growth rates were calculated over the first 10-years of radial growth. Values for seedlings and saplings were combined.

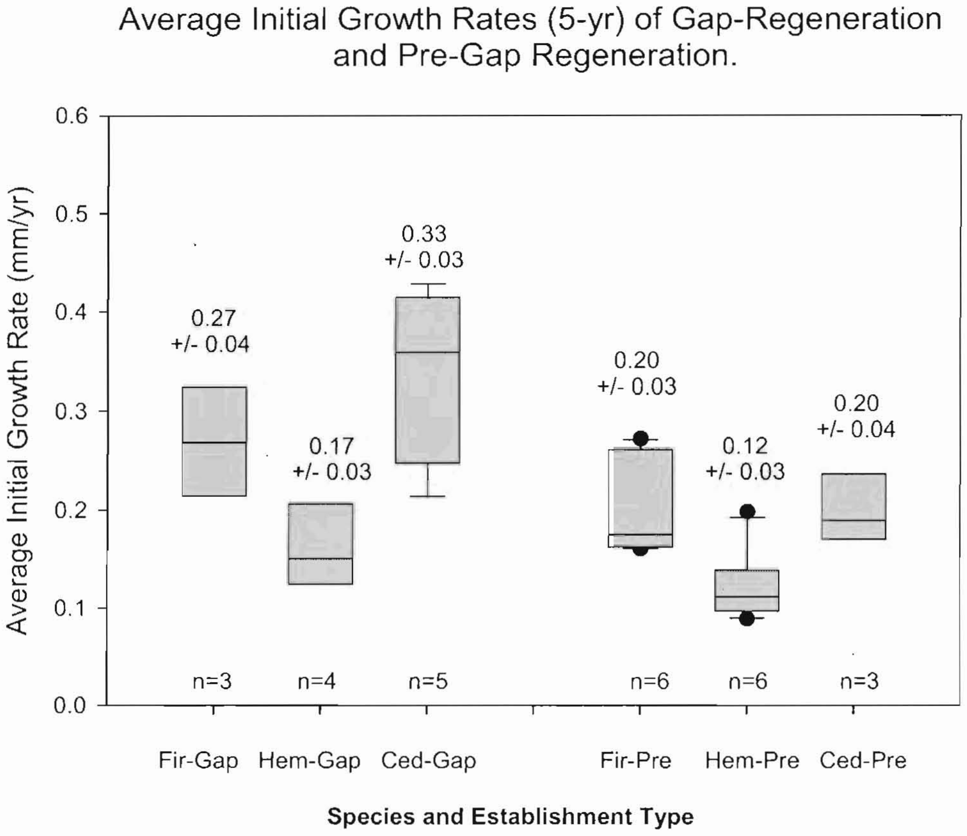


Figure 11 Average initial growth rates of Pacific silver fir (Fir), western hemlock (Hem), and western redcedar (Ced) seedlings and saplings that established in gap plots within ± 10-years of the gap-formation dates (Gap = gap-regeneration), and that established in gap and forest plots at least 10-years prior to the gap-formation dates (Pre = pre-gap regeneration).
Growth rates were calculated over first 5-years of radial growth. Seedlings and saplings were combined.

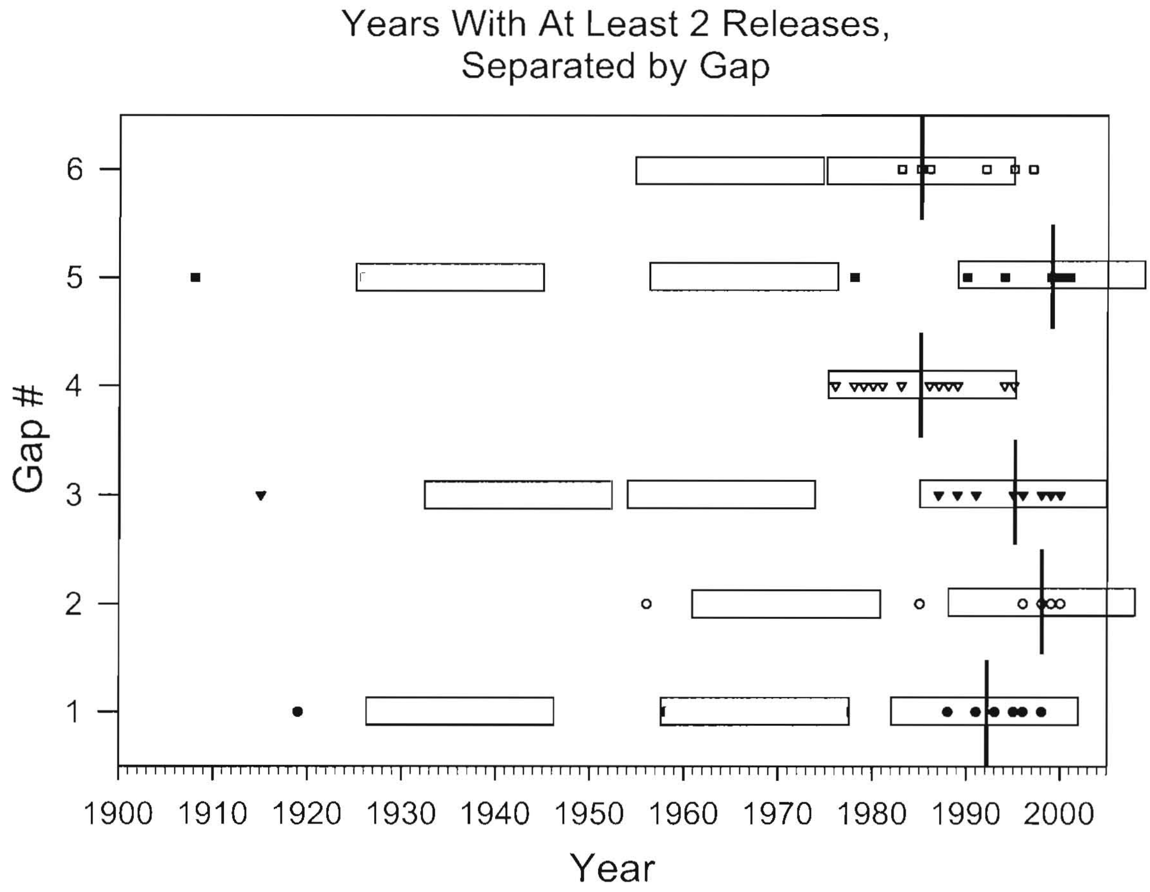


Figure 12 Years in which at least two samples in each site initiated release, separated by site. Vertical lines indicate the gap-formation dates associated with each site. Horizontal bars show periods of twenty years bracketing the gap-formation dates (solid grey shading) and periods of twenty years that contain multiple years with at least 2 saplings experiencing radial growth release (cross-hatched grey shading). Samples collected from forest plots were assigned to the nearest gap location (i.e. forest samples were not pooled within watersheds as in all other analyses).

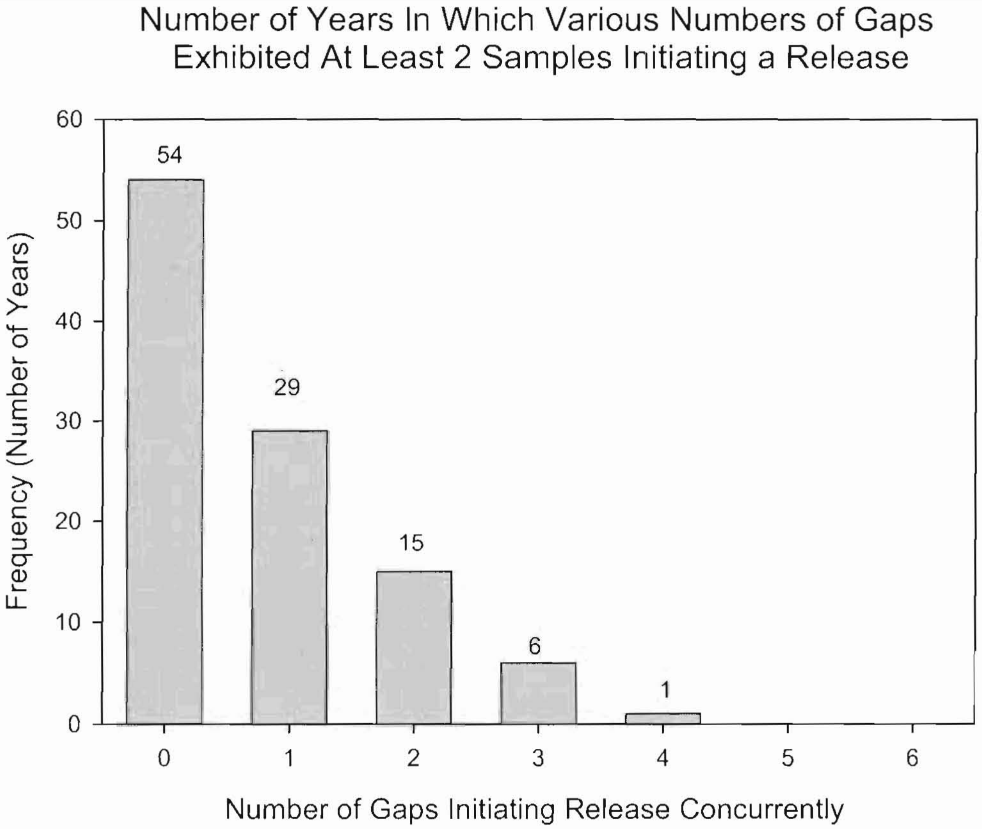


Figure 13 Number of years in which various numbers of gaps (0 gaps to all 6 gaps) simultaneously exhibited at least two releases in any given year.
Releases that occurred during the 20-year periods bracketing the gap-formation dates were excluded to ensure that releases were independent of the current gaps.

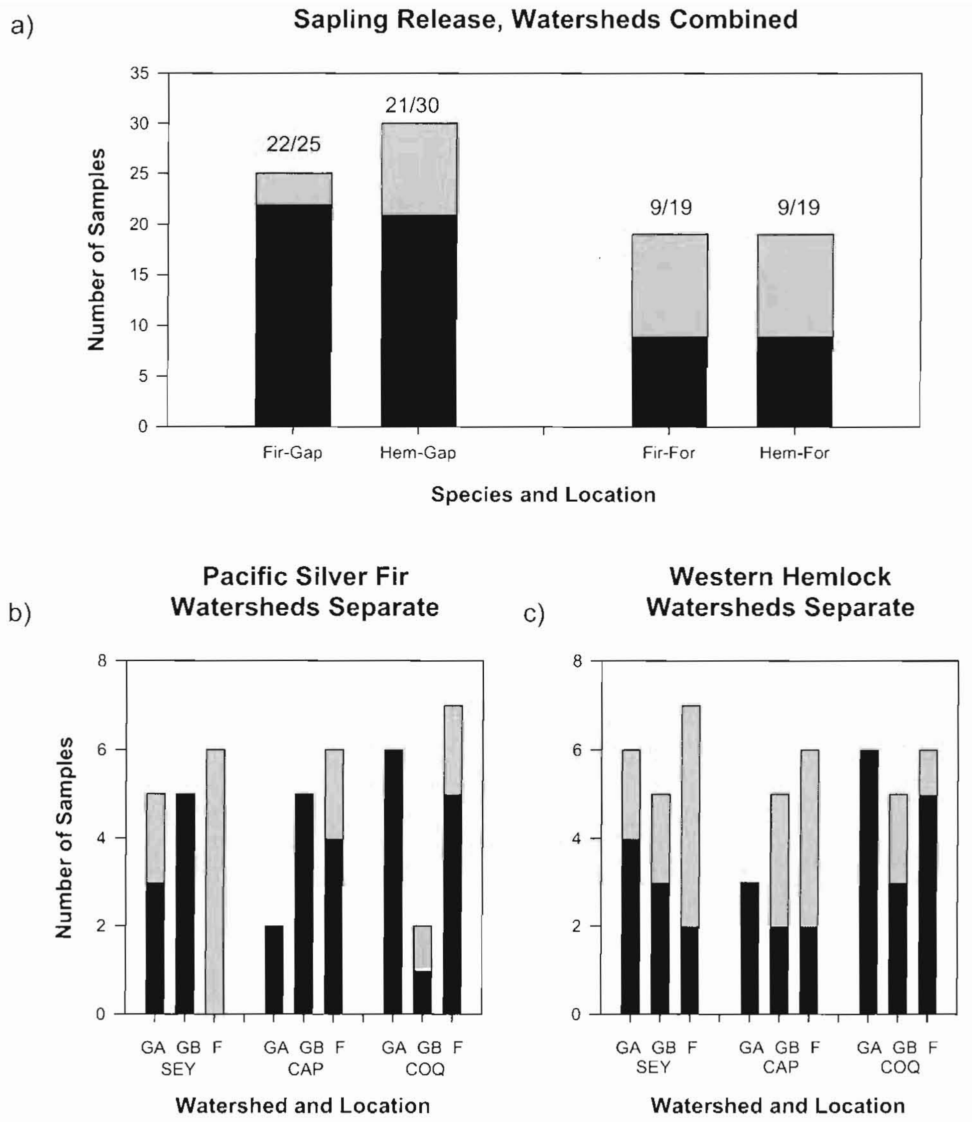


Figure 14 Number of saplings that did and did not exhibit radial growth release within +/- 10 years of the gap-formation dates, separated by species, location and watershed. a) Number of saplings that did (black bars) and did not (grey bars) exhibit radial growth release within +/- 10 years of the gap-formation dates, separated by species (Pacific silver fir =Fir, and western hemlock = Hem) and location (gap and forest sites). The fractions of samples that released within 10-years of the gap-formation dates across all three watersheds are shown above each bar. b-c) Number of Pacific silver fir and western hemlock saplings that did (black bars) and did not (grey bars) exhibit radial growth release within +/- 10 years of the gap-formation dates, separated by watershed (Seymour = SEY, Capilano = CAP, and Coquitlam =COQ River) and sites within each watershed (Gap-A, Gap-B, and Forest).

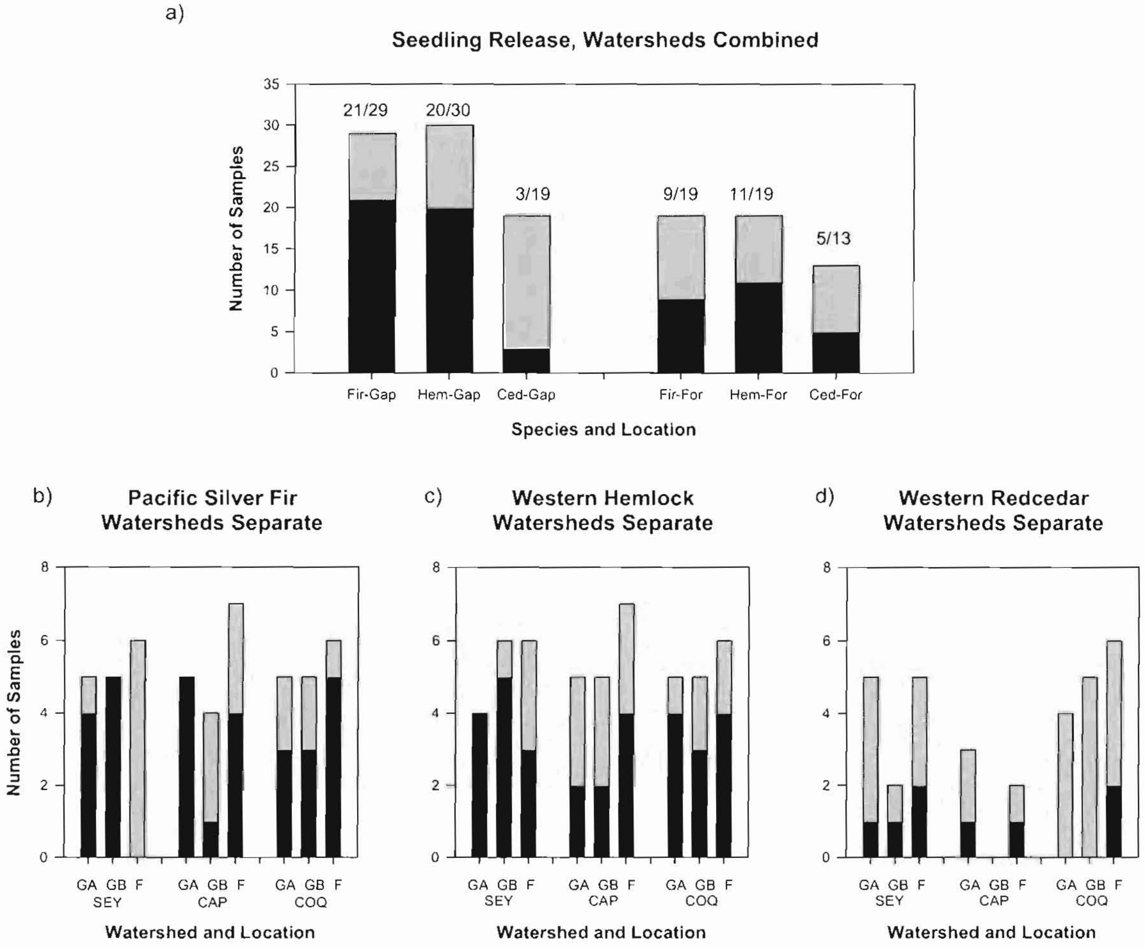


Figure 15 Number of seedlings that did and did not exhibit radial growth release within +/- 10 years of the gap-formation dates, separated by species, location and watershed. a) Number of seedlings that did (black bars) and did not (grey bars) exhibit radial growth release within +/- 10 years of the gap-formation dates, separated by species (Pacific silver fir = Fir, western hemlock = Hem, and western redcedar = Ced) and location (gap and forest sites). The fractions of samples that released within 10-years of the gap-formation dates across all three watersheds are shown above each bar. b-d) Number of Pacific silver fir, western hemlock, and western redcedar seedlings that did (black bars) and did not (grey bars) exhibit radial growth release within +/- 10 years of the gap-formation dates, separated by watershed (Seymour = SEY, Capilano = CAP, and Coquitlam =COQ River) and sites within each watershed (Gap-A, Gap-B, and Forest).

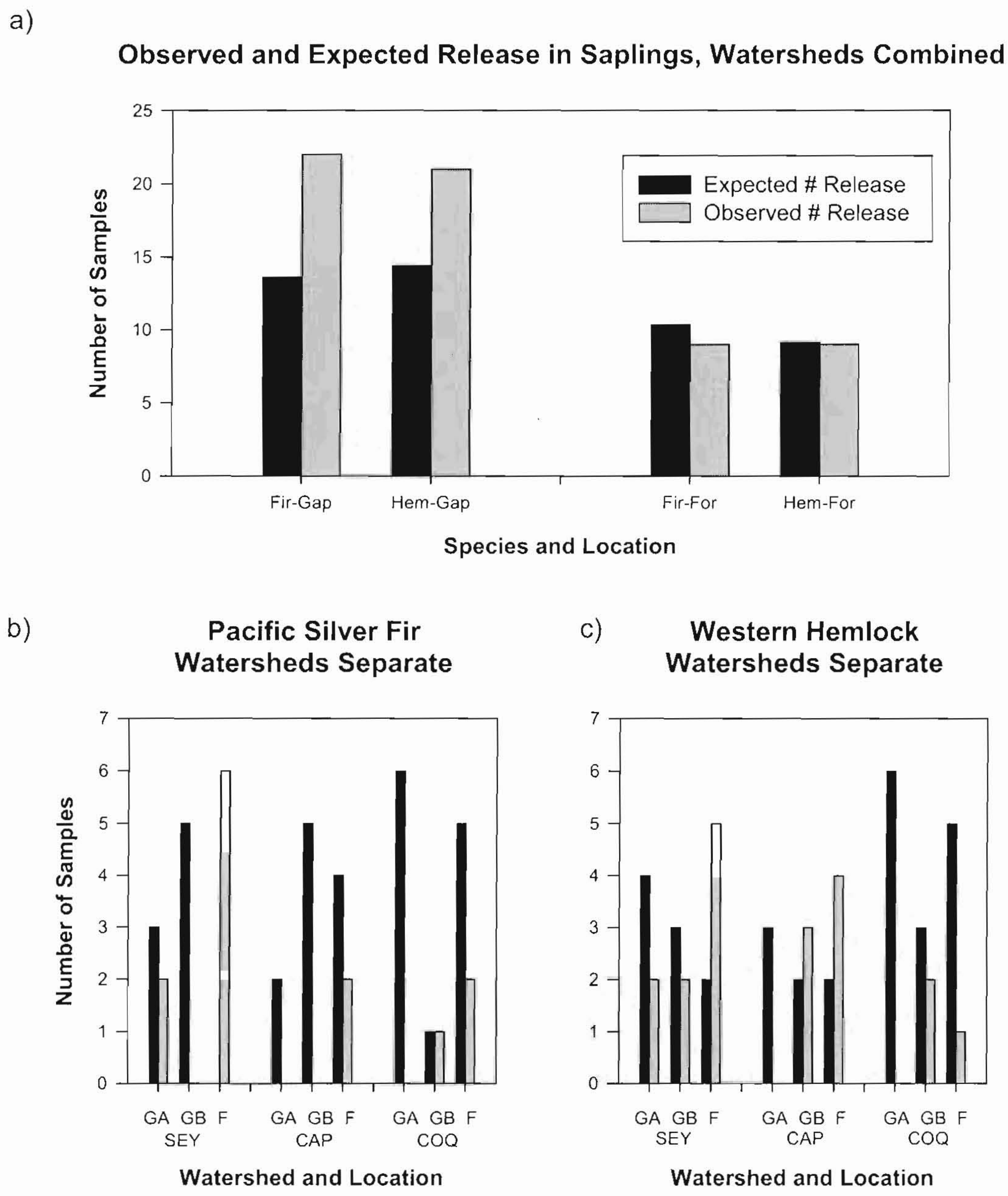


Figure 16 Observed and expected frequencies of release in saplings, separated by species, location and watershed.
a) Observed and expected frequencies of release in saplings, separated by species ((Pacific silver fir = Fir, western hemlock = Hem) and location (gap and forest sites).
b-c) Observed and expected release frequencies in Pacific silver fir and western hemlock saplings, separated by watershed (Seymour = SEY, Capilano = CAP, and Coquitlam =COQ River) and sites within each watershed (Forest, Gap-A, Gap-B). Observed frequencies of release correspond to the number of samples that exhibited a radial growth release within 10-years of the gap-formation dates. Expected frequencies of release correspond to the number of releases expected to occur during the 21-year period bracketing each gap-formation date, and are based on historic rates of release calculated for each species at each gap and forest site.

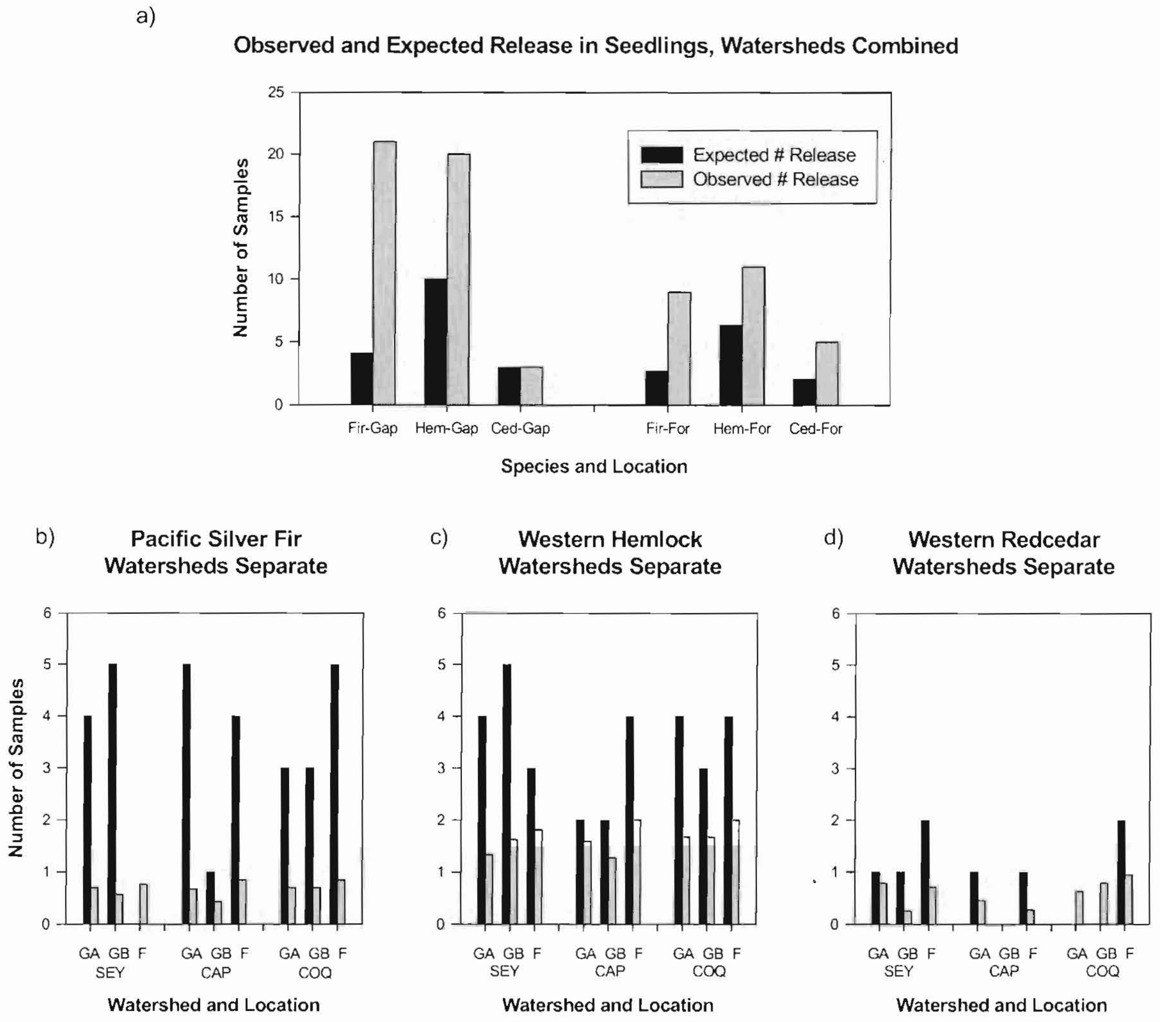


Figure 17 Observed and expected frequencies of release in seedlings, separated by species, location and watershed.
a) Observed and expected frequencies of release in seedlings, separated by species (Pacific silver fir = Fir, western hemlock = Hem, and western redcedar = Ced) and location (gap and forest sites). b-d) Observed and expected release frequencies in Pacific silver fir, western hemlock and western redcedar seedlings, separated by watershed (Seymour = SEY, Capilano = CAP, and Coquitlam =COQ River) and sites within each watershed (Forest, Gap-A, Gap-B). Observed frequencies of release correspond to the number of samples that exhibited a radial growth release within 10-years of the gap-formation dates. Expected frequencies of release correspond to the number of releases expected to occur during the 21-year period bracketing each gap-formation date and are based on historic rates of release calculated for each species at each gap and forest site.

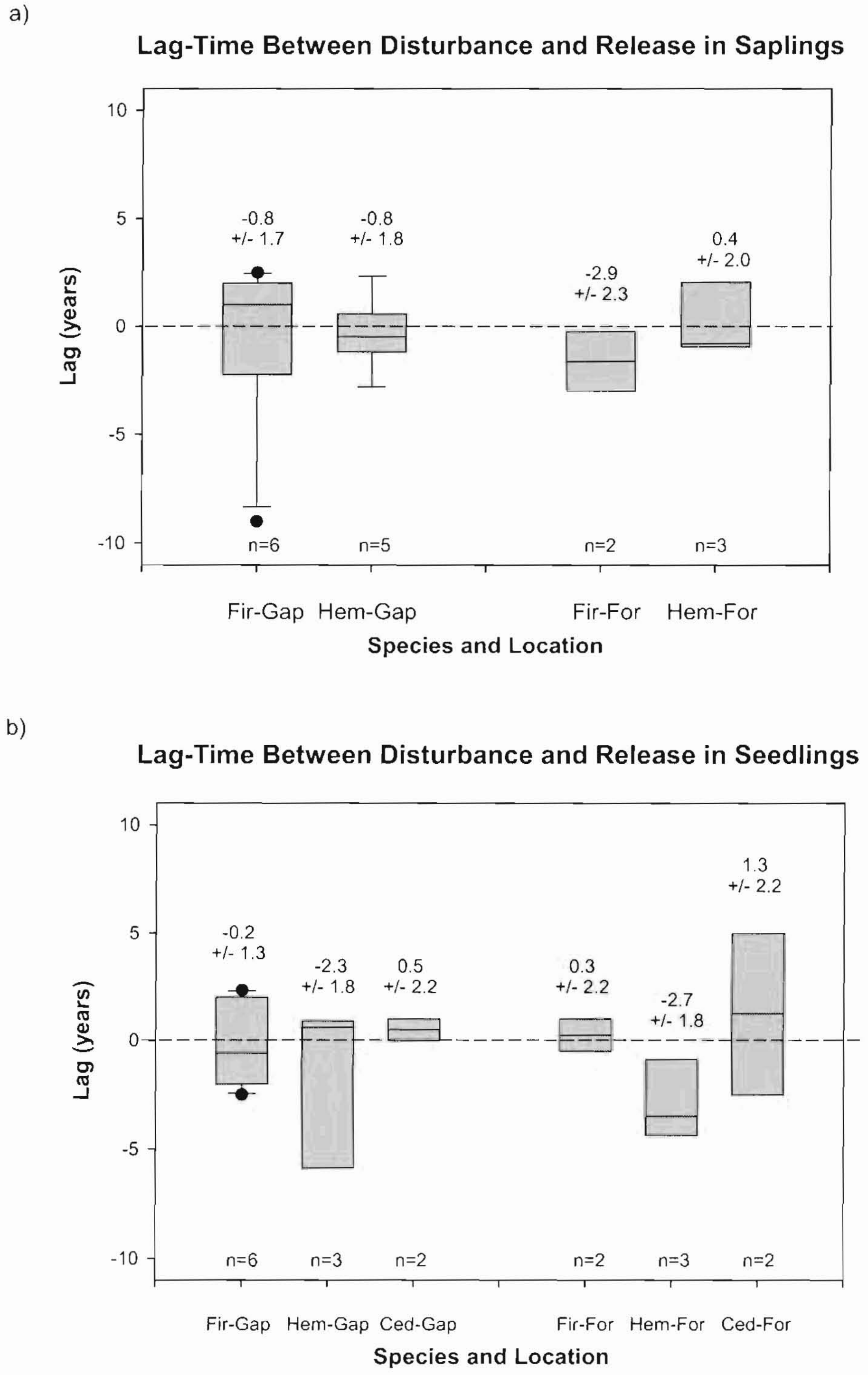


Figure 18 Average difference in years (lag-time) between the date of gap-formation and the start of radial-growth release in (a) saplings and (b) seedlings, separated by species (Pacific silver fir =Fir, western hemlock = Hem, and western redcedar = Ced) and location (gap and forest sites).

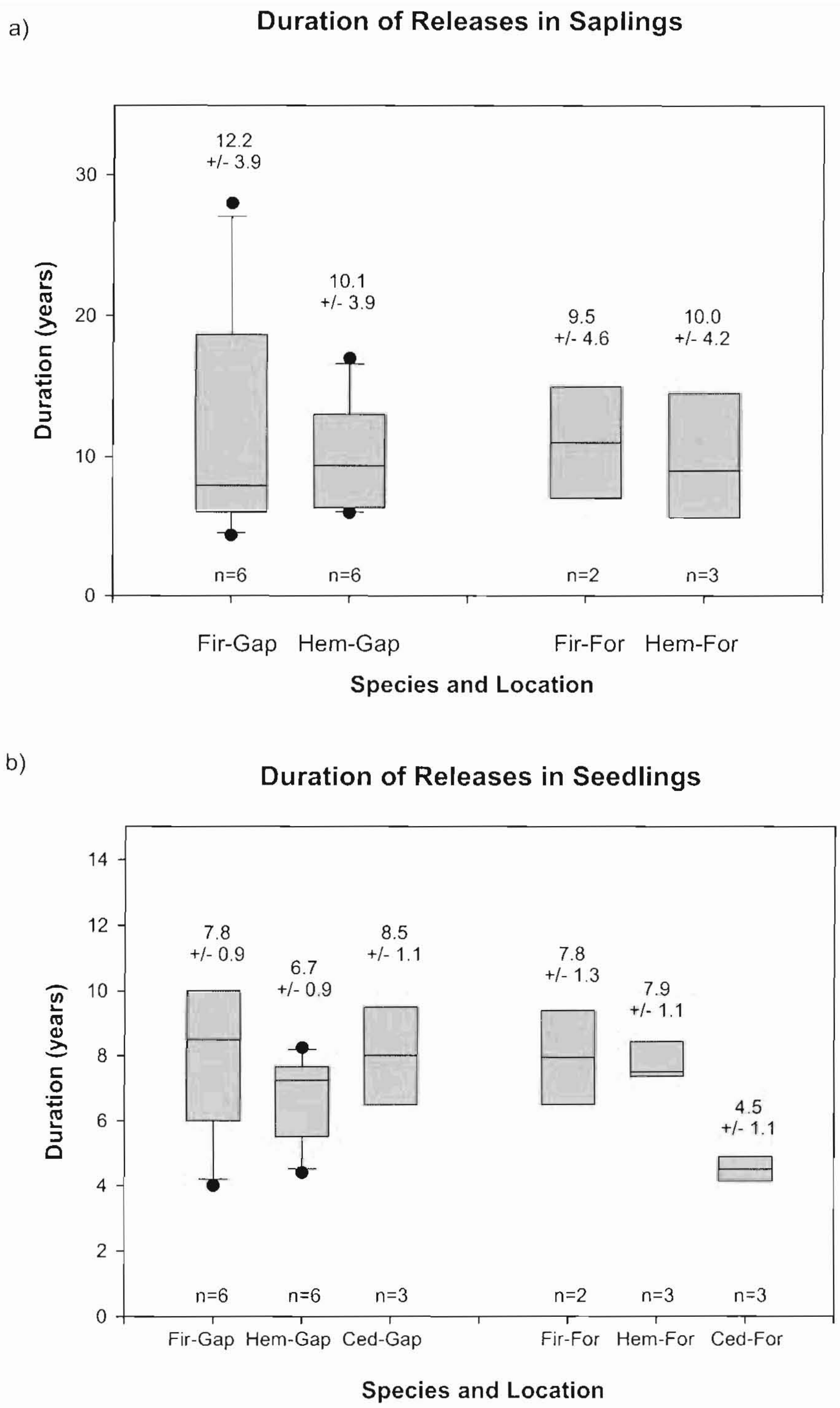


Figure 19 Average duration of radial-growth releases that occurred in (a) saplings and (b) seedlings within ± 10-years of the date of gap-formation, separated by species (Pacific silver fir =Fir, western hemlock = Hem, and western redcedar = Ced) and location (gap and forest sites).

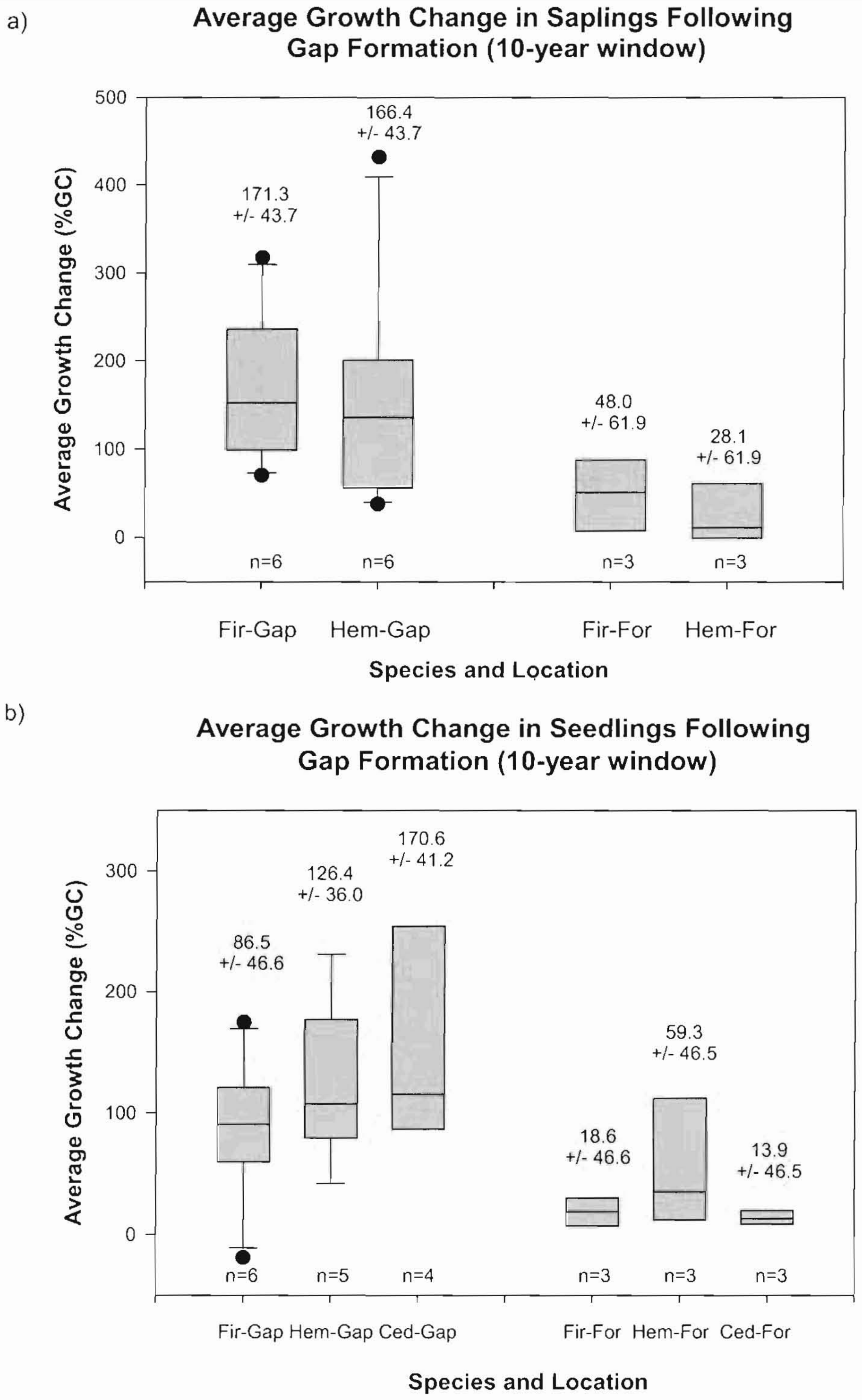


Figure 20 Average magnitudes (max %GC) of radial-growth releases that occurred in (a) saplings and (b) seedlings within ± 10-years of the dates of gap-formation, separated by species (Pacific silver fir =Fir, western hemlock = Hem, and western redcedar = Ced) and location (gap and forest sites).

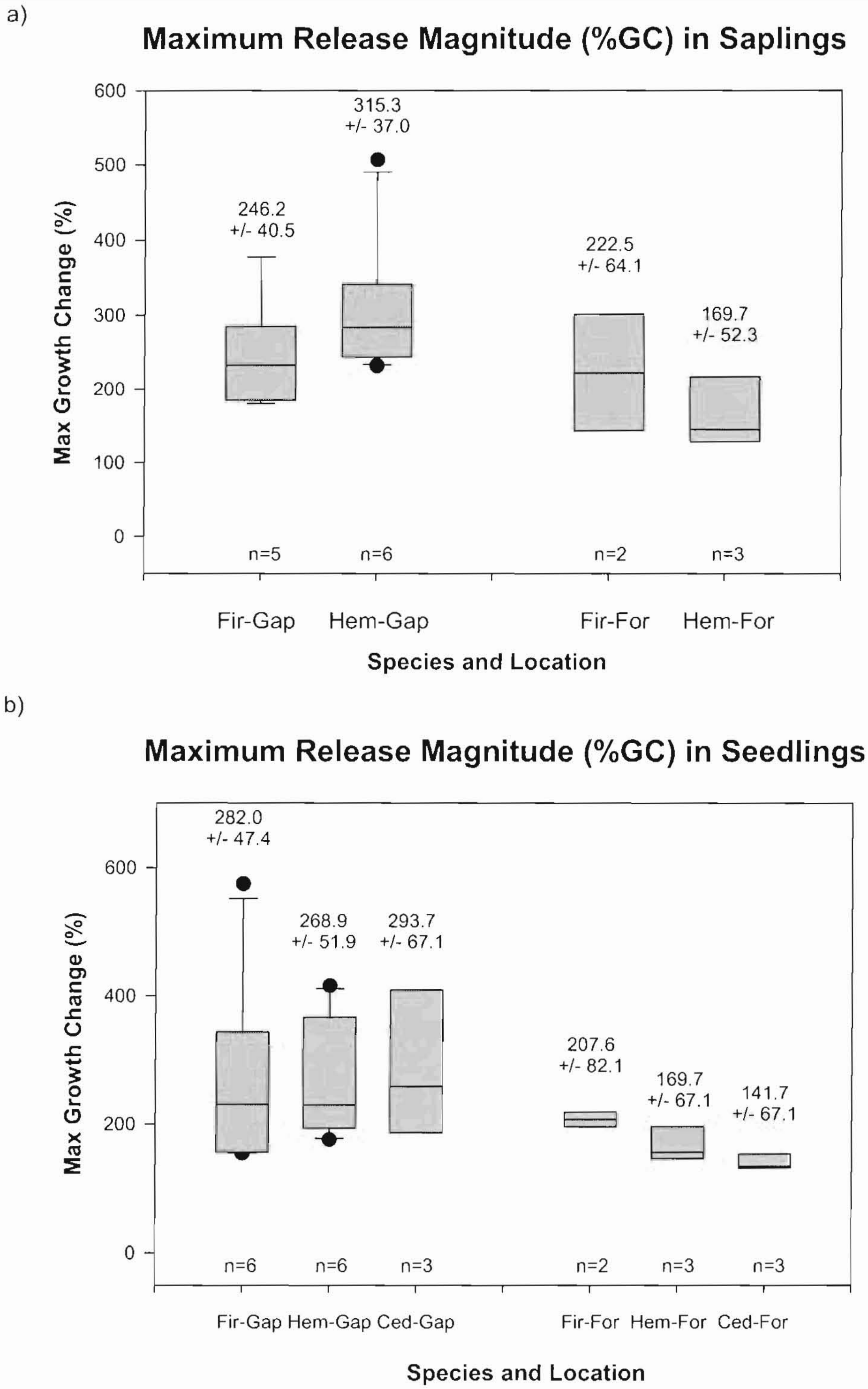


Figure 21 Average changes in radial growth (%GC) in (a) saplings and (b) seedlings between the periods 10-years preceding and subsequent to the dates of gap-formation, separated by species (Pacific silver fir =Fir, western hemlock = Hem, and western redcedar = Ced) and location (gap and forest sites).