

GROWTH RELEASE OF TREES
FOLLOWING FINE-SCALE CANOPY DISTURBANCES
IN OLD-GROWTH FORESTS OF COASTAL BRITISH COLUMBIA, CANADA

by

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Abstract

Growth release of trees following canopy disturbances is of interest to ecological scientists and forest managers. Using dendroecological techniques, I examined growth release of canopy and subcanopy trees following the formation of natural, fine-scale canopy gaps in old-growth, western redcedar-western hemlock forests of coastal British Columbia. I aimed to quantify detailed information on release of the three shade-tolerant tree species that constitute these stands: western redcedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*), and Pacific silver fir (*Abies amabilis*).

As a first step, I calibrated the radial-growth averaging method to account for regional-scale variability and capture a more complete range of growth releases that may occur following the formation of fine-scale gaps in the study stands. A 25% threshold, 5-year moving average, and 10-year window emerged as appropriate parameters for detecting releases using radial-growth averaging. Basal area increment was also the most appropriate growth index for detecting releases. Establishing these empirically-based criteria was important for quantifying the magnitude and duration of releases.

Tree diameter and growth rate prior to release were the most important predictors of the magnitude and duration of releases, but identity of the tree species and distance from the gap center were also important predictors. Western hemlock and Pacific silver fir were often growing slowly both in the canopy and subcanopy, giving them tremendous potential to release. For these species, releases were generally intensive and persistent. In contrast, western redcedar were often growing quickly both in the canopy and subcanopy, giving them less potential to release. Compared to western hemlock and Pacific silver fir, western redcedar releases were less intensive and persistent. Patterns related to distance from the gap

center emerged for trees growing along the north-south axis of gaps. Regardless of species, increasing distance from the gap center resulted in decreasing magnitude and duration of releases. However, patterns for duration were complex, as the distance effect was greater for trees north of the gap center.

Information on growth release of trees is useful for reconstructing the history of past canopy disturbances, elucidating mechanisms of tree species coexistence, and assessing and predicting stand changes due to forest management in coastal British Columbia.

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Co-authorship Statement

This thesis presents research conducted by Amanda Stan, in collaboration with her supervisor, Lori Daniels. Amanda Stan was the author of the thesis and primary investigator of the research, responsible for its design and the collection, analysis, and interpretation of data. Lori Daniels, along with the other members of the supervisory committee (Valerie LeMay, Roy Turkington, and Greg Henry) provided consultation and editorial assistance throughout the research and writing process.

1. Introduction

1.1. Fine-scale disturbances in forests

In forests where stand-destroying disturbances are infrequent, fine-scale disturbances that create gaps in the canopy through the death of single trees or small groups of trees strongly influence forest development and dynamics (Sousa 1984, White and Pickett 1985, Frelich 2002). Fine-scale processes of gap dynamics are responsible for creating and maintaining late-successional or old-growth forest communities by affecting the structure of dead wood, the growth of new or established plants, and aspects of ecosystem function such as decomposition and nutrient cycling (Franklin et al. 2002). Understanding processes of gap dynamics is essential for evaluating past and present ecological condition, particularly in areas where old-growth forests dominated historical landscapes.

Fine-scale processes of gap dynamics dominate the natural disturbance regime of the wetter parts of the coastal temperate rain forest from southern British Columbia, Canada, to southeastern Alaska, USA (Veblen and Alaback 1996, Lertzman et al. 2002, Wong et al. 2003, Daniels and Gray 2006). Using the Biogeoclimatic Ecosystem Classification system of British Columbia, this includes forests of the wetter subzones of the Coastal Western Hemlock and Mountain Hemlock zones (Meidinger and Pojar 1991). These forests are dominated by shade-tolerant cedars (*Thuja* and *Chamaecyparis* spp.), hemlocks (*Tsuga* spp.), and true firs (*Abies* spp.) (Meidinger and Pojar 1991). Historically, stand-destroying disturbances due to fire were infrequent and often constrained by topography. For example, retrospective studies using soils, lake sediments, and tree rings found that mean fire return intervals were usually greater than 1000 years, and some sites had not burned in many thousands of years (Lertzman et al. 2002, Gavin et al. 2003a, b, Hallett et al. 2003). Most

sites that burned within the past 1000 years were on south-facing slopes (Gavin et al. 2003a, b). Wind could also act as an agent of stand-destroying disturbance in coastal British Columbia, but it too has been reported as being constrained by topography. Pearson (2000) found no evidence of stand-level windthrow over a 50-year aerial photo record in protected valleys on the west coast of Vancouver Island, British Columbia. In nearby Alaska (Kramer et al. 2001) and Oregon (Harcombe et al. 2004), stand-level windthrow was confined to exposed portions of the landscape, corroborating findings from British Columbia. These disturbance patterns explain the structure of most unmanaged forests throughout coastal British Columbia. In the absence of stand-destroying disturbances, long periods of fine-scale gap forming and filling processes have led to old, structurally complex forests (Figure 1.1) (Lertzman and Krebs 1991, Lertzman et al. 1996, Wells et al. 1998, Daniels 2003).

1.2. Growth release of trees following fine-scale canopy disturbances

Fine-scale canopy disturbances influence a number of ecological processes in forests. Growth release of trees following the formation of a canopy gap, as determined using dendroecological techniques, is one process of interest to ecological scientists and forest managers. Information on growth releases in natural forest stands is useful for interpreting stand developmental history (Lorimer and Frelich 1989, Frelich 2002). In turn, understanding the development and dynamics of natural forest stands provides a benchmark to which current management practices can be compared and evaluated for long-term ecological sustainability (Landres et al. 1999, Franklin et al. 2002).

Growth releases are often used to reconstruct the long-term history of canopy disturbances in forests. This approach is particularly useful where tree-age distribution is weakly related to disturbance history, as in old-growth forests dominated by shade-tolerant



Figure 1.1. Top: Fine-scale death of canopy trees is the dominant natural disturbance in forests of coastal British Columbia, Canada. Bottom: Long periods of gap forming and filling processes lead to structurally complex, old-growth forests. Both photos are from old-growth, western redcedar-western hemlock stands in the Capilano River watershed in the Coast Mountains of southwestern British Columbia.

tree species. Radial-growth averaging (Henry and Swan 1974, Lorimer and Frelich 1989, Nowacki and Abrams 1997) is the most commonly used method for reconstructing canopy disturbances using releases (Rubino and McCarthy 2004). This method involves detecting releases by comparing average radial growth for successive periods and identifying peak growth-change values above a minimum threshold.

Applying the radial-growth averaging method to many trees in a stand can be a powerful way of estimating the frequency and intensity of past disturbance events. However, the strength of this approach depends on recognizing and addressing the limitations of the radial-growth averaging method. Several factors can influence radial-growth patterns and response to disturbance, some of which are: (i) interannual variation in climate, (ii) tree species, age, diameter, genetics, position in the canopy, and proximity to canopy gaps, (iii) disturbance type and intensity, and (iv) site conditions. Thus, calibrating the radial-growth averaging method to better account for these factors will help to more accurately reconstruct past canopy disturbances (Lorimer and Frelich 1989, Nowacki and Abrams 1997, Black and Abrams 2003, 2004). In addition, combining radial-growth averaging with stem maps of live and dead trees can improve reconstructions by offering a better understanding of the spatial and temporal aspects of individual disturbance events, including the size, shape, and location of past canopy gaps (Payette et al. 1990, Parish and Antos 2004, 2006, Fraver and White 2005). Reconstructions could be further improved with information on releases that goes beyond binary classification of release or no release.

Information on growth release following the formation of canopy gaps might also be useful for better understanding tree species coexistence in forests dominated by shade-tolerant individuals. While shade-tolerant tree species often establish beneath a closed

canopy, gaps may be necessary for individuals to grow into the canopy strata and thus critical for canopy tree replacement. For example, some shade-tolerant tree species may need a single, large gap created by the death of multiple trees to grow into the canopy strata (Parish and Antos 2004, 2006, Antos et al. 2005), others may need many, small gaps (Canham 1989, Daniels and Klinka 1996), and others may not require any gaps to grow into the canopy strata (Canham 1989).

Considering the mechanisms by which tree species ascend to the canopy, together with other life-history traits from juvenile to adult life stages (Lusk and Smith 1998), may help to clarify community dynamics in old-growth forests dominated by shade-tolerant tree species. Studies in subalpine, old-growth forests have recognized the importance of differential life-history traits across life stages for the coexistence of long-lived, shade-tolerant trees (e.g. Veblen 1986, Lertzman 1992, Yamamoto 1995, Parish and Antos 2004, 2006, Taylor et al. 2006, Mori et al. 2007). Different strategies for growing into the canopy strata, combined with other individual life-history traits, could be important for the coexistence of long-lived, shade-tolerant western redcedar (*Thuja plicata* Donn ex D. Don), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and Pacific silver fir (*Abies amabilis* Dougl. ex J. Forbes) in mid-elevation, old-growth forests of coastal British Columbia (Daniels 2003). In these stands, population size and age structures are complex, and trees show evidence of suppression and release associated with canopy gaps, with patterns that may differ among species (Daniels and Klinka 1996, Daniels 2003). These structural characteristics and growth patterns of trees suggest a need to further assess what mechanisms contribute to individual tree species persistence in coastal, old-growth stands and whether they permit long-term coexistence.

Understanding growth release of trees following gap formation is also important to forest management. While the change from clearcuts to variable retention silvicultural systems (Scientific Panel for Sustainable Forest Practices in Clayoquot Sound 1995, Franklin et al. 1997) that aim to emulate natural disturbances is an important step towards ecosystem management, we do not yet possess the tools to properly assess the sustainability of these systems. Quantifying growth release following gap formation will better prepare us for predicting potential changes in stand composition and structure resulting from variable retention silviculture at both the stand and landscape scales (Coates and Burton 1997).

1.3. Research objectives

The overall objective of my research is to examine growth release of trees following the formation of natural, fine-scale canopy gaps in old-growth, western redcedar-western hemlock forests of coastal British Columbia. My three specific objectives are to (1) calibrate the radial-growth averaging method to detect release of western redcedar, western hemlock, and Pacific silver fir following gap formation in these forests, (2) quantify attributes of growth releases, including magnitude and duration, following gap formation, and (3) discuss how to use this information to (i) improve approaches for reconstructing the history of canopy disturbances, (ii) better understand mechanisms of tree species coexistence, and (iii) improve ecosystem management of old-growth forests of coastal British Columbia.

1.4. Thesis overview

The remainder of this thesis comprises three research chapters and a concluding chapter. The research chapters are meant to be stand-alone manuscripts, though each builds on ideas and data from previous chapters. In the first research chapter (Chapter 2), I examined how climatic/regional-scale factors contribute to radial growth and release. In

addition, I explored the influences of different variations of the radial-growth averaging method on the number of trees that showed a release pattern following the formation of natural canopy gaps of known timing of origin. Combined, these analyses provided details on the functioning of the radial-growth averaging method relative to the population of trees in the study stands. I applied these results in subsequent chapters to detect, and quantify attributes of, growth releases following gap formation. In the second research chapter (Chapter 3), I quantified the duration and magnitude of releases of trees growing around the boundary of, or within, natural gaps and estimated the influence of tree- and gap-level variables on these two release attributes. I used this information to (i) discuss ways to improve current approaches for reconstructing the history of fine-scale canopy disturbances and (ii) better understand mechanisms of tree species coexistence, in old-growth forests of coastal British Columbia. In the third research chapter (Chapter 4), I expanded on previous results and estimated the influence of additional tree-level variables on the duration and magnitude of releases of trees growing along north-south transects extending through the gaps and into the adjacent forest. I then discussed the results in relation to forest management practices in coastal British Columbia. In the concluding chapter (Chapter 5), I presented a summary of my major findings.

1.5. Literature cited

- Antos, J.A., H.J. Guest, and R. Parish. 2005. The tree seedling bank in an ancient montane forest: stress tolerators in a productive habitat. *Journal of Ecology* 93:536-543.
- Black, B.A. and M.D. Abrams. 2003. Use of boundary-line growth patterns as a basis for dendroecological release criteria. *Ecological Applications* 13:1733-1749.
- Black, B.A. and M.D. Abrams. 2004. Development and application of boundary-line release criteria. *Dendrochronologia* 22:31-42.
- Canham, C.D. 1989. Different responses to gaps among shade-tolerant tree species. *Ecology* 70:548-550.
- Coates, K.D. and P.J. Burton. 1997. A gap-based approach for development of silvicultural systems to address ecosystem management objectives. *Forest Ecology and Management* 99:337-354.
- Daniels, L.D. 2003. Western redcedar population dynamics in old-growth forests: contrasting ecological paradigms using tree rings. *Forestry Chronicle* 79:517-530.
- Daniels, L.D. and R.W. Gray. 2006. Disturbance regimes in coastal British Columbia. *BC Journal of Ecosystems and Management* 7:44-56.
- Daniels, L.D. and K. Klinka. 1996. The dynamics of old-growth *Thuja-Tsuga* forests near Vancouver, British Columbia. Pages 379-393 in J.S. Dean, D.M. Meko, and T.W. Swetnam, editors. *Tree rings, environment, and humanity*.

- Franklin, J.F., D.R. Berg, D.A. Thornburgh, and J.C. Tappeiner. 1997. Alternative silvicultural approaches to timber harvesting: variable retention harvest systems. Pages 111-139 in K.A. Kohm and J.F. Franklin, editors. Creating a forestry for the 21st century: the science of ecosystem management. Island Press, Washington, DC, USA.
- Franklin, J.F., T.A. Spies, R. Van Pelt, A.B. Carey, D.A. Thornburgh, D.R. Berg, D.B. Lindenmayer, M.E. Harmon, W.S. Keeton, D.C. Shaw, K. Bible, and J. Chen. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *Forest Ecology and Management* 155:399-423.
- Fraver, S. and A.S. White. 2005. Disturbance dynamics of old-growth *Picea rubens* forests of northern Maine. *Journal of Vegetation Science* 16:597-610.
- Frelich, L.E. 2002. Forest dynamics and disturbance regimes: studies from temperate evergreen-deciduous forests. Cambridge University Press, Cambridge, UK.
- Gavin, D.G, L.B. Brubaker, and K.P. Lertzman. 2003a. An 1800-year record of the spatial and temporal distribution of fire from the west coast of Vancouver Island, Canada. *Canadian Journal of Forest Research* 33:573-586.
- Gavin, D.G, L.B. Brubaker, and K.P. Lertzman. 2003b. Holocene fire history of a coastal temperate rain forest based on soil charcoal radiocarbon dates. *Ecology* 84:186-201.

- Hallett, D.J., D.S. Lepofsky, R.W. Mathewes, and K.P. Lertzman. 2003. 11000 years of fire history and climate in the mountain hemlock rain forests of southwestern British Columbia based on sedimentary charcoal. *Canadian Journal of Forest Research* 33:292-312.
- Harcombe, P.A., S.E. Greene, M.G. Kramer, S.A. Acker, T.A. Spies, and T. Valentine. 2004. The influence of fire and windthrow dynamics on a coastal spruce-hemlock forest in Oregon, USA, based on aerial photographs spanning 40 years. *Forest Ecology and Management* 194:71-82.
- Henry, J.D. and J.M.A. Swan. 1974. Reconstructing forest history from live and dead plant material - an approach to the study of forest succession in southwest New Hampshire. *Ecology* 55:772-783.
- Kramer, M.G., A.J. Hansen, M.L. Taper, and E.J. Kissinger. 2001. Abiotic controls on long-term windthrow disturbance and temperate rain forest dynamics in southeast Alaska. *Ecology* 82:2749-2768.
- Landres, P.B., P. Morgan, and F.J. Swanson. 1999. Overview of the use of natural variability concepts in managing ecological systems. *Ecological Applications* 9:1179-1188.
- Lertzman K.P. 1992. Patterns of gap-phase replacement in a subalpine, old-growth forest. *Ecology* 73:657-669.
- Lertzman, K., D. Gavin, D. Hallett, L. Brubaker, D. Lepofsky, and R. Mathewes. 2002. Long-term fire regime estimated from soil charcoal in coastal temperate rainforests. *Conservation Ecology* 6:5. [online] URL: <http://www.consecol.org/vol6/iss2/art5>.

- Lertzman, K.P. and C.J. Krebs. 1991. Gap-phase structure of a subalpine old-growth forest. *Canadian Journal of Forest Research* 21:1730-1741.
- Lertzman, K.P., G.D. Sutherland, A. Inselberg, and S.C. Saunders. 1996. Canopy gaps and the landscape mosaic in a coastal temperate rain forest. *Ecology* 77:1254-1270.
- Lorimer, C.G. and L.E. Frelich. 1989. A methodology for estimating canopy disturbance frequency and intensity in dense temperate forests. *Canadian Journal of Forest Research* 19:651-663.
- Lusk, C.H. and B. Smith. 1998. Life history differences and tree species coexistence in an old-growth New Zealand rain forest. *Ecology* 79:795-806.
- Meidinger, D.V. and J. Pojar, editors. 1991. *Ecosystems of British Columbia*. Special Report Series 6. British Columbia Ministry of Forests, Victoria, British Columbia, Canada.
- Mori, A.S., E. Mizumachi, and A. Komiyama. 2007. Roles of disturbance and demographic non-equilibrium in species coexistence, inferred from 25-year dynamics of a late-successional old-growth subalpine forest. *Forest Ecology and Management* 241:74-83.
- Nowacki, G.J. and M.D. Abrams. 1997. Radial-growth averaging criteria for reconstructing disturbance histories from presettlement-origin oaks. *Ecological Monographs* 67:225-249.
- Parish, R. and J.A. Antos. 2004. Structure and dynamics of an ancient montane forest in coastal British Columbia. *Oecologia* 141:562-576.

- Parish, R. and J.A. Antos. 2006. Slow growth, long-lived trees, and minimal disturbance characterize the dynamics of an ancient, montane forest in coastal British Columbia. *Canadian Journal of Forest Research* 36:2826-2838.
- Payette, S., L. Filion, and A. Delwaide. 1990. Disturbance regime of a cold temperate forest as deduced from tree-ring patterns: the Tantaré Ecological Reserve, Quebec. *Canadian Journal of Forest Research* 20:1228-1241.
- Pearson, A.F. 2000. Natural disturbance patterns in a coastal temperate rain forest watershed, Clayoquot Sound, British Columbia. Ph.D. dissertation. University of Washington, Seattle, Washington, USA.
- Rubino, D.L. and B.C. McCarthy. 2004. Comparative analysis of dendroecological methods used to assess disturbance events. *Dendrochronologia* 21:97-115.
- Scientific Panel for Sustainable Forest Practices in Clayoquot Sound. 1995. Sustainable ecosystem management in Clayoquot Sound: planning and practices. Scientific Panel for Sustainable Forest Practices in Clayoquot Sound, Victoria, British Columbia, Canada.
- Sousa, W.P. 1984. The role of disturbance in natural communities. *Annual Review of Ecology and Systematics* 15:353-391.
- Taylor, A.H., J.S. Wei, Z.L. Jun, L.C. Ping, M.C. Jin, and H. Jinyan. 2006. Regeneration patterns and tree species coexistence in old-growth *Abies-Picea* forests in southwestern China. *Forest Ecology and Management* 223:303-317.
- Veblen, T.T. 1986. Treefalls and the coexistence of conifers in subalpine forests of the central Rockies. *Ecology* 67:644-649.

- Veblen, T.T. and P.B. Alaback. 1996. A comparative review of forest dynamics and disturbance in the temperate rainforests of North and South America. Pages 173-213 *in* R.G. Lawford, P.B. Alaback, and E. Fuentes, editors. High-latitude rainforests and associated ecosystems of the West Coast of the Americas: climate, hydrology, ecology, and conservation. Springer-Verlag, New York, New York, USA.
- Wells, R.W., K.P. Lertzman, and S.C. Saunders. 1998. Old-growth definitions for the forests of British Columbia, Canada. *Natural Areas Journal* 18:279-292.
- White, P.S. and Pickett, S.T.A. 1985. Natural disturbance and patch dynamics: an introduction. Pages 3-13 *in* S.T.A. Pickett and P.S. White, editors. The ecology of natural disturbance and patch dynamics. Academic Press, New York, New York, USA.
- Wong, C., H. Sandmann, and B. Dorner. 2003. Historical variability of natural disturbances in British Columbia: a literature review. FORREX Series 12. FORREX-Forest Research Extension Partnership, Kamloops, British Columbia, Canada.
- Yamamoto, S. 1995. Gap characteristics and gap regeneration in subalpine old-growth coniferous forests, central Japan. *Ecological Research* 10:31-39.

2. Calibrating the radial-growth averaging method for detecting releases in old-growth forests of coastal British Columbia¹

2.1. Introduction

Radial-growth release detection methods are often used to reconstruct canopy disturbances in forest stands. Releases, i.e. abrupt increases in radial growth, are an appealing approach to the study of canopy disturbance history, as tree rings can preserve a record of past disturbance events at a high spatial and temporal resolution (Fritts and Swetnam 1989, Frelich 2002). Of the radial-growth release detection methods in the literature, the most widely used is radial-growth averaging (Rubino and McCarthy 2004). This method involves detecting releases by comparing average radial growth for successive periods and identifying peak growth-change values above a minimum threshold (Henry and Swan 1974, Lorimer and Frelich 1989, Nowacki and Abrams 1997). In the current literature, radial-growth averaging is often expressed using the formula:

$$\%GC = (M_2 - M_1) / M_1 \times 100,$$

where %GC is percent-growth change for a single year, M_1 is the mean or median radial growth preceding that year, and M_2 is the mean or median radial growth following that year (Nowacki and Abrams 1997, Rubino and McCarthy 2004). By applying percent-growth change to consecutive years of a large number of tree-ring series from a stand and noting the

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occurrence of peak values above a set threshold, it is possible to elucidate the history of release episodes and thus infer past disturbances to the forest canopy.

For radial-growth averaging to be most useful, it must be calibrated to filter out growth increases unrelated to canopy disturbance events. To do this, the threshold (i.e. %GC) and moving average (i.e. M_1 and M_2) parameters are adjusted to account for factors that influence radial growth and release potential, including tree species, diameter, position in the canopy, growth rate prior to release, age, and interannual climatic variation. The expected lesser response of larger, overstory versus smaller, understory trees following a disturbance event is often addressed by lowering the threshold value (Lorimer and Frelich 1989, Nowacki and Abrams 1997). In addition, a lower threshold value is considered more appropriate for less shade-tolerant species, which typically do not experience the severe radial-growth suppression associated with intense releases (Black and Abrams 2003, 2004). Moving average is usually set to screen out increases in radial growth caused by recovery from adverse climatic conditions (Lorimer 1980, Lorimer and Frelich 1989, Nowacki and Abrams 1997). A 10-year moving average is common in many studies, particularly those from forests of eastern North America (e.g. Glitzenstein et al. 1986, Lorimer and Frelich 1989, Tardif and Bergeron 1999, Fraver and White 2005a, Hart and Grissino-Mayer 2008). The moving average is also meant to reflect the average duration of releases following a disturbance event, estimates which are usually derived from studies of managed stands (Nowacki and Abrams 1997, Rentch et al. 2002). Overall, these adjustments to the threshold and moving average parameters are intended to increase confidence in detecting release events resulting from canopy disturbance in specific forest types.

Fine-scale death of canopy dominants is the primary natural disturbance in the wetter parts of the coastal temperate rain forest of British Columbia, Canada (Lertzman and Krebs 1991, Lertzman et al. 1996, Daniels and Gray 2006). Because of infrequent coarse-scale fire at time scales up to thousands of years (Lertzman et al. 2002, Gavin et al. 2003), many stands without a history of human disturbance are old and contain an abundance of canopy gaps as well as live and dead trees of varying ages and sizes (Lertzman et al. 1996, Wells et al. 1998). At mid-elevations, western redcedar (*Thuja plicata* Donn ex D. Don), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and Pacific silver fir (*Abies amabilis* Dougl. ex J. Forbes) dominate the canopy of old-growth stands (Meidinger and Pojar 1991). All three species are shade tolerant (Klinka et al. 1990, Carter and Klinka 1992), but capable of large increases in radial growth upon the formation of a canopy gap (Daniels and Klinka 1996).

The general objective of this study was to calibrate the radial-growth averaging method to detect release of western redcedar, western hemlock, and Pacific silver fir following fine-scale canopy disturbance in mid-elevation, old-growth forests of coastal British Columbia. To do this, I examined trees (diameter at breast height (dbh) ≥ 10 cm) growing within and adjacent to natural canopy gaps of known timing of origin. My specific objectives were to (1) determine the contribution of climatic/regional-scale factors to patterns of radial growth and release and (2) use sensitivity analysis to systematically explore the influences of different variations of the radial-growth averaging method. In relation to the second, specific objective, I addressed three questions: (i) How do the parameters that constitute different variations of the radial-growth averaging method influence the number of trees that show a release pattern following the formation of a canopy gap? (ii) Do outcomes vary among co-dominant, shade-tolerant species? (iii) Do outcomes vary when ring-width

versus basal area increment values are used to detect releases? This last question is important because many studies use basal area increment to quantify growth. Ultimately, results from this study provide information useful for establishing the best combination of parameters and growth index for capturing a more complete range of growth releases (i.e. low/high magnitude and short/long duration) that may occur following the formation of fine-scale gaps in old-growth forests of coastal British Columbia. Establishing these empirically-based criteria is an important first step towards quantifying attributes of growth release for trees in these stands.

2.2. Study area

I conducted this research in the Capilano, Seymour, and Coquitlam River watersheds in the Coast Mountains of southwestern British Columbia (Figure 2.1). These drainages encompass an area of approximately 58,500 ha that is managed by Metro Vancouver for water supply to municipalities in the greater Vancouver area. In the past, processes of glacial erosion impacted the area and helped create the overall rugged topography and steep slopes that exist today (Ryder 1981). Relief in the watersheds ranges from 1300 to 1600 m, and slopes commonly exceed 35°, particularly at higher elevations. Across the terrain, several ecosystem types occur that are typical of those present throughout coastal British Columbia. Using the Biogeoclimatic Ecosystem Classification system of British Columbia, these include the Coastal Western Hemlock, Mountain Hemlock, and Alpine Tundra zones (Meidinger and Pojar 1991).

I restricted the study sites to mid-elevation (300-700 m a.s.l.), old-growth forests within the watersheds. The sites are located in the Very Wet Maritime subzone of the Coastal Western Hemlock zone, which has a wet, humid climate, with cool summers and

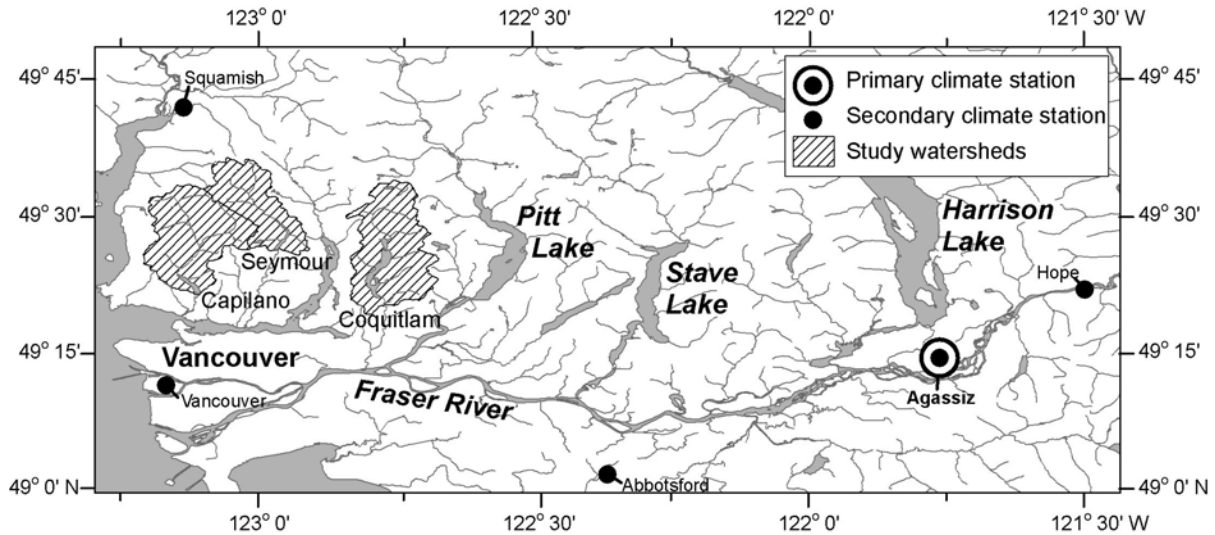


Figure 2.1. Location of the Capilano, Seymour, and Coquitlam River watersheds, British Columbia, Canada, and of the climate stations used to examine climate-growth relations for western redcedar, western hemlock, and Pacific silver fir.

mild winters (Meidinger and Pojar 1991). Based on spatially-interpolated monthly climate normals for the period 1961-1990 (Wang et al. 2006), mean annual temperature at all study sites ranged from 6.0 to 7.5°C, with a mean of 15 to 16°C in August and -1 to 1°C in December. Total annual precipitation was between 3000 to 4000 mm. Total growing season (May to September) precipitation ranged from 600 to 800 mm. At all study sites, soils are mostly Humo-Ferric Podzols derived from colluvium and glacial till (Valentine et al. 1978). Sites are located on Coast Plutonic Complex intrusions of Mid-Cretaceous quartz diorite in Capilano and Seymour and of Late-Jurassic to Early-Cretaceous quartz diorite in Coquitlam (Monger and Journeay 1994).

Historically, most low- and mid-elevation forests in the watersheds were old growth, as evidenced by an abundance of standing dead and downed trees, canopy gaps, and trees greater than 250 years of age (Acres International Limited 1999). These old-growth stands resulted from long periods of fine-scale gap forming and filling processes occurring in the

absence of catastrophic disturbances such as fire (Lertzman et al. 1996, Wells et al. 1998, Gavin et al. 2003). Until the early 1990s, many of these forests were impacted by harvesting (Acres International Limited 1999). Consequently, low- and mid-elevations in the watersheds are a mosaic of second-growth stands, interspersed with patches of remnant old-growth forest.

Shade-tolerant western redcedar, western hemlock, and Pacific silver fir, and a small number of shade-intolerant Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) constitute mid-elevation, old-growth stands in the watersheds (Meidinger and Pojar 1991). Life spans are ≥ 360 years for Pacific silver fir, ≥ 450 years for western hemlock, and ≥ 1000 for western redcedar and Douglas-fir (Daniels 1994). Pacific silver fir reaches ≥ 100 cm dbh, western hemlock ≥ 120 cm dbh, and western redcedar and Douglas-fir ≥ 250 cm dbh (Daniels 1994).

Stand developmental processes contribute greatly to the overall openness of mid-elevation, old-growth forests in the watersheds. Approximately 74% of the area of old-growth, western redcedar-western hemlock stands (Stan and Daniels, *unpublished data*) is in gaps of developmental origin (i.e. those created by the mortality of canopy dominants; Lertzman et al. 1996), including both canopy and expanded gaps. A canopy gap is the vertical projection onto the ground of an opening in the canopy, and an expanded gap is defined by the boles of the trees whose crowns delineate a canopy gap (Runkle 1982). Only 13% of the area of these stands is closed canopy (Stan and Daniels, *unpublished data*).

2.3. Methods

2.3.1. *Selecting study sites*

I used a combination of watershed ecological inventory data and field reconnaissance to locate canopy gaps. From forest cover maps of the watersheds (Acres International Limited 1999), I identified remnant patches of old-growth, western redcedar-western hemlock forest situated on slopes $\leq 30^\circ$ between 300 and 700 m a.s.l. All stands $\geq 20\%$ western redcedar and $\leq 20\%$ Douglas-fir by volume were considered appropriate for this study. In coastal British Columbia, Douglas-fir establishes primarily after stand-destroying disturbances and therefore can be a minor component of very old stands. Approximately 3000 ha of forest stands met the above criteria. I randomly selected stands and inspected them to verify old-growth structural and compositional characteristics, along with site features and accessibility. Stands that were poorly drained, difficult to access because of topographic features (e.g. stream crossing), or too small to contain canopy gaps not influenced by edge effects from roads or major streams were omitted from further sampling.

Stands confirmed appropriate through field reconnaissance were systematically searched for gaps that were (1) created by one or two uprooted canopy dominant(s) and (2) likely formed within the last 50 years. I focused on gaps that were created by uprooted trees in order to maintain consistency in terms of their mode of formation. While modes of gap-forming mortality in coastal British Columbia include standing death, snapping, and uprooting (Lertzman and Krebs 1991, Arsenault 1995, Lertzman et al. 1996), the last has the greatest potential to offer the most information for determining the timing of gap formation using dendroecological methods. In addition, “recently” formed gaps were best suited for determining the timing of gap formation using dendroecological methods. Over time,

information such as outer-ring dates of gapmakers can become less accurate due to loss of bark and decay, and in addition, secondary gap expansion or formation of adjacent gaps can result in complex growth patterns of trees growing around and within gaps, making older gaps less desirable for use in this study. I used the five-class system of log decomposition described by Maser et al. (1979) to facilitate identification of gaps that met the appropriate age criterion. Based on this system, gaps were marked for more rigorous assessment of timing of formation only if the gapmakers were in decay classes I, II, or III. Logs in the first three decay classes correspond to the least decayed individuals and therefore should represent the most recently created gaps (Daniels et al. 1997).

For each marked gap, I attempted to determine the year of death and year of fall of the gapmaker(s). To determine year of death, I took multiple increment cores from the least decayed sections of each bole to ensure that (1) enough intact rings, including the outermost rings, were available for crossdating and (2) when possible, samples included the bark and sapwood (Dynesius and Jonsson 1991, Daniels et al. 1997). Cores were mounted and sanded following the procedures of Stokes and Smiley (1968). I measured ring widths to the nearest 0.001 mm with a stereozoom microscope and Velmex sliding-stage micrometer interfaced with MeasureJ2X software. The program COFECHA (Holmes 1983, Grissino-Mayer 2001) was used to statistically crossdate ring-width series from gapmakers against preliminary master-dating series developed from cores collected from nearby living trees; crossdating was later verified against regional-scale, species-specific final master-dating series. By crossdating cores, I was able to assign a calendar year to each tree ring and thus estimate the last year of growth of the gapmakers. To determine year of fall, I collected partial or whole-stem cross sections from any live trees scarred or crushed by the gapmaker. In addition, I

sampled cross sections from seedlings or saplings growing on the gapmaker. Cross sections were sanded (Stokes and Smiley 1968) and visually crossdated (Yamaguchi 1991) to determine year of establishment of seedlings and saplings (an estimate of maximum year of fall) along with year of scar or reaction wood formation in injured trees. Gapmakers that could not be successfully dated to year of death or fall were rejected and no further sampling was conducted at those sites. Although 45 gaps were located during field reconnaissance, only 20 gaps were dated with confidence and these were used for subsequent sampling.

2.3.2. Sampling and crossdating trees

At each of the 20 dated gaps, I extracted two increment cores from all trees (dbh \geq 10 cm) that defined the boundary of, or occurred within, the gaps. The boundary of a gap was delineated using the crown of canopy dominant, co-dominant, and intermediate trees nearest to the gapmaker(s). All trees were cored on the side facing the center of the gap at a height of approximately 30 cm above the ground. Cores were mounted and sanded according to Stokes and Smiley (1968).

I developed a rigorous multi-step, multi-scale approach to crossdating because preliminary attempts were unsuccessful for western hemlock and Pacific silver fir from these stands, and there were no published chronologies for mid-elevation forests of coastal British Columbia. First, I visually crossdated (Yamaguchi 1991) the two cores collected from an individual tree relative to each other. Examining cores from an individual tree together allowed me to identify locally absent rings, i.e. those that were missing along one or more radii of the tree (Fritts 1976, Norton et al. 1987). The frequent occurrence of modest to severe suppression of western hemlock and Pacific silver fir that grow in these stands is one likely cause of locally absent rings. In addition, radial growth of these species is sometimes

asymmetrical and can result in rings that are missing along certain radii. Second, I measured ring widths to the nearest 0.001 mm with a stereozoom microscope and Velmex sliding-stage micrometer interfaced with MeasureJ2X software and inserted zero values to account for rings that were present in one core and absent in the other. Third, I used COFECHA to statistically verify my visual inspection of the two cores and ensure accurate within-tree crossdating. Finally, I combined cores from all gaps, along with additional cores collected from trees growing in the forest immediately adjacent to each gap, and used COFECHA to statistically crossdate all ring-width series from a single species. Subsets of the best-dated cores with the highest series-intercorrelation values were pooled into final master-dating series for each species. Specifically, cores with r -values ≥ 0.30 as determined by COFECHA were included in the final master-dating series for each species; some cores were truncated to remove earlier segments for which the r -value was < 0.30 . In general, cores with the greatest number of suppressions and/or releases were difficult to statistically crossdate, and at best, could only be visually crossdated using narrow and wide marker rings.

2.3.3. Estimating the influence of climate and other regional-scale factors on radial growth and release

I used the final master-dating series to explore the influence of climate, or other regional-scale factors, on growth of western redcedar, western hemlock, and Pacific silver fir. The final master-dating series for each species comprises individual ring-width series with the best-matching patterns across all gaps. Thus, these sets represent trees that are more influenced by a common, regional-scale factor (e.g. climate) than localized processes of gap dynamics (Fritts 1976).

To examine the influence of interannual variation in climate, ring-width series were standardized to remove low-frequency variation, such as age- and size-related trends in growth, along with decadal-scale climatic variation and stand dynamics. I used the program ARSTAN (version 40c for Windows XP; Cook 1985) to fit 40-year cubic splines with 50% frequency response to individual ring-width series (Cook and Peters 1981). This single-detrending procedure is appropriate because the age-/size-related trend in growth is less pronounced in the three study species, which are all shade-tolerant and experience low initial growth rates (i.e. narrow rings) in shaded conditions. I used the Expressed Population Signal (EPS; Wigley et al. 1984) to assess the quality of the chronologies produced by ARSTAN. EPS remained above 0.85 for the chronologies of each of the study species, which is the threshold recommended to ensure that ring-width patterns accurately reflect growth in the chronology.

I compared residual chronologies to temperature and precipitation data (Fritts 1976). Monthly mean temperature and total precipitation data were obtained from the Agassiz CDA (Canadian Department of Agriculture) station (station 1100120; 49° 15' N, 121° 46' W; elev. 15 m), located approximately 115 km east of Vancouver, British Columbia (Figure 2.1). Agassiz data extend back to 1895 and represent the most complete record of temperature and precipitation in the region; missing values occur in < 1% of the combined records at this station. The Agassiz temperature and precipitation records are highly correlated with records from stations in nearby Vancouver (station 1108447; 49° 12' N, 123° 11' W; elev. 3 m), Abbotsford (station 1100030; 49° 02' N, 122° 22' W; elev. 58 m), Squamish (station 1047660; 49° 42' N, 123° 08' W; elev. 31 m), and Hope (station 1113540; 49° 23' N, 121° 32' W; elev. 39 m). Missing values in the Agassiz record were estimated by linear regression

using data from the other stations. I used response function analysis to test the relation between the residual chronologies and monthly mean temperature and total precipitation data (Fritts 1976, Blasing et al. 1984). In response functions, the coefficients computed between the tree-ring chronologies and monthly climatic variables are multivariate estimates from a principal component regression model (Briffa and Cook 1990). This analysis allowed me to directly assess climate as a cause of regional-scale growth patterns in the study species. Analyses were performed using DENDROCLIM2002 (Biondi and Waikul 2004). This program uses a bootstrapped procedure with 1000 replications to evaluate statistical significance at the 0.05 level (Guiot 1991).

I then applied the radial-growth averaging method with a moving average of 5, 10, and 15 years to the residual chronologies of western redcedar, western hemlock, and Pacific silver fir. Calculating percent-growth change for each year of each residual chronology was a way of estimating the upper limits of the effects of interannual climatic variation (i.e. high-frequency variation) and other regional-scale environmental factors on growth increases. The results were comparable to those obtained when examining growth increases caused by local-scale canopy disturbances (Lorimer and Frelich 1989, Nowacki and Abrams 1997).

2.3.4. Sensitivity analysis – detecting release of trees

In the sensitivity analysis, I systematically tested three parameters of the radial-growth averaging method. The goal of the analysis was to explore how specific parameters, and unique combinations of values for these parameters, influenced the number of trees that showed a release pattern following the formation of a canopy gap. In total, 30 variations of the radial-growth averaging method were applied to individual trees of each of the study species. The variations were derived by altering the values for the threshold, moving

average, and window parameters (Figure 2.2). Threshold values to detect a release were a 25, 50, 100, 200, and 250% increase in growth rate. Moving averages were set for periods of 5, 10, and 15 years. Values for threshold and moving average were selected to reflect the range reported in the literature (Rubino and McCarthy 2004). Window refers to the period associated with the independently determined date of gap formation (e.g. year of death or fall) during which a tree may release. In this study, it was necessary to define a window in order to objectively identify releases related to particular openings in the canopy. The window was set at ± 5 and ± 10 years around the outer-ring date (i.e. year of death) of each independently dated gapmaker (Figure 2.2). Setting the window to include several years both before and after the year of death of the gapmaker is useful for reducing errors in capturing releases following canopy disturbances. Specifically, trees may show a release pattern prior to the year of death because of slow opening of the canopy from cambial and crown dieback of the gapmaker, or trees may show a lag in response after the year of death because new resources are allocated to other vital functions and structures before radial growth (Oliver and Larson 1996). In addition, the window will help reduce errors in capturing releases that can result from uncertainty in the exact year of death because of decay of the outermost rings of the gapmaker.

I applied the 30 variations to a subset of trees growing around the boundary of, or within, the study gaps. In this study, I required 25 years of growth before and after the independently determined date of gap formation to objectively identify releases using all variations of the radial-growth averaging method. The 25 years resulted from the 15-year moving average, which required 15 years of growth data before and after each percent-growth-change value, coupled with the 10-year window. I applied the 30 variations to all

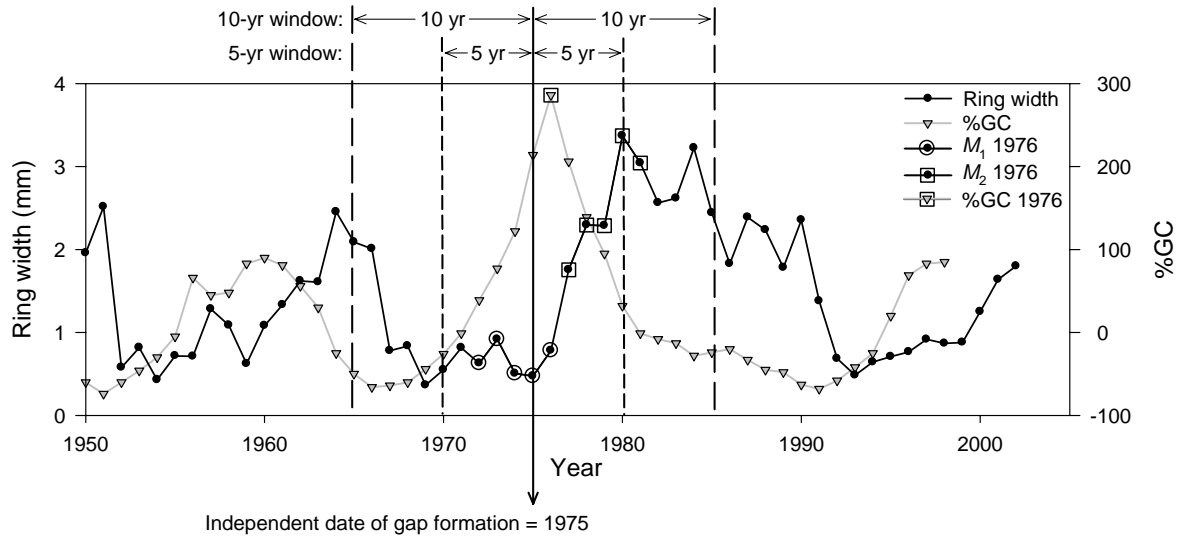


Figure 2.2. Schematic depicting the detection of a release for a tree growing around or within a natural canopy gap of known timing of origin using the radial-growth averaging method with a 5-year moving average. Percent-growth change (%GC) for a single year is equal to $(M_2 - M_1) / M_1 \times 100$, where M_1 is the mean ring width for the five years preceding that year, and M_2 is the mean ring width for the five years following that year (Nowacki and Abrams 1997). %GC is highlighted for a release detected within windows surrounding 1975, the year of gap formation (i.e. year of death or fall).

trees that met this age criterion, which included 37 western redcedar, 63 western hemlock, and 25 Pacific silver fir growing around or within seven gaps. I used mean original ring-width and basal area increment values of individual trees (i.e. average of two cores per tree) to calculate percent-growth change. Basal area increment (BAI) was calculated from the bark towards the pith using the following equations:

$$D_{t-1} = D_t - (R_t \times 2)$$

$$\text{BAI} = \pi \left(\frac{D_t}{2} \right)^2 - \pi \left(\frac{D_{t-1}}{2} \right)^2,$$

where D_{t-1} is the diameter (mm) at coring height (dch; inside bark) for year $t-1$, D_t is the dch (inside bark) for year t , and R_t is ring width (mm) for year t . For the outermost ring of each

core, D_t was estimated using the dch value derived from field measurements. The initial value for R_t for each core was the total width of the outermost ring and bark. In each variation of the radial-growth averaging method, I identified a release as the highest peak percent-growth-change value, above or equal to the specified threshold, within the window that surrounded the year of death of the gapmaker (Figure 2.2). I quantified the number of releases detected for each threshold-moving average-window combination for both ring width and basal area increment.

2.4. Results

2.4.1. Influence of climate and other regional-scale factors on radial growth and release

In total, 196 western redcedar, 95 western hemlock, and 39 Pacific silver fir ring-width series were included in the regional chronologies, which had series intercorrelations of 0.59, 0.50, and 0.48, respectively (Table 2.1). Each chronology contained series from trees in all three watersheds. Mean sensitivity was 0.16 for western redcedar, 0.18 for western hemlock, and 0.30 for Pacific silver fir (Table 2.1). Mean sensitivity is a measure of the relative change in ring width from year to year and is calculated as the absolute difference between adjacent indices divided by their mean value (Fritts 1976).

According to the response function analyses, there were some significant ($P < 0.05$) associations between climatic variables and growth of western redcedar and western hemlock, but no significant associations between climatic variables and growth of Pacific silver fir (Figure 2.3). Growth of western hemlock and western redcedar was significantly, negatively associated with July temperature of the growing season prior to ring formation. The association of growth and August precipitation of the previous growing season was

Table 2.1. Descriptive statistics for regional residual ring-width chronologies of western redcedar, western hemlock, and Pacific silver fir. Chronologies were developed using the best-matching series from trees growing around the boundary of, within, or in the forest adjacent to 20 canopy gaps from three watersheds.

Species	No. sites [§]	No. trees	No. radii	Record period	Series intercor.	Missing rings [¶] (%)	Mean sensitivity [‡]	Auto cor. [*]
western redcedar	20 (3)	102	196	1359-2003	0.59	0.03	0.16	0.00
western hemlock	18 (3)	60	95	1857-2003	0.50	0.11	0.18	0.04
Pacific silver fir	10 (3)	24	39	1741-2003 [†]	0.48	0.29	0.30	0.07

[§]Number of sites from which the cores were sampled. Values in parentheses are number of watersheds.

^{||}Mean Pearson's correlation coefficient calculated from the pairwise comparison of all ring-width series in the chronology using COFECHA.

[¶]Missing rings in each chronology.

[‡]Measure of the relative change in ring width from year to year and is calculated as the absolute difference between adjacent indices divided by the mean of the two indices (Fritts 1976).

^{*}First-order autocorrelation, i.e. serial correlation coefficient for the chronology at a lag of one year.

[†]Sample depth is only two cores until 1902 and becomes 10 cores at 1921.

positive for all three species, but significant only for western hemlock. Growth of western redcedar showed a significant, negative association with June temperature of the current growing season, while growth of western hemlock and Pacific silver fir showed a non-significant, negative association with temperature in that same month. In the intermediate season, significant, positive associations between temperature and growth occurred in January and March for western hemlock and in February for western redcedar.

Percent-growth change derived for 5-, 10-, and 15-year moving averages using the residual chronologies of each species was < 25% in all but five years from 1895 to 2003 (Figure 2.4a, b, c). In the case of a 5-year moving average for western hemlock, percent-growth change reached 26, 30, and 33% in 1930, 1931, and 1932, respectively (Figure 2.4b). While percent-growth change also reached 30% in 1900 and 33% in 1903 for Pacific silver, both values occurred when there were only two series (one tree) in the chronology (Figure 2.4c). In general, the highest percent-growth-change values occurred in or around years with

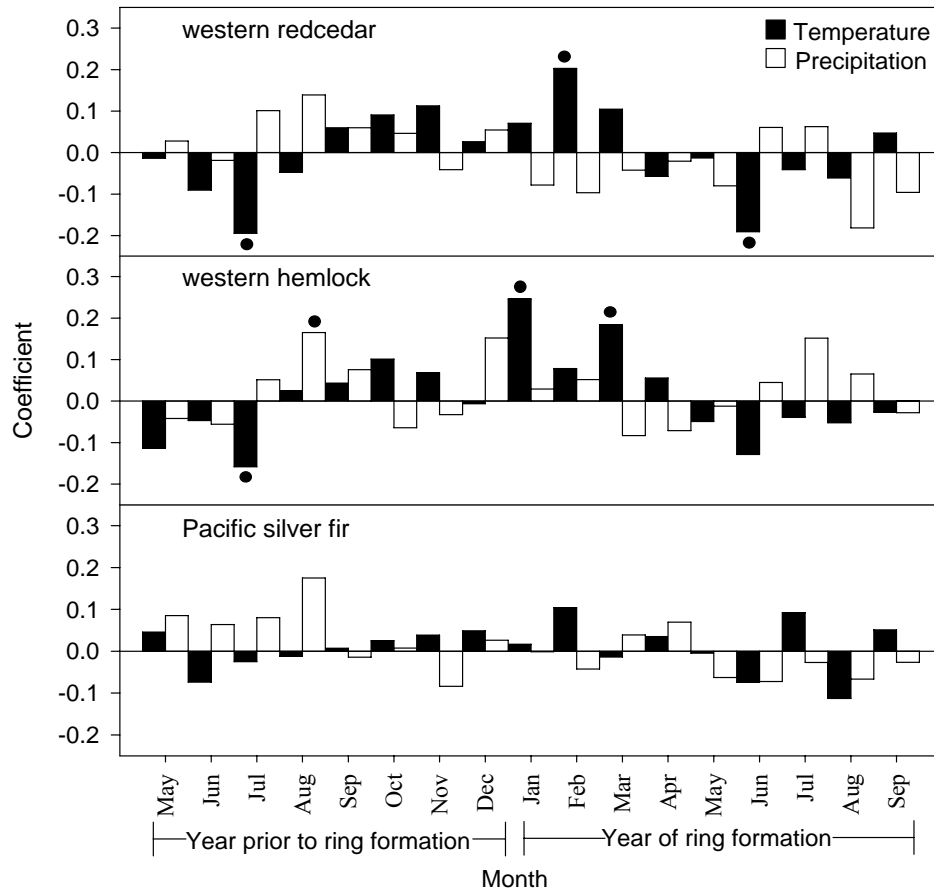
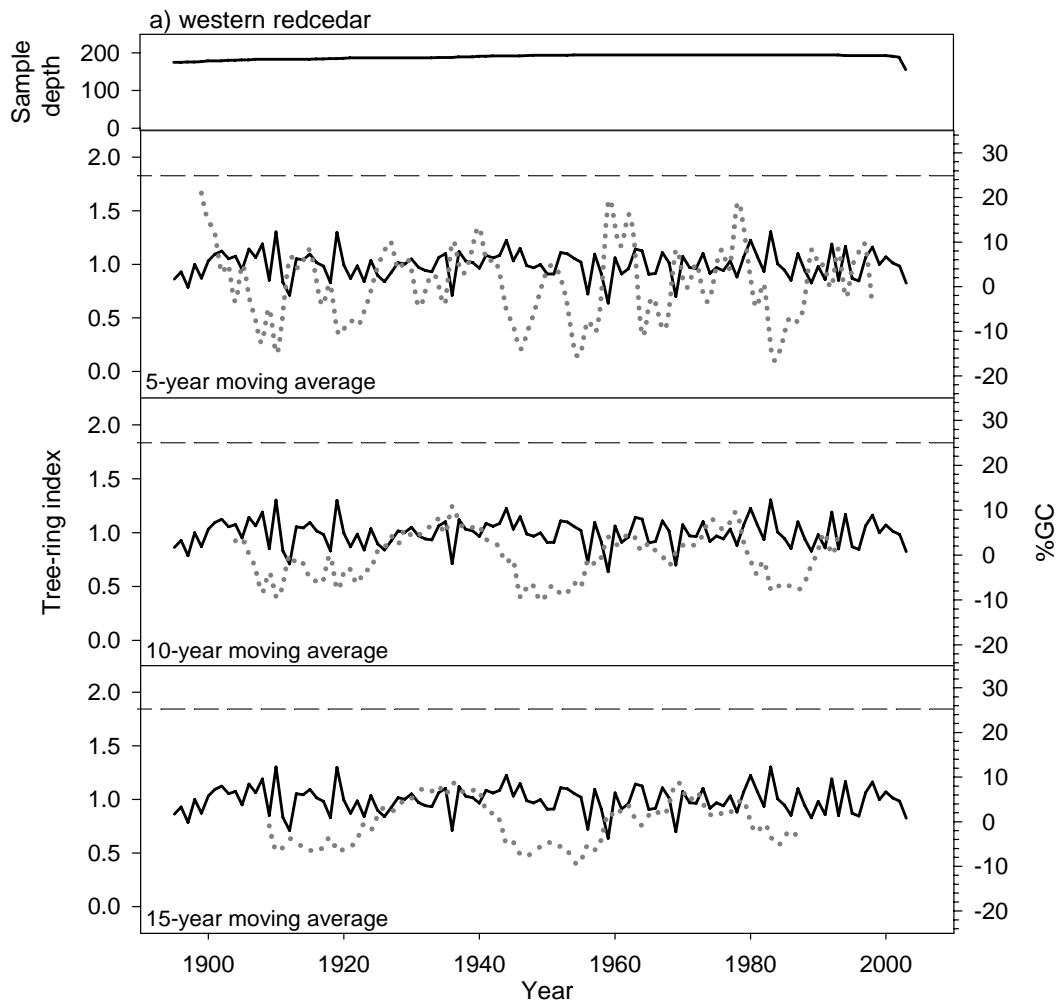


Figure 2.3. Response function analyses for western redcedar, western hemlock, and Pacific silver fir. Coefficients are for residual ring-width chronologies against monthly mean temperature and total precipitation for the period 1896-2003. Dots indicate statistical significance ($P < 0.05$).

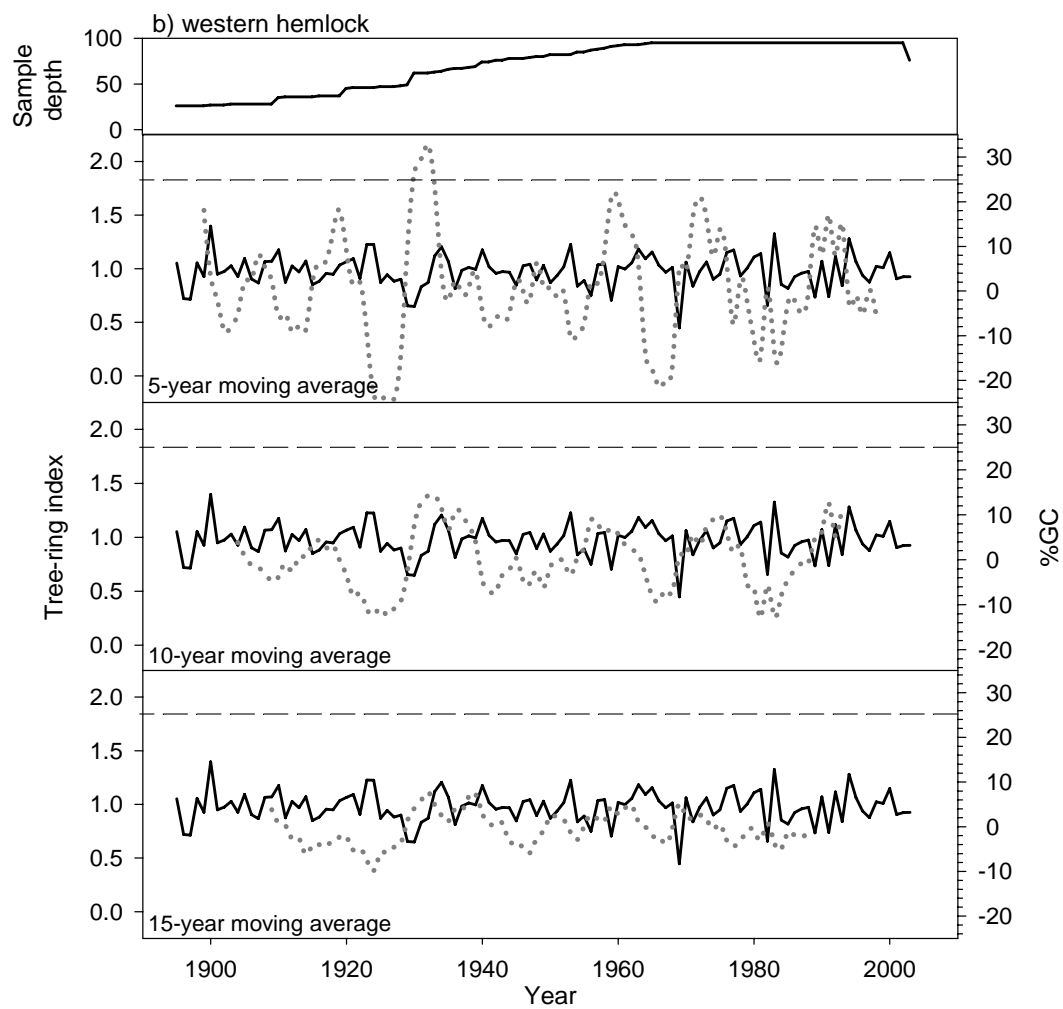
the lowest tree-ring index values and decreased (i.e. were smoothed) as the moving average increased from 5 to 15 years (Figure 2.4a, b, c).

2.4.2. Sensitivity analysis – release of trees

The number of trees that showed a release pattern differed among the 30 variations of the radial-growth averaging method (Figure 2.5a, b). In relation to the threshold, moving average, and window parameters, two general trends were common to all three species. First, as threshold increased, the number of trees that showed a release pattern decreased.



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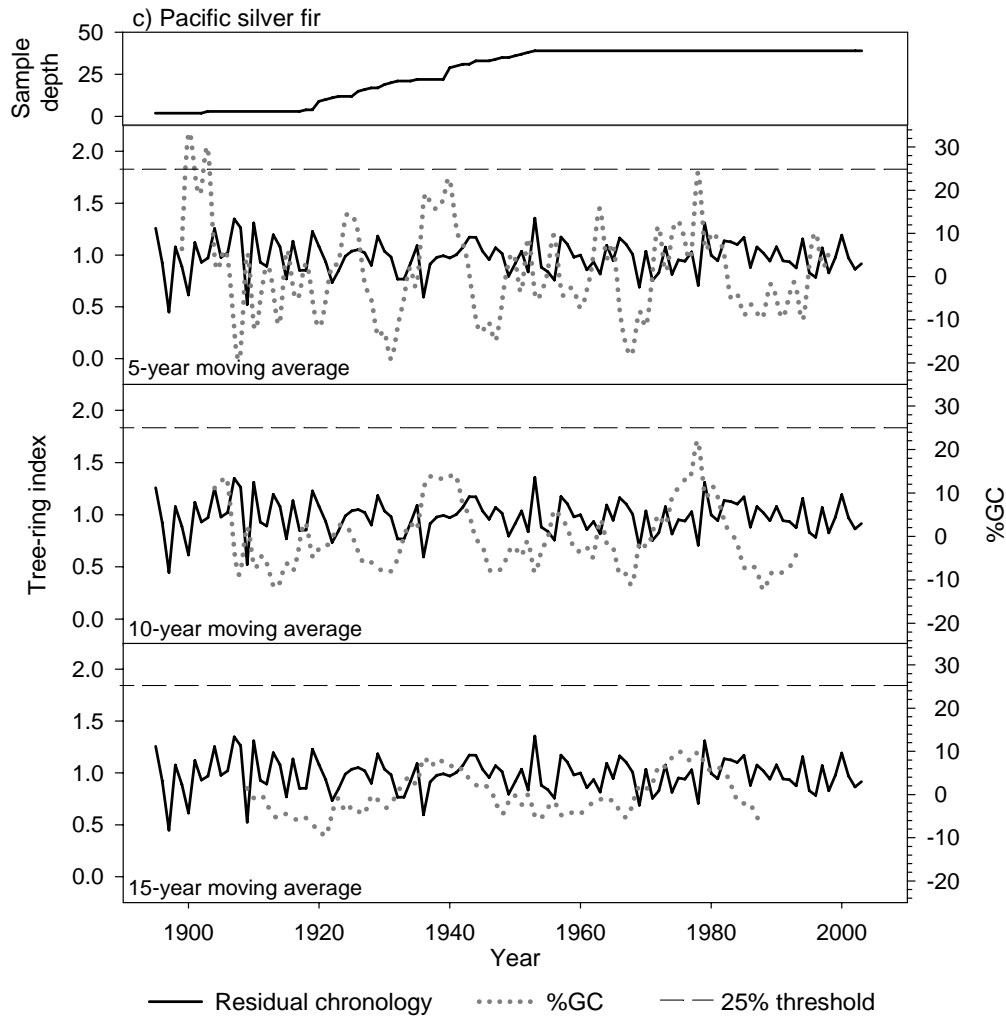


Figure 2.4. Residual ring-width chronologies and percent-growth change (%GC) for the period 1895-2003 based on 5-, 10-, and 15-year moving averages for (a) western redcedar, (b) western hemlock, and (c) Pacific silver fir.

Threshold level had the greatest influence on the number of western redcedar that showed a release pattern. Specifically, when the 100 versus 50% threshold was applied, the proportion of western redcedar that showed a release pattern was reduced by as much as 0.57 (5-year moving average and 10-year window) and 0.51 (5-year moving average and 10-year window) for ring width and basal area increment, respectively (Figure 2.5a, b). Second, a higher number of trees showed a release pattern using a 10- versus a 5-year window. This pattern was most consistent for western redcedar and western hemlock. Yet, in a few cases,

the number of western hemlock that showed a release pattern was more affected by the moving average as opposed to the window parameter (Figure 2.5a, b). For Pacific silver fir, the moving average parameter often had a greater influence than the window parameter, particularly when ring-width values were used (Figure 2.5a).

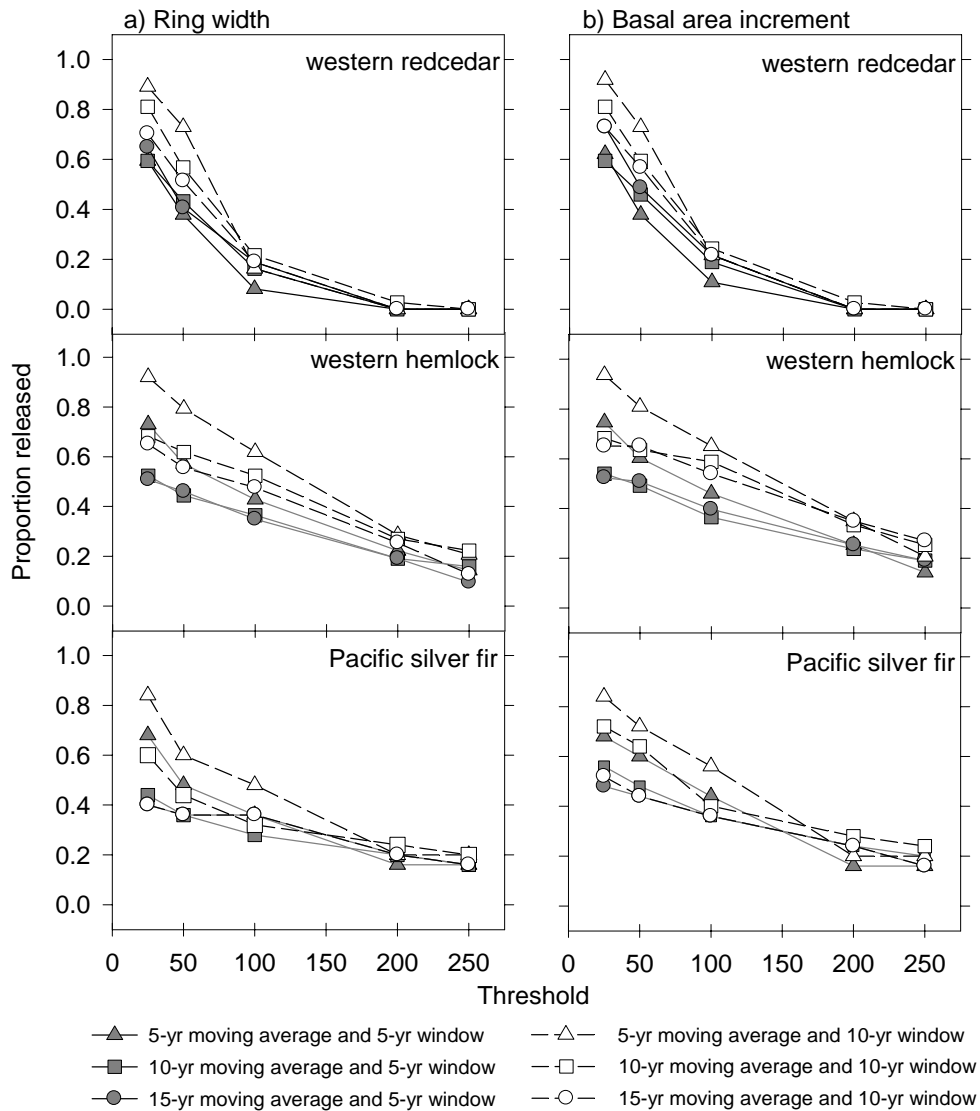


Figure 2.5. Comparison of the proportion of trees that showed a release pattern for the 30 variations of the radial-growth averaging method for (a) ring width and (b) basal area increment for western redcedar, western hemlock, and Pacific silver fir.

Across the 30 variations of the radial-growth averaging method, the greatest number of trees showed a release pattern using the combination of a 25% threshold, 5-year moving average, and 10-year window for both ring width and basal area increment (Figure 2.5a, b). However, the total proportion of trees that showed a release pattern was 0.02, 0.05, and 0.06 higher for western redcedar, western hemlock, and Pacific silver fir, respectively, when basal area increment values were used as opposed to ring-width values. A detailed breakdown of the 30 variations showed that up to 0.08, 0.14, and 0.20 more western redcedar, western hemlock, and Pacific silver fir, respectively, showed a release pattern when basal area increment was used rather than ring width (Table 2.2). For western hemlock, the greatest differences occurred using a 15-year moving average. For Pacific silver fir, the greatest differences occurred at thresholds $\leq 100\%$. No discernable patterns occurred for western redcedar (Figure 2.5a, b).

2.5. Discussion

The linear aggregate model is used to describe the group of factors that are responsible for growth variation in a tree-ring series over time (Cook 1987). According to this model, growth in any single year is a function of age- and size-related trends due to tree maturation, climate, disturbances from within and outside the stand, and unexplained year-to-year variability. In theory, the environmental signal of interest in a study is best maximized when the other factors that influence growth are minimized. Thus, in practice, dendrochronologists aim to sample trees in which one specific environmental factor such as climate or disturbance is the primary control on radial growth. A particular challenge for dendroecologists is the need to directly filter the climatic signal from tree-ring series in order to evaluate the disturbance signal. Climate, unlike disturbance, is a regional-scale

Table 2.2. Proportional differences between the number of trees that showed a release pattern using basal area increment versus ring width for each of the 30 variations of the radial-growth averaging method. Darker shading indicates a greater difference between the number of trees that showed a release pattern, i.e. difference of 0.00, difference of 0.01-0.05, difference of 0.06-0.10, and difference of > 0.10.

Window		5			10			
Moving avg		5	10	15	5	10	15	
Threshold (%GC)	25	0.03	0.00	0.08	0.03	0.00	0.03	western redcedar
	50	0.00	0.03	0.08	0.00	0.03	0.05	
	100	0.03	0.03	0.03	0.05	0.03	0.03	
	200	0.00	0.00	0.00	0.00	0.00	0.00	
	250	0.00	0.00	0.00	0.00	0.00	0.00	
	25	0.02	0.02	0.02	0.02	0.00	0.00	western hemlock
	50	0.03	0.05	0.05	0.02	0.02	0.10	
	100	0.03	0.00	0.05	0.03	0.06	0.06	
	200	0.03	0.05	0.06	0.06	0.06	0.10	
	250	0.00	0.03	0.10	0.00	0.03	0.14	
	25	0.00	0.12	0.08	0.00	0.12	0.12	Pacific silver fir
	50	0.12	0.12	0.08	0.12	0.20	0.08	
	100	0.08	0.08	0.00	0.08	0.08	0.00	
	200	0.00	0.04	0.04	0.00	0.04	0.04	
	250	0.00	0.04	0.00	0.00	0.04	0.00	

environmental factor whose effects are not as easily minimized thorough site selection.

Thus, estimating the influence of short-term changes in temperature and precipitation on growth of species at different sites is important to dendroecologists studying growth releases caused by canopy disturbances. Understanding species- and site-specific growth responses to climatic factors will allow growth increases resulting from within-stand disturbances to be more accurately quantified.

Several techniques, including visual (Lorimer and Frelich 1989), regression (Nowacki and Abrams 1997), response function (Rentch et al. 2002), and boundary line (Black and Abrams 2003, 2004) analyses, have been used to filter growth increases in tree-ring series caused by climatic variation or other factors not of direct interest in a study. For this study, I use traditional dendroclimatological procedures and the radial-growth averaging method to

estimate the maximal influence of interannual variation in growth on release and thus establish the lower boundaries of release due to fine-scale canopy disturbance. In addition, the sensitivity analysis provides a detailed understanding of the functioning of the radial-growth averaging method relative to trees surrounding natural canopy gaps of known timing of origin. Overall, these procedures allow for a thorough calibration of the radial-growth averaging method and provide a starting point for a more in-depth calibration of specific attributes of release following the formation of fine-scale gaps in old-growth forests of coastal British Columbia.

2.5.1. Influence of climate and other regional-scale factors on radial growth and release

Growth of western redcedar and western hemlock was significantly associated with some monthly climatic variables. Because of this sensitivity to interannual climatic variability, it was appropriate to look at climate-growth relations in greater detail in order to better understand growth increases that were unrelated to canopy disturbances, i.e. false releases. For the radial-growth averaging method, false releases occur as a result of the strong influence of growth rate prior to release on percent-growth change (Lorimer 1980, Black and Abrams 2003, 2004). Specifically, at a fixed threshold value, this method is predisposed to detect more releases at low rates of prior growth (i.e. false positive releases) and fewer releases at high rates of prior growth (i.e. false negative release). When climate is less favorable for growth, narrow (i.e. negative marker) tree rings may form. Individual, or sequences of, negative marker rings followed by wider rings from years of average or above average growth can cause false positive releases in trees. Thus, understanding the effects of

temperature and precipitation on growth is crucial for determining an appropriate variation of the radial-growth averaging method for use in a study (Lorimer and Frelich 1989).

Despite significant climate-growth relations, the overall influence of regional-scale factors on growth in these stands was weak compared to localized processes of gap dynamics. This was apparent when percent-growth-change values for warm and dry periods were evaluated against those that followed the formation of canopy gaps. Specifically, warm and dry conditions produced negative marker rings that caused relatively higher percent-growth-change values than those in years with more average climatic conditions. For example, 1958 was the most moisture-limited year and growing season to occur over the entire instrumental record from 1895 to 2003 (Environment Canada station 1100120, McCloskey 2007). In 1959, the year following these particularly warm and dry conditions, western redcedar and western hemlock produced a negative marker ring. Applying the radial-growth averaging method to residual chronologies gave percent-growth-change values of 19 and 21% for western redcedar and western hemlock, respectively, in 1959. Thus, the influence of warm and dry conditions was apparent in the tree rings in the form of negative marker rings, but the effects of these conditions on growth increases at the multi-year scale were minimal. In addition, these growth increases were well below the majority that occurred for individual trees as a result of canopy disturbance. Specifically, growth increases as high as 800% (data not shown) occurred following the formation of a fine-scale canopy gap, while those related to regional-scale factors rarely exceeded 25%.

Percent-growth-change values calculated from the residual chronology of western hemlock reached above 25% in just one instance between 1930 and 1932. The increase to 33% coincided with a period of higher moisture that followed drought conditions

(Environment Canada station 1100120). In addition, the higher percent-growth-change values occurred immediately after a known outbreak of the defoliating insect western hemlock looper (*Lambdina fiscellaria lugubrosa* (Hulst)) in the Coquitlam watershed from 1927-1929 (Parfett et al. 1995). Although the history of this outbreak is unknown at the stand level, it is possible that defoliation and subsequent recovery explain some of the observed growth increase in western hemlock, the looper's preferred host tree, in the early 1930s. This possibility is supported by the fact that western redcedar and Pacific silver fir do not show the same growth pattern as western hemlock during that period, and western redcedar and western hemlock have similar climate-growth relations. While percent-growth change also reached above 25% for Pacific silver fir in the early 1900s, this occurred when there was only one tree in the chronology and thus might reflect other factors besides regional-scale variability. Overall, these findings further suggest a minimal influence of climate on tree growth compared to within-stand disturbances in old-growth forests of coastal British Columbia.

2.5.2. Parameters of the radial-growth averaging method

The proportion of trees that showed a release pattern varied from 0 to > 0.90 depending on the combination of threshold-moving average-window parameters. A closer look at the results of the 30 variations of the radial-growth averaging method revealed that altering the parameters had an effect on not only *if* a growth increase was identified as a release, but also *which* growth increase was identified as a release. Consistent with Rubino and McCarthy (2004), the threshold parameter ultimately controlled *if* a growth increase qualified as a release. Specifically, at low threshold values, many growth increases qualified as releases, while at high threshold values, only the most intense growth increases, thus

fewer, qualified as releases. Sometimes, the moving average and window parameters had a considerable influence on the year of the highest peak percent-growth-change value and thus *which* growth increase was identified as a release in response to gap formation. This was the case for trees with variable growth around the time of gap formation and weak growth increases in response to gap formation (i.e. low in magnitude and short in duration). For trees with these growth patterns, several peaks of low magnitude were possible within the window that surrounded the year of death of the gapmaker. Using a low threshold value meant that the year of the highest peak percent-growth change could differ by many years among moving averages, particularly within larger windows. In contrast, for trees with intense growth increases in response to gap formation (i.e. high in magnitude and long in duration), varying the moving average and window parameters caused peak percent-growth-change values to differ by only a few years. Thus, the parameters did not actually influence which release was identified, but only the specific year it initiated. These results ultimately relate back to the desire to use threshold and moving-average values that filter out minor fluctuations in growth and thus qualify only the most intense growth increases as responses to canopy disturbances (Lorimer 1980, Lorimer and Frelich 1989, Nowacki and Abrams 1997, Black and Abrams 2003, 2004). Inspecting all tree-ring series will help to reduce errors in identifying releases, both in terms of their status as valid releases and also for their timing of onset.

2.5.3. Ring width versus basal area increment

Using basal area increment versus ring width caused notable and methodologically interesting differences in the number of trees that showed a release pattern across the 30 variations. A greater number of trees released when basal area increment values were used.

Ring width is subject to a decrease over time, even when approximately the same cross-sectional area of wood is added to a stem annually. Because of this size-related trend, the M_1 values were relatively larger for smaller diameter trees when ring width as opposed to basal area increment was applied in the radial-growth averaging method. Because larger M_1 values resulted in lower percent-growth-change values (Black and Abrams 2003, 2004), fewer releases were detected for smaller diameter trees using ring width versus basal area increment (Figure 2.6).

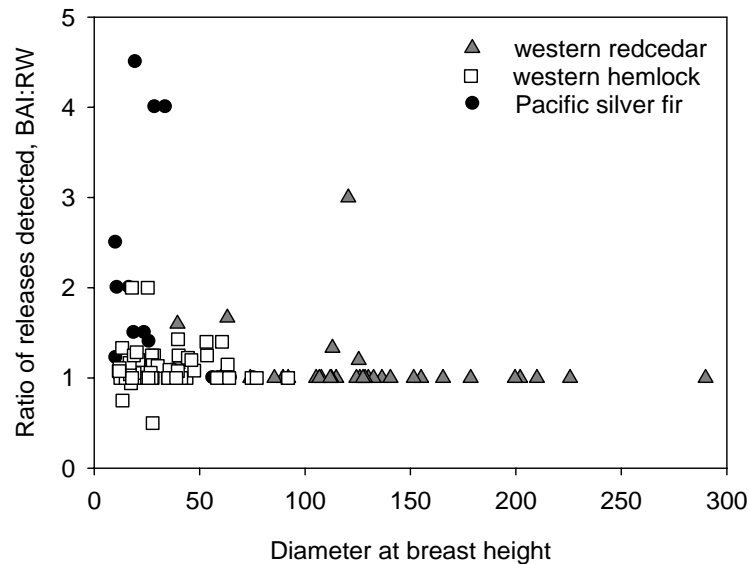


Figure 2.6. Ratio of releases detected over the 30 variations of the radial-growth averaging method using basal area increment (BAI) versus ring width (RW) relative to diameter at breast height for each western hemlock ($n = 60$), Pacific silver fir ($n = 23$), and western redcedar ($n = 34$) in the sensitivity analysis. Ratios could not be calculated for eight trees because of RW values of zero.

My results indicate that basal area increment is better suited than ring width to assess stands with large inter- and intra-species variation in tree size. In old-growth forests of coastal British Columbia, the population size structures of western redcedar, western hemlock, and Pacific silver fir differ considerably (Daniels 2003). Western redcedar is found predominantly in larger size classes in the canopy strata. Western hemlock occurs frequently

in both larger and smaller size classes in the canopy and subcanopy strata, although it does not grow as large as western redcedar. Pacific silver fir is mostly found in smaller size classes in the subcanopy strata. Because western hemlock and Pacific silver fir occur in smaller size classes relative to western redcedar, they are more biased towards having fewer releases detected when ring-width values are applied in the radial-growth averaging method (Figure 2.6). Thus, based on these findings, basal area increment is the more appropriate choice of growth index for detecting releases in structurally complex, old-growth forests of coastal British Columbia.

2.6. Conclusions

Given the influence of the parameters and growth index on the detection of a release, it is necessary to consider which overall version of the radial-growth averaging method is most appropriate for the study goals and species under review. In general, the version should be inclusive and capture the full range of growth increases (i.e. low/high magnitude and short/long duration) that occur for tree species following a particular type of disturbance event, yet account for the effects of climatic variability, or other regional-scale factors, on radial growth and release. In this study, the results are meant to provide a version of the radial-growth averaging method that is calibrated to detect growth release of trees following the formation of fine-scale canopy gaps in old-growth stands of coastal British Columbia. A 25% threshold, 5-year moving average, and 10-year window represent appropriate parameters for identifying releases due to canopy gaps in these stands. These parameters will minimize growth increases occurring as a result of more regional-scale factors, such as climate, and yet be as inclusive as possible to those following fine-scale canopy disturbances. In addition, using basal area increment will help to reduce errors that result from the size-

related trend in original ring-width values. The ability to minimize errors is an important characteristic of any release-detection method (Fraver and White 2005b, Py et al. 2006, Thompson et al. 2007). However, not all errors can be avoided; thus, it is necessary to recognize the ways in which the methods applied in a particular study influence the outcomes.

In summary, proper calibration of the radial-growth averaging method is a necessary starting point for a more thorough calibration of growth response to canopy disturbance events. Specifically, attributes of release, including magnitudes and durations, can be quantified, providing detailed information on how trees respond to the formation of natural canopy gaps. By improving our knowledge of attributes of release of individual tree species, studies can be better designed to capture the variability of past disturbance events and predict changes in forest structure and composition over time.

2.7. Literature cited

Acres International Limited. 1999. Annex to the Analysis Report, Watershed Management Plan #5, Volumes I-III. Greater Vancouver Regional District Watershed Ecological Inventory Program, Burnaby, British Columbia, Canada.

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

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

Black, B.A. and M.D. Abrams. 2004. Development and application of boundary-line release criteria. *Dendrochronologia* 22:31-42.

Blasing, T.J., A.M. Solomon, and D.N. Duvick. 1984. Response functions revisited. *Tree-Ring Bulletin* 44:1-15.

Biondi, F. and K. Waikul. 2004. DENDROCLIM2002: a C++ program for statistical calibration of climate signals in tree-ring chronologies. *Computers and Geosciences* 30:303-311.

Briffa, K. and E. Cook. 1990. Methods of response function analysis. Pages 240-247 *in* E.R. Cook and L.A. Kairiukstis, editors. *Methods of dendrochronology: applications in the environmental sciences*. Kluwer Academic Publishers, Dordrecht, The Netherlands.

- Carter, R.E. and K. Klinka. 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.
- Cook, E.R. 1985. A time series analysis approach to tree ring standardization. Ph.D. dissertation. The University of Arizona, Tucson, Arizona, USA.
- Cook, E.R. 1987. The decomposition of tree-ring series for environmental studies. *Tree-Ring Bulletin* 47:37-59.
- Cook, E.R. and K. Peters. 1981. The smoothing spline: a new approach to standardizing forest interior tree-ring width series for dendroclimatic studies. *Tree-Ring Bulletin* 41:45-53.
- Daniels, L.D. 1994. Structure and regeneration of old-growth *Thuja plicata* stands near Vancouver, British Columbia. M.Sc. thesis. University of British Columbia, Vancouver, British Columbia, Canada.
- Daniels, L.D. 2003. Western redcedar population dynamics in old-growth forests: contrasting ecological paradigms using tree rings. *Forestry Chronicle* 79:517-530.
- Daniels, L.D., J. Dobry, K. Klinka, and M.C. Feller. 1997. Determining year of death of logs and snags of *Thuja plicata* in southwestern coastal British Columbia. *Canadian Journal of Forest Research* 27:1132-1141.
- Daniels, L.D. and R.W. Gray. 2006. Disturbance regimes in coastal British Columbia. *BC Journal of Ecosystems and Management* 7:44-56.

- Daniels, L.D. and K. Linka. 1996. The dynamics of old-growth *Thuja-Tsuga* forests near Vancouver, British Columbia. Pages 379-393 in J.S. Dean, D.M. Meko, and T.W. Swetnam, editors. Tree rings, environment, and humanity.
- Dynesius, M. and B.G. Jonsson. 1991. Dating uprooted trees: comparison and application of eight methods in a boreal forest. Canadian Journal of Forest Research 21:655-665.
- Fraver, S. and A.S. White. 2005a. Disturbance dynamics of old-growth *Picea rubens* forests of northern Maine. Journal of Vegetation Science 16:597-610.
- Fraver, S. and A.S. White. 2005b. Identifying growth releases in dendrochronological studies of forest disturbance. Canadian Journal of Forest Research 35:1648-1656.
- Frelich, L.E. 2002. Forest dynamics and disturbance regimes: studies from temperate evergreen-deciduous forests. Cambridge University Press, Cambridge, UK.
- Fritts, H.C. 1976. Tree rings and climate. Academic Press, New York, New York, USA.
- Fritts, H.C. and T.W. Swetnam. 1989. Dendroecology: a tool for evaluating variations in past and present forest environments. Advances in Ecological Research 19:111-189.
- Gavin, D.G., L.B. Brubaker, and K.P. Lertzman. 2003. Holocene fire history of a coastal temperate rain forest based on soil charcoal radiocarbon dates. Ecology 84:186-201.
- Glitzenstein, J.S., P.A. Harcombe, and D.R. Streng. 1986. Disturbance, succession, and maintenance of species diversity in an east Texas forest. Ecological Monographs 56:243-258.
- Grissino-Mayer, H.D. 2001. Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. Tree-Ring Research 57:205-221.

- Guiot, J. 1991. The bootstrapped response function. *Tree-Ring Bulletin* 51:39-41.
- Hart, J.L. and H.D. Grissino-Mayer. 2008. Vegetation patterns and dendroecology of a mixed hardwood forest on the Cumberland Plateau: implications for stand development. *Forest Ecology and Management* 255:1960-1975.
- Henry, J.D. and J.M.A. Swan. 1974. Reconstructing forest history from live and dead plant material - an approach to the study of forest succession in southwest New Hampshire. *Ecology* 55:772-783.
- Holmes, R.L. 1983. Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bulletin* 43:69-78.
- Klinka, K., R.E. Carter, and M.C. Feller. 1990. Cutting old-growth forests in British Columbia: ecological considerations for forest regeneration. *Northwest Environmental Journal* 6:221-242.
- Lertzman, K., D. Gavin, D. Hallett, L. Brubaker, D. Lepofsky, and R. Mathewes. 2002. Long-term fire regime estimated from soil charcoal in coastal temperate rainforests. *Conservation Ecology* 6:5. [online] URL: <http://www.consecol.org/vol6/iss2/art5>.
- Lertzman, K.P. and C.J. Krebs. 1991. Gap-phase structure of a subalpine old-growth forest. *Canadian Journal of Forest Research* 21:1730-1741.
- Lertzman, K.P., G.D. Sutherland, A. Inselberg, and S.C. Saunders. 1996. Canopy gaps and the landscape mosaic in a coastal temperate rain forest. *Ecology* 77:1254-1270.
- Lorimer, C.G. 1980. Age structure and disturbance history of a southern Appalachian virgin forest. *Ecology* 61:1169-1184.

- Lorimer, C.G. and L.E. Frelich. 1989. A methodology for estimating canopy disturbance frequency and intensity in dense temperate forests. *Canadian Journal of Forest Research* 19:651-663.
- Maser, C., R.G. Anderson, K. Cromack, Jr., J.T. Williams, and R.E. Martin. 1979. Dead and down woody material. Pages 78-95 in J.W. Thomas, editor. *Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington*. USDA Forest Service, Agriculture Handbook 553.
- McCloskey, S.P.J. 2007. Western hemlock looper: a biological agent of disturbance in coastal forests of British Columbia. Ph.D. dissertation. University of British Columbia, Vancouver, British Columbia, Canada.
- Meidinger, D.V. and J. Pojar, editors. 1991. *Ecosystems of British Columbia*. Special Report Series 6. British Columbia Ministry of Forests, Victoria, British Columbia, Canada.
- Monger, J.W.H. and J.M. Journeay. 1994. Guide to the geology and tectonic evolution of the southern Coast Mountains. Open File 2490. Geological Survey of Canada, Vancouver, British Columbia, Canada.
- Norton, D.A., J.G. Palmer, and J. Ogden. 1987. Dendroecological studies in New Zealand 1. An evaluation of tree age estimates based on increment cores. *New Zealand Journal of Botany* 25:373-383.
- Nowacki, G.J. and M.D. Abrams. 1997. Radial-growth averaging criteria for reconstructing disturbance histories from presettlement-origin oaks. *Ecological Monographs* 67:225-249.

- Oliver, C.D. and B.C. Larson. 1996. Forest stand dynamics. John Wiley and Sons, New York, New York, USA.
- Parfett, N., I.S. Otvos, and A. Van Sickle. 1995. Historical western hemlock looper outbreaks in British Columbia: input and analysis using a geographic information system. FRDA Report 235. Canadian Forest Service, Victoria, British Columbia, Canada.
- Py, C., J. Bauer, P.J. Weisberg, and F. Biondi. 2006. Radial growth responses of singleleaf pinyon (*Pinus monophylla*) to wildfire. *Dendrochronologia* 24:39-46.
- Rentch, J.S., F. Desta, and G.W. Miller. 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.
- Rubino, D.L. and B.C. McCarthy. 2004. Comparative analysis of dendroecological methods used to assess disturbance events. *Dendrochronologia* 21:97-115.
- Runkle, J.R. 1982. Patterns of disturbance in some old-growth mesic forests of eastern North America. *Ecology* 63:1533-1546.
- Ryder, J.M. 1981. Geomorphology of the southern part of the Coast Mountains of British Columbia. *Zeitschrift für Geomorphologie* 37:120-147.
- Stokes, M.A. and T.L. Smiley. 1968. An introduction to tree-ring dating. University of Chicago Press, Chicago, Illinois, USA.
- Tardif, J. and Y. Bergeron. 1999. Population dynamics of *Fraxinus nigra* in response to flood-level variations in northwestern Quebec. *Ecological Monographs* 69:107-125.

- Thompson, R.D., L.D. Daniels, and K.J. Lewis. 2007. A new dendroecological method to differentiate growth responses to fine-scale disturbance from regional-scale environmental variation. *Canadian Journal of Forest Research* 37:1034-1043.
- Valentine, K.W.G., P.N. Sprout, T.E. Baker, and L.M. Lavkulich, editors. 1978. The soil landscapes of British Columbia. British Columbia Ministry of Environment, Victoria, British Columbia, Canada.
- Wang, T., A. Hamann, D.L. Spittlehouse, and S.N. Aitken. 2006. Development of scale-free climate data for western Canada for use in resource management. *International Journal of Climatology* 26:383-397.
- Wells, R.W., K.P. Lertzman, and S.C. Saunders. 1998. Old-growth definitions for the forests of British Columbia, Canada. *Natural Areas Journal* 18:279-292.
- Wigley, T.M.L., K.R. Briffa, and P.D. Jones. 1984. On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. *Journal of Climate and Applied Meteorology* 23:201-213.
- Yamaguchi, D.K. 1991. A simple method for cross-dating increment cores from living trees. *Canadian Journal of Forest Research* 21:414-416.

3. Quantifying attributes of growth releases for reconstructing canopy disturbances in old-growth forests of coastal British Columbia¹

3.1. Introduction

Canopy disturbance is a primary process in forests that influences the growth of new and established trees (Sousa 1984, White and Pickett 1985). Where stand-destroying disturbances are infrequent, forest canopies are opened periodically by the death of single trees or small groups of trees. Changes in growth brought about by these fine-scale disturbances are often assessed by inspecting the radial-growth patterns of trees that survive the disturbances, as they can provide insight into the compositional and structural development of the stand (Lorimer and Frelich 1989, Frelich 2002).

Two approaches are generally used to study canopy disturbance and the radial growth of surviving trees in natural systems. In the first approach, we know when the disturbance occurred and measure its effect on the radial growth of surviving trees. The date of disturbance is known either because the disturbance is a result of a documented event, as in the case of a wind or ice storm (e.g. Merrens and Peart 1992, Lafon and Speer 2002, Smith and Shortle 2003, Beaudet et al. 2007), or because it is derived by estimating year of death of logs or standing dead trees using dendroecological methods (e.g. Fraver and White 2005a, Thompson et al. 2007). In the second approach, we do not know when the disturbance

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occurred and use the radial growth of surviving trees to measure and reconstruct it. This technique uses abrupt increases in radial growth, i.e. releases, as a proxy for canopy disturbance (Lorimer 1985).

Radial-growth releases have been used to reconstruct the frequency and intensity of past canopy disturbances in temperate forests worldwide that are dominated by fine-scale processes of gap dynamics (e.g. Lorimer 1980, Taylor 1990, Frelich and Lorimer 1991, Orwig and Abrams 1994, Lusk and Smith 1998, Ishikawa et al. 1999, Ziegler 2002, Rozas 2003, Gutiérrez et al. 2004, Taylor et al. 2006). Radial-growth averaging (Henry and Swan 1974, Lorimer and Frelich 1989, Nowacki and Abrams 1997) is the most commonly used method for reconstructing canopy disturbances using releases (Rubino and McCarthy 2004). This method involves detecting releases by comparing average radial growth for successive periods and identifying peak growth-change values above a minimum threshold. Radial-growth averaging is not always calibrated, and thresholds are commonly applied without explicitly considering factors that may influence radial growth and release potential. Studies that do calibrate attempt to filter out growth increases that result from climatic factors or account for tree size and growth rate prior to release as influences on the amount of growth increase that is possible for a particular tree (Lorimer and Frelich 1989, Nowacki and Abrams 1997, Black and Abrams 2003, 2004). While calibrating for these influences is an important step towards correctly identifying releases due to canopy disturbances, it is not the only step. Thus, some studies use release-detection methods, in conjunction with stem maps, to link spatial and temporal characteristics of live and dead trees (Payette et al. 1990, Parish and Antos 2004, 2006, Fraver and White 2005b). By relating the temporal record of release

of individual trees to their location within a stand, along with temporal and spatial aspects of dead trees, one can gain a detailed understanding of historical disturbance events.

A potentially more powerful approach to quantify the history of canopy disturbances is to measure species-specific tree response to extant canopy gaps and use this information to calibrate gap reconstructions at the stand level. In this approach, the first step is to determine the timing of formation of natural, extant canopy gaps. The second step is to quantify the release of trees surrounding these gaps. Building on existing methods, the radial-growth averaging method is initially calibrated to account for regional-scale variability (Chapter 2). Then, this method is used to assess temporal and spatial attributes of growth releases following the formation of gaps of known timing of origin. Specifically, the duration and magnitude of individual releases can be quantified and related to tree- and gap-level variables. This species- and ecosystem-specific information provides the starting point from which to reconstruct gap disturbances at the stand level.

Fine-scale death of canopy dominants is the primary natural disturbance in the wetter parts of the coastal temperate rain forest of British Columbia, Canada (Lertzman and Krebs 1991, Lertzman et al. 1996, Daniels and Gray 2006). Because of infrequent coarse-scale fire at time scales up to thousands of years (Lertzman et al. 2002, Gavin et al. 2003), the forest landscape comprises many old stands. These stands have complex structures, with fine-scale canopy gaps and live/dead trees that can reach great ages and massive sizes (Meidinger and Pojar 1991, Lertzman et al. 1996, Wells et al. 1998). At mid-elevations, western redcedar (*Thuja plicata* Donn ex D. Don), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and Pacific silver fir (*Abies amabilis* Dougl. ex J. Forbes) dominate the canopy of old-growth stands (Meidinger and Pojar 1991). All three species are shade tolerant (Klinka et al. 1990,

Carter and Klinka 1992), but capable of large increases in radial growth upon the formation of a canopy gap (Daniels and Klinka 1996). This combination of infrequent coarse-scale disturbances and long-lived, highly shade-tolerant tree species makes it possible to reconstruct the long-term history of fine-scale gap disturbances in coastal, old-growth stands using release-detection methods. However, to do this will first require short-term information from these forests on growth release following the formation of extant gaps.

Information on growth release following the formation of canopy gaps might also be useful for better understanding tree species coexistence in forests with complex population structures. In old-growth forests of coastal British Columbia, the population structures of western redcedar, western hemlock, and Pacific silver fir differ considerably (Daniels 2003). Western redcedar is found predominantly in the canopy strata. Western hemlock occurs frequently in both the canopy and subcanopy strata. Pacific silver fir is found mostly in the subcanopy strata. Seedlings and saplings of western hemlock and Pacific silver fir are common, while those of western redcedar are much less so. Considering the mechanisms by which these species grow into the canopy strata may help to clarify community dynamics in these stands (Canham 1989). Western redcedar, western hemlock, and Pacific silver fir all show evidence of suppression and release associated with canopy gaps, with patterns that may differ among species (Daniels and Klinka 1996). These patterns suggest a need to further assess the role of gaps for individual tree species persistence in old-growth stands and whether they contribute to long-term coexistence.

The objectives of this study were to quantify attributes of growth releases following gap formation in old-growth, western redcedar-western hemlock forests of coastal British Columbia and to discuss how to use this information to (i) improve approaches for

reconstructing the history of canopy disturbances and (ii) better understand mechanisms of tree species coexistence in these stands. I addressed the objectives by (1) determining the timing of origin of natural, extant canopy gaps, (2) quantifying the number of trees that showed a release pattern following the formation of these gaps, (3) quantifying the duration and magnitude of releases in response to gap formation, and (4) estimating the influence of different tree- and gap-level variables on the duration and magnitude of releases. I sought to capture the full range of growth releases that were associated with fine-scale gaps, including those of short to long duration and low to high magnitude. Understanding details of tree release following gap formation provides a foundation for accurately reconstructing stand history and assessing mechanisms of species coexistence.

3.2. Study area

I conducted this research in the Capilano, Seymour, and Coquitlam River watersheds in the Coast Mountains of southwestern British Columbia (Figure 3.1). These drainages encompass an area of approximately 58,500 ha that is managed by Metro Vancouver for water supply to municipalities in the greater Vancouver area. In the past, processes of glacial erosion impacted the area and helped create the overall rugged topography and steep slopes that exist today (Ryder 1981). Relief in the watersheds ranges from 1300 to 1600 m, and slopes commonly exceed 35°, particularly at higher elevations. Across the terrain, several ecosystem types occur that are typical of those present throughout coastal British Columbia. Using the Biogeoclimatic Ecosystem Classification system of British Columbia, these include the Coastal Western Hemlock, Mountain Hemlock, and Alpine Tundra zones (Meidinger and Pojar 1991).

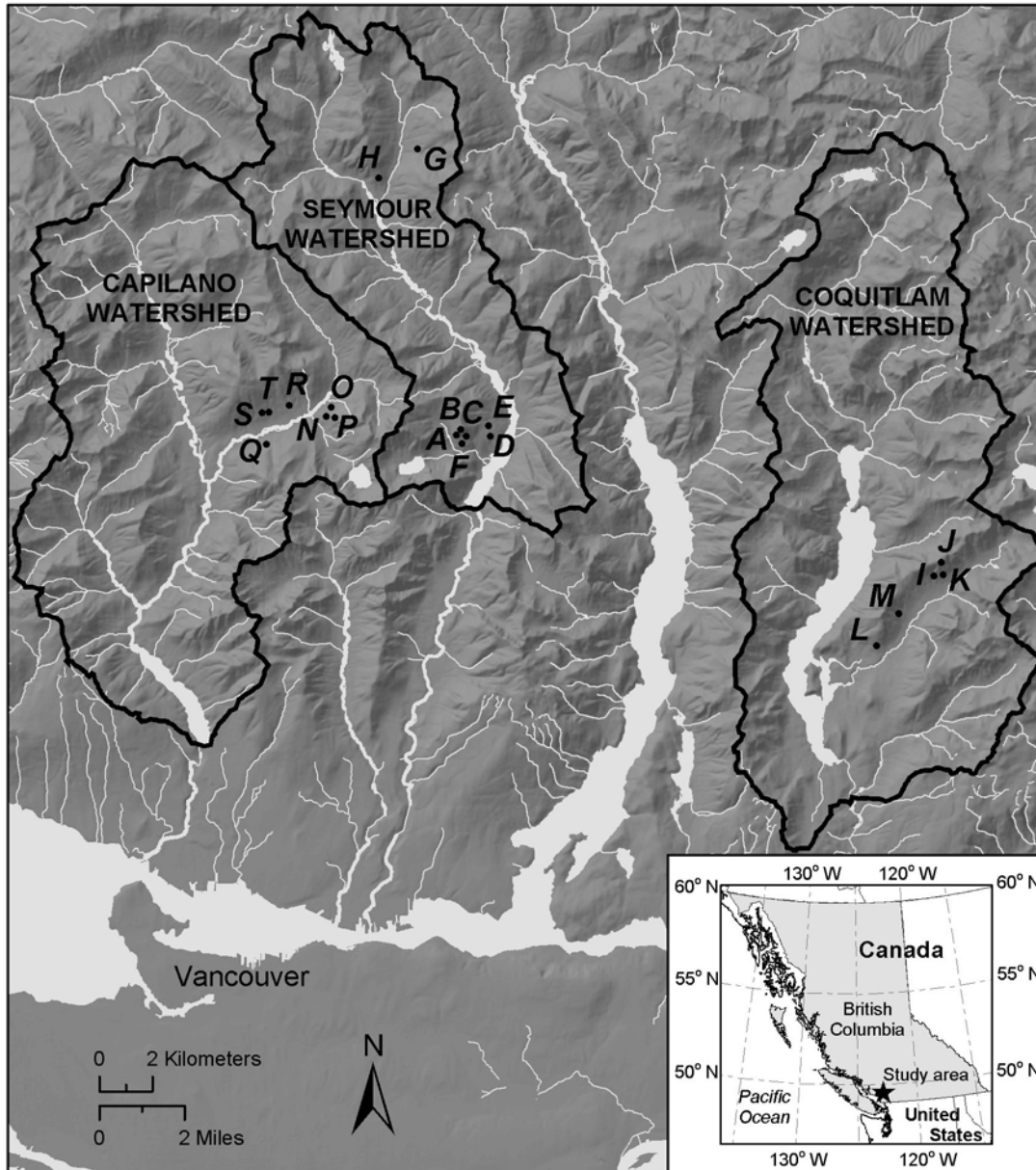


Figure 3.1. Location of the study area and sites in the Capilano, Seymour, and Coquitlam River watersheds, British Columbia, Canada.

I restricted the study sites to mid-elevation (300-700 m a.s.l.), old-growth forests within the watersheds. The sites are located in the Very Wet Maritime subzone of the Coastal Western Hemlock zone, which has a wet, humid climate, with cool summers and mild winters (Meidinger and Pojar 1991). Based on spatially-interpolated monthly climate normals for the period 1961-1990 (Wang et al. 2006), mean annual temperature at all study

sites ranged from 6.0 to 7.5°C, with a mean of 15 to 16°C in August and -1 to 1°C in December. Total annual precipitation was between 3000 to 4000 mm. Total growing season (May to September) precipitation ranged from 600 to 800 mm. At all study sites, soils are largely Humo-Ferric Podzols derived from colluvium and glacial till (Valentine et al. 1978). Sites are located on Coast Plutonic Complex intrusions of Mid-Cretaceous quartz diorite in Capilano and Seymour and of Late-Jurassic to Early-Cretaceous quartz diorite in Coquitlam (Monger and Journeay 1994).

Historically, most low- and mid-elevation forests in the watersheds were old growth, as evidenced by an abundance of standing dead and downed trees, canopy gaps, and trees greater than 250 years of age (Acres International Limited 1999). These stands resulted from long periods of fine-scale gap forming and filling processes occurring in the absence of catastrophic disturbances such as fire (Lertzman et al. 1996, Wells et al. 1998, Gavin et al. 2003). Until the early 1990s, many of these forests were impacted by harvesting (Acres International Limited 1999). Consequently, low- and mid-elevations in the watersheds are a mosaic of second-growth stands, interspersed with remnant patches of old-growth forest.

Shade-tolerant western redcedar, western hemlock, and Pacific silver fir, and a small number of shade-intolerant Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) constitute mid-elevation, old-growth stands in the watersheds (Meidinger and Pojar 1991). Life spans are ≥ 360 years for Pacific silver fir, ≥ 450 years for western hemlock, and ≥ 1000 for western redcedar and Douglas-fir (Daniels 1994). Pacific silver fir reaches ≥ 100 cm diameter at breast height (dbh), western hemlock ≥ 120 cm dbh, and western redcedar and Douglas-fir ≥ 250 cm dbh (Daniels 1994).

Stand developmental processes contribute greatly to the overall openness of mid-elevation, old-growth forests in the watersheds. Approximately 74% of the area of old-growth, western redcedar-western hemlock stands (Stan and Daniels, *unpublished data*) is in gaps of developmental origin (i.e. those created by the mortality of canopy dominants; Lertzman et al. 1996), including both canopy and expanded gaps. A canopy gap is the vertical projection onto the ground of an opening in the canopy, and an expanded gap is defined by the boles of the trees whose crowns delineate a canopy gap (Runkle 1982). Only 13% of the area of these stands is closed canopy (Stan and Daniels, *unpublished data*).

3.3. Methods

3.3.1. *Selecting study sites*

I used a combination of watershed ecological inventory data and field reconnaissance to locate canopy gaps. From forest cover maps of the watersheds (Acres International Limited 1999), I identified remnant patches of old-growth, western redcedar-western hemlock forest situated on slopes $\leq 30^\circ$ between 300 and 700 m a.s.l. All stands $\geq 20\%$ western redcedar and $\leq 20\%$ Douglas-fir by volume were considered appropriate for this study. In coastal British Columbia, Douglas-fir establishes primarily after stand-destroying disturbances and therefore can be a minor component of very old stands. Approximately 3000 ha of forest stands met the above criteria. I randomly selected stands and inspected them to verify old-growth structural and compositional characteristics, along with site features and accessibility. Stands that were poorly drained, difficult to access because of topographic features (e.g. stream crossing), or too small to contain canopy gaps not influenced by edge effects from roads or major streams were omitted from further sampling.

Stands confirmed appropriate through field reconnaissance were systematically searched for gaps that were (1) created by one or two uprooted canopy dominant(s) and (2) likely formed within the last 50 years. I focused on gaps that were created by uprooted trees in order to maintain consistency in terms of their mode of formation. While modes of gap-forming mortality in coastal British Columbia include standing death, snapping, and uprooting (Lertzman and Krebs 1991, Arsenault 1995, Lertzman et al. 1996), the last has the greatest potential to offer the most information for determining the timing of gap formation using dendroecological methods. In addition, “recently” formed gaps were best suited for determining the timing of gap formation using dendroecological methods. Over time, information such as outer-ring dates of gapmakers can become less accurate due to loss of bark and decay, and in addition, secondary gap expansion or formation of adjacent gaps can result in complex growth patterns of trees growing around and within gaps, making older gaps less desirable for use in this study. I used the five-class system of log decomposition described by Maser et al. (1979) to facilitate identification of gaps that met the appropriate age criterion. Based on this system, gaps were marked for more rigorous assessment of timing of formation only if the gapmakers were in decay classes I, II, or III. Logs in the first three decay classes correspond to the least decayed individuals and therefore should represent the most recently created gaps (Daniels et al. 1997).

For each marked gap, I attempted to determine the year of death and year of fall of the gapmaker(s). To determine year of death, I took multiple increment cores from the least decayed sections of each bole to ensure that (1) enough intact rings, including the outermost rings, were available for crossdating and (2) when possible, samples included the bark and sapwood (Dynesius and Jonsson 1991, Daniels et al. 1997). Cores were mounted and sanded

following the procedures of Stokes and Smiley (1968). I measured ring widths to the nearest 0.001 mm with a stereozoom microscope and Velmex sliding-stage micrometer interfaced with MeasureJ2X software. The program COFECHA (Holmes 1983, Grissino-Mayer 2001) was used to statistically crossdate ring-width series from gapmakers against preliminary master-dating series developed from cores collected from nearby living trees; crossdating was later verified against regional-scale, species-specific final master-dating series (Chapter 2). By crossdating cores, I was able to assign a calendar year to each tree ring and thus estimate the last year of growth of the gapmakers. To determine year of fall, I collected partial or whole-stem cross sections from any live trees scarred or crushed by the gapmaker. In addition, I sampled cross sections from seedlings or saplings growing on the gapmaker. Cross sections were sanded (Stokes and Smiley 1968) and visually crossdated (Yamaguchi 1991) to determine year of establishment of seedlings and saplings (an estimate of maximum year of fall) along with year of scar or reaction wood formation in injured trees. Gapmakers that could not be successfully dated to year of death or fall were rejected and no further sampling was conducted at those sites. Although 45 gaps were located during field reconnaissance, only 20 gaps were dated with confidence and these were used for subsequent sampling (Table 3.1).

3.3.2. Sampling and crossdating trees

At each of the 20 dated gaps, I extracted two increment cores from all trees (dbh \geq 10 cm) that defined the boundary of, or occurred within, the gaps (Table 3.2). The boundary of a gap was delineated using the crown of canopy dominant, co-dominant, and intermediate trees nearest to the gapmaker(s). All trees were cored on the side facing the center of the gap

Table 3.1. Summary of data collected to determine timing of formation of 20 gaps using dendroecological methods.

Gap ID	Species of gapmaker	dbh (cm)	Cores from gapmaker [§]	Mean corr. [†]	Scars or reaction wood	Seedlings or saplings	Year of death [‡]	Year of fall [*]
A	western redcedar	110	7	0.64	0	1	1973	<i>1979</i>
B	western redcedar	180	2	0.65	2	1	1991	1992
C	western redcedar	132	5	0.61	0	0	1998	n/a
D	western redcedar	140	5	0.49	1	0	1998	n/a
E	western redcedar	108	9	0.42	1	1	1956	<i>1966</i>
F	western redcedar	74	3	0.53	3	0	1974	1981
	western hemlock ⁺	53	2	n/a				
G	Pacific silver fir	93	2	0.39	2	1	1995	1993/1998
H	western redcedar	99	6	0.52	1	0	1967	1978
I	western redcedar	106	4	0.51	0	0	1973	n/a
J	western hemlock	66	3	n/a	1	0	n/a	1985
K	western hemlock	99	2	n/a	1	0	n/a	1985
L	western redcedar	172	5	0.40	1	0	n/a	1963
M	western redcedar	160	3	0.56	1	0	1959	1976
N	western redcedar ⁺	106	7	0.51	1	0	1995	1996
	western hemlock	30	0					
O	Pacific silver fir ⁺	53	3	0.33	1	0	2000	1999
	western hemlock	21	3	0.39				
P	western redcedar	200	3	0.70	0	0	1989	n/a
Q	western redcedar	165	2	0.55	1	0	1977	1978
R	western redcedar	312	3	0.44	1	0	1977	1999
S	western hemlock ⁺⁺	99	0		0	0	2000	n/a
T	western redcedar	147	3	0.59	0	0	2000	n/a
	western hemlock	84	0					

[§]Number of statistically crossdated ring-width series.

[†]Mean Pearson's correlation coefficient between the ring-width series and the final master-dating series of each species calculated by program COFECHA.

[‡]Determined using the date of the outermost ring of the statistically crossdated ring-width series.

^{*}Determined using dates of scars or reaction wood formation in trees hit by the gapmaker. Years in italics refer to the maximum year of fall as determined from pith dates of seedlings or saplings that established on the gapmaker.

⁺Gapmakers were on the same root plate.

⁺⁺Dated using information from gap T, which was 30 m away and likely formed during the same storm.

^{||}Two scars were located on the same radii. Gapmaker likely fell in 1993 and shifted its position in 1998.

Note: n/a indicates that no data were available to sample or information could not be extracted from the sample(s) to determine year of death or fall. Gaps were sampled during 2003 and 2004.

at a height of approximately 30 cm above the ground. Cores were mounted and sanded

according to Stokes and Smiley (1968).

Table 3.2. Characteristics of the 20 study gaps and the number of trees growing around or within the gaps (n = 348).

Gap ID	Watershed	Gap area (m ²) [§]	Elevation (m)	Slope (°)	Aspect (°)	Canopy openness (%) [†]	No. of trees		
							Ced	Hem	Fir
A	Seymour	328	627	25	198	5.43	7	7	7
B	Seymour	429	633	25	202	9.49	7	8	4
C	Seymour	381	635	30	200	10.20	5	10	7
D	Seymour	317	440	15	188	8.42	5	6	3
E	Seymour	217	440	15	30	7.60	3	8	2
F	Seymour	174	540	14	174	5.25	4	9	1
G	Seymour	205	660	12	288	10.29	0	9	9
H	Seymour	153	460	27	167	7.04	6	7	1
I	Coquitlam	439	625	15	207	8.40	5	13	14
J	Coquitlam	359	631	18	206	6.69	3	11	8
K	Coquitlam	127	625	23	206	6.60	0	6	9
L	Coquitlam	118	420	12	160	8.76	5	5	1
M	Coquitlam	190	530	29	150	4.77	7	8	1
N	Capilano	351	537	18	237	5.80	6	13	4
O	Capilano	383	534	19	238	6.32	7	9	5
P	Capilano	317	563	17	271	5.88	4	9	0
Q	Capilano	324	420	15	18	8.42	4	12	0
R	Capilano	248	497	17	225	9.37	3	5	5
S	Capilano	164	505	23	174	6.22	3	8	0
T	Capilano	560	510	23	192	5.38	3	17	0

[§]Area of the expanded gap as defined by the boles of the trees whose crowns delineated the opening in the canopy (Runkle 1982).

[†]Determined from hemispherical photographs taken a meter above the forest floor within the gaps.

Note: Slope and aspect were estimated using a clinometer and compass, respectively. Ced = western redcedar, Hem = western hemlock, and Fir = Pacific silver fir.

I took a rigorous approach to crossdating because the frequent occurrence of modest to severe suppression within western hemlock and Pacific silver fir that grow in these stands made it difficult to match their ring patterns. First, the two cores collected from each tree were visually crossdated (Yamaguchi 1991) relative to each other to identify locally absent rings, i.e. those that were missing along one or more radii of the tree (Fritts 1976, Norton et al. 1987). Then, ring widths of all cores were measured to the nearest 0.001 mm using a stereozoom microscope and Velmex sliding-stage micrometer interfaced with MeasureJ2X software and statistically crossdated (Holmes 1983, Grissino-Mayer 2001) both within individual trees and among all trees of a single species. In general, cores with the greatest

number of suppressions and/or releases were difficult to statistically crossdate, and at best, could only be visually crossdated using narrow and wide marker rings.

3.3.3. *Identifying release of trees*

I assessed all trees growing around or within the 20 dated gaps for growth release. I converted ring width into basal area increment and used a species- and ecosystem-specific version of the radial-growth averaging method (Chapter 2) to determine if individual trees showed a release pattern following the formation of a canopy gap of known timing of origin. As formalized by Nowacki and Abrams (1997), this method is expressed using the equation:

$$\%GC = (M_2 - M_1) / M_1 \times 100,$$

where %GC is percent-growth change for a single year, M_1 is the mean basal area increment preceding that year, and M_2 is the mean basal area increment following that year. I applied the percent-growth change equation with a 5-year moving average (i.e. M_1 and M_2) to basal area increment values of individual trees (i.e. mean of two cores per tree) and identified a release as the highest peak growth-change value $\geq 25\%$, within the 10-year window that surrounded the year of death of the gapmaker (Figure 3.2). The peak percent-growth-change value represented the year prior to the onset of a release (Nowacki and Abrams 1997). If a peak $\geq 25\%$ did not occur, I then assessed whether the last calculated growth-change value within the window was $\geq 25\%$. This subsequent inspection was particularly useful for the younger gaps for which it was not always possible to determine if a tree released using a peak value. An adjustment was made for trees from gaps with information on only the year of fall of the gapmaker (Table 3.1). For those trees, I established the window relative to the year of fall and shortened the portion after fall to five years (Figure 3.2) because it was

unlikely that any associated releases occurred beyond that time. I used all the releases detected in these analyses in later analyses of duration and magnitude.

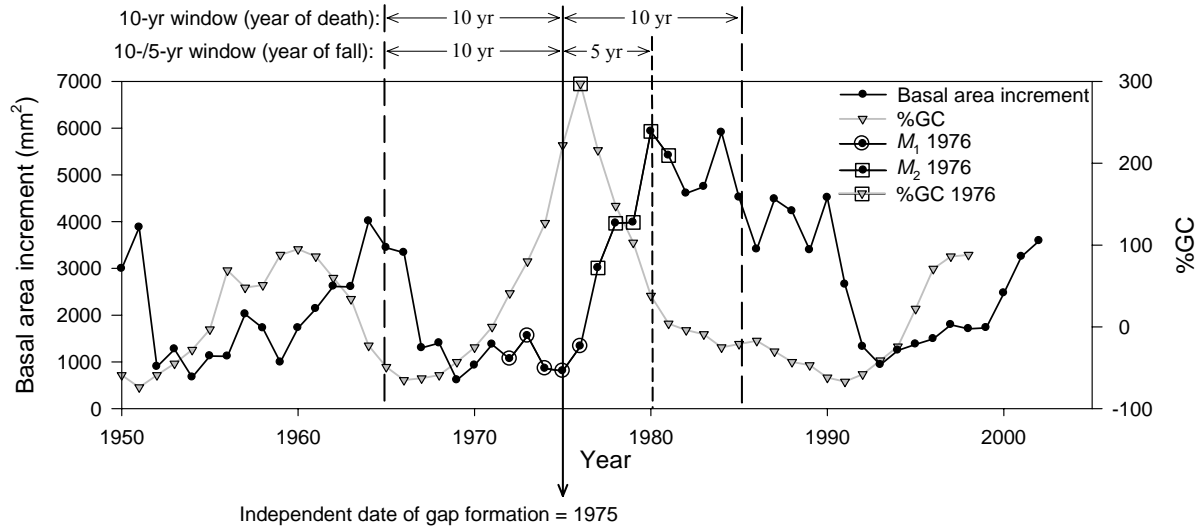


Figure 3.2. Schematic depicting the detection of a release for a tree growing around or within a natural canopy gap of known timing of origin using the radial-growth averaging method with a 5-year moving average. Percent-growth change (%GC) for a single year is equal to $(M_2 - M_1) / M_1 \times 100$, where M_1 is the mean basal area increment for the five years preceding that year, and M_2 is the mean basal area increment for the five years following that year (adapted from Nowacki and Abrams 1997). %GC is highlighted for a release detected within windows surrounding 1975, the year of gap formation (i.e. year of death or fall).

I used the CATMOD procedure (SAS Institute Inc. 2007) to conduct a log-linear analysis of a three-way contingency table of species, canopy position, and release. In addition to the number of trees that showed a release pattern, this procedure allowed me to assess the association of western redcedar, western hemlock, and Pacific silver fir in canopy (co-dominant and dominant trees) and subcanopy (suppressed and intermediate trees) positions.

Given the large size of the canopy trees in these stands, a release might occur following both the death and fall of a gapmaker. Therefore, I determined the number of trees that showed a release pattern based on both independent dates of gap formation. I examined

94 trees from a subset of the six oldest gaps with information on both the year of death and fall of the gapmaker(s) (Table 3.1). To do this, I applied the same techniques used to detect releases relative to year of death and fall but adjusted the window for the latter to include only the five years after fall. Trees were placed into categories based on whether a release was detected relative to the year of death, year of fall, or both. In the instance that the same release was detected for both dates of gap formation, it was counted as being associated with the year of death.

3.3.4. Duration of releases

Duration is the number of years from the onset to the end of a release. To determine the duration of a release, M_1 for the year of peak percent-growth change was held constant as M_2 was shifted successively one year at a time (Figure 3.2). A release was considered to have ended when percent-growth change decreased below the 25% threshold. Thus, the end of a release was defined as the last calendar year in M_2 when percent-growth change was still $\geq 25\%$ (Figure 3.2). Some releases were sustained, i.e. percent-growth change was $\geq 25\%$ at the time of sampling and thus the end of the release was not observed.

I assessed the duration of releases using survival analysis. This class of statistical procedures is concerned with studying the time until a specific event occurs (Kalbfleish and Prentice 1980, Klein and Moeschberger 1997, Fox 2001, Lee and Wang 2003). Besides accommodating strongly skewed distributions, survival analysis allows for the inclusion of censored observations, i.e. those in which the event of interest is not observed. These methods are widely used in the biomedical, social, and engineering sciences (Collett 2003, Lee and Wang 2003). Plant ecologists have applied survival analysis to address questions such as stand growth until or since a fire (Johnson and Gutsell 1994), time until a tree is

attacked by an insect (He and Alfaro 2000), time to emergence of a seed or flowering of a plant (Fox 2001), the lifespan of a leaf (Dungan et al. 2003), and time until death of a seedling (Beckage and Clark 2003).

I calculated both nonparametric and parametric survival functions. The survival function $S(t)$ is the probability that a release survives beyond time t , i.e. $\Pr(T > t)$, where T is a continuous random variable that represents the number of years from the onset to the end of a release (i.e. duration). Nonparametric survival functions do not require any assumptions of distribution. Parametric survival functions require selecting a distribution, thus allowing for a regression analysis with explanatory variables.

I estimated nonparametric survival functions using the product-limit (Kaplan-Meier) estimate of the survival function (Kaplan and Meier 1958). The product-limit estimate accounts for censored observations. In this study, observations were right censored because a release could continue beyond the date of sampling. This method estimates the survival function $S(t)$ as a product of t conditional observed survival probabilities:

$$S(t) = p_1 \times p_2 \times \dots \times p_t,$$

where $1, 2, \dots, t$ are distinct times at which releases end, $p_i = (n_i - d_i)/n_i$ is the proportion of releases surviving the i th year after they have survived $i - 1$ years, where n_i is the number of releases at risk of ending at t_i (i.e. the number of uncensored releases just prior to t_i), and d_i is the number of releases ending at t_i . Analysis was done using the LIFETEST procedure (SAS Institute Inc. 2007).

I fit a parametric survival model to duration of releases. The model was an accelerated failure time model in which the explanatory variables multiplicatively affected

failure time of a release, or linearly affected the natural logarithm of a failure time, $\ln(T)$ (Kalbfleish and Prentice 1980, Klein and Moeschberger 1997, Fox 2001). The model is of the form:

$$\ln(T) = \mathbf{X}\boldsymbol{\beta} + \sigma\epsilon,$$

where \mathbf{X} is an $n \times p$ matrix of explanatory variables for n observations and p variables, $\boldsymbol{\beta}$ is a $p \times 1$ vector of unknown parameters, σ is a scale parameter, and ϵ is a $n \times 1$ vector of random errors from a specified survival distribution that is independent of \mathbf{X} . In this study, I used a model in which T was defined as a Weibull distribution. This distribution is commonly used in survival analysis because it is flexible and appropriate for a range of monotonic survival functions (Kalbfleish and Prentice 1980, Klein and Moeschberger 1997, Fox 2001).

In the model, I tested explanatory variables reported to be important in previous studies of tree growth relative to canopy gaps (e.g. Canham 1988a, Canham et al. 1990). Tree-level variables were: species as a dummy variable, diameter in the year of release (cm), prior growth (cm^2), distance from the center of the gap (m), and an index of north-south tree position around or within the gap. Tree diameter in the year of release was calculated by subtracting rings formed after release to better represent diameter at coring height (inside bark) at the time of the event. Prior growth was mean basal area increment for the five years prior to the year of the peak percent-growth-change value associated with the onset the release. This variable was included because percent-growth change has been shown to decline exponentially as prior growth increases (Black and Abrams 2003, 2004). The gap center was the location of the root mound of the gapmaker. The north-south index was determined by calculating the cosine of the tree bearing relative to the gap center. Gap-level

variables were: area of the expanded gap (m^2), an index of north-south hillslope aspect (i.e. cosine of aspect), percent canopy openness, and percent hillslope gradient (Table 3.2). The expanded gap was defined by the boles of the trees whose crowns delineated the opening in the canopy (Runkle 1982). Canopy openness was determined from hemispherical photographs taken with a Nikon F 35-mm camera equipped with a Nikkor 8mm f/2.8 fisheye lens. At each gap, photos were taken a meter above the forest floor within quadrants established relative to the gap center and analyzed using Gap Light Analyzer, version 2.0 (Frazer et al. 1999). Results of the four photos were averaged to obtain a single value for canopy openness at each gap.

To determine which variables most influenced the duration of releases, I started with a model containing species, added tree-level then gap-level variables one at time, and tested for their significance. After entry of a variable, I subsequently tested its interaction with species. In addition, I tested the interaction of diameter in the year of release and prior growth. All significant ($P < 0.05$) terms were kept in the model, where the dummy variables for species or species by continuous variables were considered a single term. Tree diameter in the year of release and prior growth were transformed using the natural logarithm to improve model fit. All analyses were done using the LIFEREG procedure (SAS Institute Inc. 2007).

3.3.5. *Magnitude of releases*

I assessed the magnitude of releases according to the peak percent-growth-change value associated with the onset of each release. I used the GLM procedure (SAS Institute Inc. 2007) to construct a general linear model of percent-growth change, fitting in the same manner those variables used to assess the duration of releases. In addition to diameter in the

year of release and prior growth, percent-growth change was also transformed using the natural logarithm to improve model fit and normality of residuals.

3.4. Results

3.4.1. Number of trees and releases

There were 348 trees growing around or within the 20 study gaps. Trees were not evenly distributed among species and canopy positions, as indicated by the significant interaction of these variables (Table 3.3; $P < 0.001$). There were 87 western redcedar, 180 western hemlock, and 81 Pacific silver fir. Western redcedar and western hemlock occurred in the greatest numbers in the canopy, while the subcanopy was composed mostly of western hemlock and Pacific silver fir (Figure 3.3). Mean dbh was 141 ± 4.98 , 62 ± 2.55 , and 58 ± 3.52 cm for canopy western redcedar, western hemlock, and Pacific silver fir, respectively. Mean dbh was 41 ± 1.45 , 23 ± 0.85 , and 18 ± 0.79 cm for subcanopy western redcedar, western hemlock, and Pacific silver fir, respectively.

Table 3.3. Partial associations for the saturated log-linear model of species, canopy position, and release. Values in bold are significant at $P < 0.05$.

Variable	df	Wald χ^2	P
species	2	20.46	<0.001
canopy position	1	0.92	0.337
release	1	61.62	<0.001
species \times canopy position	2	42.44	<0.001
species \times release	2	5.20	0.074
canopy position \times release	1	0.05	0.816
species \times canopy position \times release	2	1.88	0.391

Note: species = western redcedar, western hemlock, or Pacific silver fir; canopy position = canopy or subcanopy; release = detected or not detected.

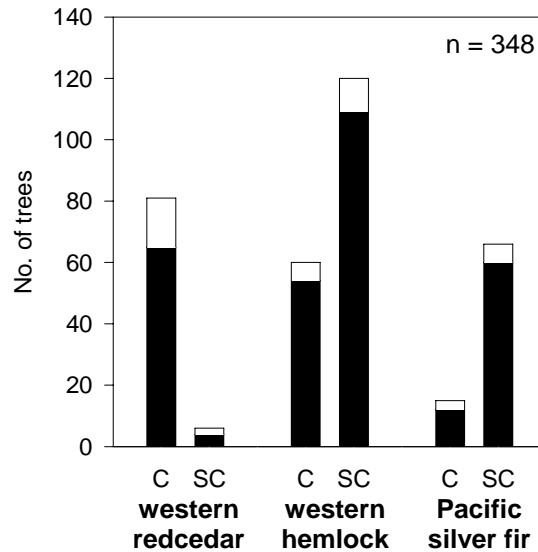


Figure 3.3. Frequency distribution of canopy (C) and subcanopy (SC) western redcedar, western hemlock, and Pacific silver fir growing around or within 20 gaps of known timing of origin. The number of trees that showed a release pattern following gap formation is depicted in black; trees that did not are in white.

A high number of western redcedar, western hemlock, and Pacific silver fir showed a release pattern following gap formation (Figure 3.3). In total, 87% (304 of 348) of all individuals had an increase in growth $\geq 25\%$ within 10 years of gap formation, a proportion that was significantly different from random (Table 3.3; $P < 0.001$). However, there was no evidence for a more complex interaction among the number of trees that released, species, or canopy position (Table 3.3; $P = 0.391$).

For the subset of six gaps for which I determined both year of death and fall of the gapmaker(s), a large number of trees showed a release pattern after both stages of gap formation (Table 3.4). Western hemlock had the highest number of releases, with 53% of the canopy and 38% of the subcanopy trees having had double release events. For western redcedar, 45% of the canopy trees released relative to both year of death and fall. Pacific

silver fir had the fewest double release events, with 22% of the subcanopy trees having had released.

Table 3.4. Percent of trees that showed a release pattern relative to year of death and fall for a subset of trees from six gaps.

Species	Canopy position	n	Releases detected relative to:			No release
			Year of death	Year of fall	Year of death and fall	
western redcedar	canopy	29	49	3	45	3
	subcanopy	2	100	0	0	0
western hemlock	canopy	17	47	0	53	0
	subcanopy	34	59	3	38	0
Pacific silver fir	canopy	3	100	0	0	0
	subcanopy	9	56	11	22	11

3.4.2. Duration of releases

For western hemlock, Pacific silver fir, and western redcedar, the median duration of releases was approximately 37, 26, and 21 years, respectively (Figure 3.4). There was a significant species \times logdiameter the year of release interaction (Table 3.5; $P = 0.045$), indicating that there were differences in the duration of releases among species. For western hemlock, increasing diameter resulted in decreasing duration of releases (Table 3.6; slope = -0.664). This pattern was opposite for western redcedar, as increasing diameter resulted in increasing duration of releases (Table 3.6; slope = 0.156). Pacific silver fir showed a pattern similar to western hemlock (Table 3.6; slope = -0.397). None of the other tree- or gap- level variables tested were significant and were not kept in the model.

3.4.3. Magnitude of releases

The magnitude of releases was greatest for western hemlock and Pacific silver fir (Figure 3.5a, b). Mean growth change of canopy trees was 136 and 191% for western hemlock and Pacific silver fir, respectively. For subcanopy trees, mean growth change was

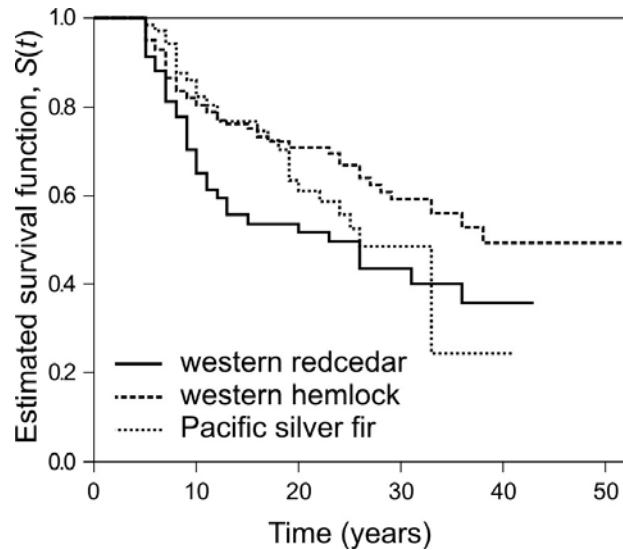


Figure 3.4. Survival functions $S(t)$ for duration of releases of western redcedar, western hemlock, and Pacific silver fir. $S(t)$ is the probability that a release will survive beyond time t , having survived to time t . The survival functions are nonparametric product-limit (Kaplan-Meier) estimates.

Table 3.5. Analysis of variance results for the Weibull survival model of duration of releases. Values in bold are significant at $P < 0.05$.

Variable	df	Deviance	Pr(Chi)
species	2	5.13	0.077
<i>logdiameter</i> the year of release	1	15.37	<0.001
species \times <i>logdiameter</i> the year of release	2	6.11	0.045

Note: Variables were added sequentially and are order dependent (see Methods). Species are western redcedar, western hemlock, and Pacific silver fir; *logdiameter* the year of release is the diameter of the tree at coring height (i.e. approximately 30 cm above the ground) in the year the release began.

191% for western hemlock and 199% for Pacific silver fir. Maximum growth change was > 1000% for western hemlock and > 800% for Pacific silver fir. These findings differ from those for western redcedar, for which maximum growth change was > 500%, and mean growth change was 83 and 98% for canopy and subcanopy trees, respectively (Figure 3.5a, b). While relative-growth change was lower for western redcedar, this species grew at an

Table 3.6. Parameter estimates for the Weibull survival model of duration of releases. Estimates are for levels of a given variable included in the model. Note: P-values for species or for species by continuous variable interactions should be interpreted for all species combined and were given in Table 3.5.

Variable	Coefficient	Standard error	<i>z</i>	<i>P</i>
intercept [§]	3.824	0.120	31.89	<0.001
species (Pacific silver fir)	-0.245	0.181	-1.36	0.174
species (western redcedar)	-0.376	0.170	-2.22	0.027
<i>logdiameter</i> the year of release ^{§†}	-0.664	0.152	-4.38	<0.001
Pacific silver fir × <i>logdiameter</i> the year of release	0.267	0.230	1.16	0.245
western redcedar × <i>logdiameter</i> the year of release	0.820	0.293	2.80	0.005

[§]Results with respect to western hemlock.

[†]Variable is centered at the corresponding species-specific mean.

Note: Species are western redcedar, western hemlock, and Pacific silver fir; *logdiameter* the year of release is the diameter of the tree at coring height (i.e. approximately 30 cm above the ground) in the year the release began.

overall faster rate both before and after release compared to western hemlock and Pacific silver fir (Figure 3.5a, b). All three species had variable growth rates (Figure 3.5a, b).

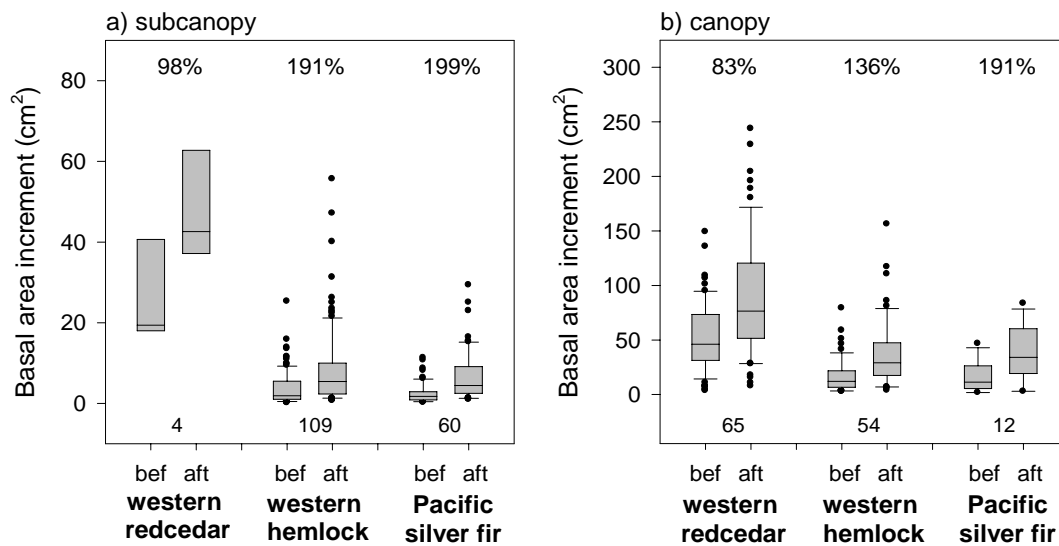


Figure 3.5. Box plots of mean basal area increment five years before (bef) and after (aft) release for (a) subcanopy and (b) canopy trees. Values at the top and bottom of the plots are mean percent-growth change and sample size, respectively. The horizontal line in each box is the median, the lower and upper limits of each box are the 25th and 75th percentiles, the lines are the 5th and 95th percentiles, and the circles are outliers.

Based on the general linear model, species and *logprior* growth explained a significant amount of variation in magnitude of release (Table 3.7; $P < 0.001$). The species \times *logdiameter* the year of release, species \times *logprior* growth, and *logdiameter* the year of release \times *logprior* growth interactions were also significant (Table 3.7; $P = 0.044$ to 0.001). None of the other tree- or gap- level variables, or three-way interactions, tested were significant and were not kept in the model.

Table 3.7. Analysis of variance results for the general linear model of magnitude of releases. Values in bold are significant at $P < 0.05$.

Variable	df	SS [†]	<i>F</i>	Pr(<i>F</i>)
species	2	20.50	23.47	<0.001
<i>logdiameter</i> the year of release	1	1.24	2.85	0.093
<i>logprior</i> growth	1	6.69	15.33	<0.001
species \times <i>logdiameter</i> the year of release	2	2.98	3.42	0.034
species \times <i>logprior</i> growth	2	2.76	3.16	0.044
<i>logdiameter</i> the year of release \times <i>logprior</i> growth	1	4.72	10.81	0.001

[†]Type III sums of squares.

Note: Variables were added sequentially and are order dependent (see Methods).

Species are western redcedar, western hemlock, and Pacific silver fir;

logdiameter the year of release is the diameter of the tree at coring height (i.e. approximately 30 cm above the ground) in the year the release began; *logprior* growth is mean basal area increment for the five years prior to the year of the peak-percent-growth change value associated with the onset of the release.

There was a pattern of decreasing percent-growth change with increasing diameter in the year of release and prior growth (Figure 3.6a, b). In addition, the effect of prior growth varied significantly among trees of different diameters (Tables 3.7 and 3.8; $P = 0.001$). For the largest diameter hemlock trees, prior growth had a minimal effect on percent-growth change. However, for the largest diameter Pacific silver fir and western redcedar trees, prior growth had a moderate effect, with higher values of prior growth resulting in lower values of percent-growth change. For the smallest diameter trees of all species, prior growth had a

more substantial effect, with higher values of prior growth resulting in lower values of percent-growth change, particularly for Pacific silver fir.

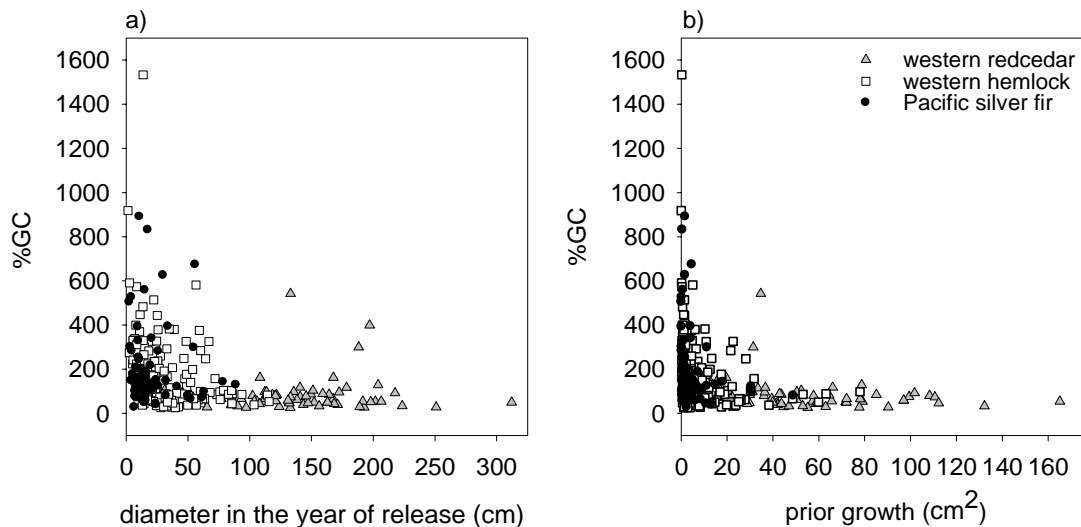


Figure 3.6. Plots of percent-growth change (%GC) with respect to (a) diameter in the year of release and (b) prior growth for western redcedar, western hemlock, and Pacific silver fir growing around or within 20 gaps of known timing of origin.

3.5. Discussion

3.5.1. Processes of gap formation

In coastal British Columbia, the formation of a gap from tree mortality is a spatially and temporally complex process. Larger, multi-tree gaps in forests of coastal British Columbia and other areas of northwestern North America often have gapmakers in varying stages of decay, implying differences in the timing of mortality of individual trees or small groups of trees and gradual gap expansion over time (Spies et al. 1990, Lertzman and Krebs 1991, Lertzman et al. 1996, Bartemucci et al. 2002, Ott and Juday 2002). Canopy gaps created by the death of single trees or the synchronous death of several trees are therefore at the beginning of the continuum of gap creation in coastal forests. These gaps represent the initial opening of the canopy at one point in space and time to create new conditions for

Table 3.8. Parameter estimates for the general linear model of magnitude of releases. Estimates are for levels of a given variable included in the model. Note: P-values for species or for species by continuous variable interactions should be interpreted for all species combined and were given in Table 3.7.

Variable	Coefficient	Standard error	<i>t</i>	<i>P</i>
intercept [§]	4.729	0.058	80.87	<0.001
species (Pacific silver fir)	0.200	0.094	2.13	0.034
species (western redcedar)	-0.540	0.098	-5.53	<0.001
<i>logdiameter</i> the year of release ^{§†}	-0.200	0.105	-1.89	0.059
<i>logprior</i> growth ^{§†}	-0.106	0.059	-1.78	0.075
Pacific silver fir × <i>logdiameter</i> the year of release	0.442	0.178	2.49	0.013
western redcedar × <i>logdiameter</i> the year of release	0.318	0.215	1.48	0.139
Pacific silver fir × <i>logprior</i> growth	-0.250	0.108	-2.31	0.022
western redcedar × <i>logprior</i> growth	-0.198	0.128	-1.55	0.123
<i>logdiameter</i> the year of release × <i>logprior</i> growth	0.110	0.033	3.29	0.001

[§]Results with respect to western hemlock.

[†]Variable is centered at the corresponding species-specific mean.

Note: $R^2 = 0.30$ and Akaike's information criterion (AIC) = 620.66; the full model with all non-significant terms included has an $R^2 = 0.32$ and an AIC = 625.83. Species are western redcedar, western hemlock, and Pacific silver fir; *logdiameter* the year of release is the diameter of the tree at coring height (i.e. approximately 30 cm above the ground) in the year the release began; *logprior* growth is mean basal area increment for the five years prior to the year of the peak-percent-growth change value associated with the onset of the release.

growth. The fine-scale canopy gaps in this study are a good point from which to begin to quantify growth change of trees as a result of gaps in these systems.

Besides being complex at the level of the gap, the process of gap formation is complex at the level of the individual tree. Gaps form by the death and fall of individual trees. Death can occur prior to fall or both can occur simultaneously, and these processes differ among species (Franklin et al. 1987). Tree death can include cambial dieback and crown senescence, leading to asymmetrical crowns over irregular time scales. Tree fall tends to be abrupt, yet can be more gradual when individual limbs snap off or whole trees get lodged on other trees while falling.

In coastal British Columbia, tree death prior to fall is very common, but the timing of these two processes differs among species. In general, death and fall occur more abruptly in western hemlock and Pacific silver fir than western redcedar. Western hemlock and Pacific silver fir often die standing (Lertzman and Krebs 1991, Hennon and McClellan 2003). Because wood decay fungi cause heart rot in live trees and rapid decay in dead trees (Kimmey 1956, Crawford and Oliver 1990, Hennon and McClellan 2003), these two species are susceptible to breakage prior to death or shortly afterward (Hennon and Loopstra 1991, Mattheck et al. 1994). Therefore, while gap formation is slow when trees die while standing, the mode of fall of western hemlock and Pacific silver fir can accelerate the process. For western redcedar, a higher proportion of gapmakers are uprooted, suggesting that gap formation is sudden compared to western hemlock and Pacific silver fir. Yet, many uprooted cedars exhibit partial cambial and crown dieback prior to falling. Partial cambial dieback is common in western redcedar (Daniels et al. 1997, Van Pelt 2001) and results in strips of dead cambium along the length of the bole alternating with strips of live cambium. Parts of the crown associated with the dead cambium die as well, causing the crown to die asymmetrically, with slow, cumulative decline over time. In reality, the formation of a canopy gap around a western redcedar snag, and many uprooted trees, can take several decades to more than a century (Daniels et al. 1997).

In this study, species-specific differences in processes of tree death and fall were important to consider when determining timing of gap formation using dendroecology. Western hemlock and Pacific silver fir were difficult to sample and crossdate, making many individual trees unsuitable for dendroecological analyses. Rapid decay subsequent to death limited opportunities to sample snags and logs that had recently died. Even those gapmakers

from which a sound core was sampled were very difficult to crossdate for year of the outermost ring due to the high frequency of suppression and release in these species (Daniels and Klinka 1996). In contrast, western redcedar is highly decay resistant (van der Kamp 1975, Jin et al. 1988), and thus easy to sample, and can be successfully crossdated. However, cambial dieback makes it difficult to assign a single year of death to each western redcedar gapmaker. Even with precise crossdating, accurately determining year of death requires corroborating evidence. For example, I collected cores from the least decayed areas around the circumference of the gapmakers and compared outermost-ring dates. In trees where the dates were consistent among cores, year of death was determined with confidence. In trees with cambial dieback, the dates were inconsistent among cores, and I used the most recent date to estimate year of death. For some gaps, cambial scars and reaction wood in trees damaged by gapmakers provided accurate dates for year of fall and thus secondary information on timing of formation (Dynesius and Jonsson 1991). Taken together, this information on cambial dieback and estimated years of death and fall is compelling evidence that gap formation involves multiple processes that occur over many years in old-growth forests of coastal British Columbia. The release of trees following both death and fall of gapmakers in this study highlights the influence of these gap-forming processes on tree growth and stand development through time.

3.5.2. Improving estimates of canopy disturbances

Radial-growth averaging (Henry and Swan 1974, Lorimer and Frelich 1989, Nowacki and Abrams 1997) is the standard method that uses releases caused by the death of overstory trees to reconstruct the frequency and intensity of past canopy disturbances (Rubino and McCarthy 2004). In some applications, the threshold (i.e. %GC) and moving average (i.e.

M_1 and M_2) parameters that constitute this method are modified to account for factors that influence tree growth and release potential, such as tree diameter, position in the canopy, species, growth rate prior to release, and interannual variation in climate. Threshold is the critical value of percent-growth change that represents a release. In most studies, threshold is a fixed value between 25 and 250%, with a lower value considered more appropriate for detecting the release of larger and/or less shade-tolerant tree species (Lorimer and Frelich 1989, Nowacki and Abrams 1997). Some studies apply a more flexible approach that allows threshold to vary as a function of growth rate prior to release, which is one of the most fundamental predictors of release potential (Black and Abrams 2003, 2004). The moving average parameter is usually set to screen out short-term reductions in radial growth and subsequent recovery resulting from adverse climatic conditions (Lorimer 1980, Lorimer and Frelich 1989, Nowacki and Abrams 1997). In most studies, moving average is a fixed period between 5 and 15 years, with a shorter period more likely to cause error when applied to detect the release of tree species that are sensitive to interannual variation in climate.

Using general guidelines to set the threshold and moving average parameters can be problematic and lead to false interpretations of stand history if, for a particular population of trees, they do not allow all growth releases (i.e. low/high magnitude and short/long duration) caused by the death of overstory trees to be detected. For example, a higher threshold and shorter moving average seem appropriate in this study because western redcedar, western hemlock, and Pacific silver fir are highly shade tolerant and not very sensitive to climatic variability (Chapter 2). Yet, a higher threshold, such as the commonly applied 100% threshold, will miss almost all the western redcedar releases. When radial-growth averaging was originally proposed, a 100% threshold was established to represent a proportional

increase in growth change of understory trees following the complete loss of overtopping canopy trees (Lorimer and Frelich 1989). Some studies fail to consider this relation of threshold with the amount of crown that is newly exposed on a surviving tree when setting the parameters of the radial-growth averaging method. Furthermore, trees of different species, size, and growth rate prior to release experience varying levels of percent-growth change, even with a 100% loss of overtopping canopy trees. In this study, I used a version of the radial-growth averaging method that was explicitly calibrated to detect the full range of growth releases that may occur for western redcedar, western hemlock, and Pacific silver fir following the formation of fine-scale gaps in old-growth stands. To establish this method, I assessed the influence of interannual variation in climate on growth and release potential and conducted a sensitivity analysis on the influence of the parameters of the radial-growth averaging method on the number of trees that showed a release pattern following gap formation (Chapter 2). Because the study species are responsive to fine-scale disturbances, and the moving average and threshold parameters are inclusive to detect short to long duration growth increases just above those caused by climate, 87% of all trees released. Setting the parameters of the radial-growth averaging method to detect a more complete range of releases that may occur for the population of trees in a stand, relative to the type of disturbance in question, is crucial for reducing error when reconstructing stand history.

In addition to detecting the release of trees following the formation of a gap, my approach provides techniques for quantifying release attributes useful for more precisely estimating past canopy disturbances. Magnitude measures the initial growth increase during the first five years of release. Duration measures the persistence of the growth increase. This detailed information from trees growing around or within gaps of known timing of origin

goes beyond the traditional binary classification of release or no release and allows for inferences about the type of gap and tree location relative to the gap. For example, a release of high magnitude and long duration suggests that the gap formed abruptly and was large, either initially or became so through expansion. The released tree might have been small in diameter, growing slowly prior to the gap forming, or located close to the center of the gap. Conversely, a release of low magnitude and short duration suggests that the gap resulted from dieback or damage to the crown and/or was small. For a release with these qualities, the tree might have been large in diameter, growing quickly prior to the gap forming, or located further away from the center of the gap. These inferences about the type of gap and tree location relative to the gap will permit historic gap boundaries to be more precisely estimated. The sample data showed a trend of decreasing magnitude and duration of release with increasing tree distance from the center of the gap. However, the lack of a statistically significant influence of many tree- and gap-level variables on magnitude and duration of release might reflect the low variability in gap characteristics and the small number of gaps from which trees were sampled.

3.5.3. Reconstructing the history of canopy disturbances

The history of canopy disturbances for a stand is often reconstructed by coring all live trees and identifying growth releases using radial-growth averaging with objectively defined criteria. In this approach, every release is assumed to indicate a disturbance to the canopy and thus the formation or expansion of a gap. For example, Daniels and Klinka (1996) used this standard approach to reconstruct stand dynamics of coastal, old-growth forests in my study area. Their objectives were to compare and contrast the growth of canopy trees (dbh > 10 cm) and determine whether western redcedar, western hemlock, and Pacific silver fir

relied on canopy gaps to reach the upper canopy. Following the moderate criteria of Lorimer and Frelich (1989), they defined a release as a growth increase of $> 50\%$, compared to the mean growth of the previous 10 years, that was sustained for at least 10 years. Based on my results, these criteria will underestimate the release of western redcedar in these stands, which are mostly canopy-dominant trees, and lead to misinterpretation of the frequency of past canopy disturbances.

To improve upon the study by Daniels and Klinka (1996), I recommend the following approach. First, calibrate the release of trees relative to natural, extant canopy gaps to generate species- and ecosystem-specific criteria. Second, use these criteria to identify all releases in ring-width series of individual trees and quantify the duration and magnitude of each release. Third, determine the spatial distribution of trees that released at similar times to estimate preliminary sizes and boundaries of gaps. Fourth, verify gaps in the field. Steps three and four involve both a spatial and temporal component. Spatially, determine if there is a gapmaker within the estimated boundary of the gap. Temporally, determine the species and decay class of the gapmaker and if it can be crossdated to year of death and/or fall. Information on species and decay class provides a general estimate of time since death, and crossdating provides a more precise estimate; both estimates can be compared to the dates of release of nearby trees. Combined, this spatial and temporal information can be used to verify whether canopy disturbance caused the release of nearby trees. Steps three and four can be done sequentially or together, where information on both live and dead trees is collected at the same time. Either way, both approaches require a final field check to verify the presence of gaps and release of nearby trees. Besides release of tree-size individuals, information on the initial or long-term growth of seedlings and saplings can be collected to

better characterize stand disturbance history. Ultimately, a detailed understanding of the spatial and temporal aspects of gap dynamics over long time spans will permit inferences of rates of gap formation, expansion, and closure.

3.5.4. Gap dynamics and species coexistence

Various mechanisms, including differences in life-history traits, environmental heterogeneity facilitated by recent and ancient disturbances, and competition between neighbors, can act alone or together to promote the coexistence of tree species (Denslow 1980, Veblen 1986, Canham 1989, Lertzman 1992, Lusk and Smith 1998, Chesson 2000, Loehle 2000, Nakashizuka 2001, Nishimura et al. 2005, Mori et al. 2007). Chance events and neutral processes can also play a role in structuring patterns of tree diversity (Brokaw and Busing 2000, Hubbell 2001, Wright 2002), but might be more important in species-rich communities (Nakashizuka 2001, Gravel et al. 2006).

In forests where fine-scale tree mortality and canopy gaps dominate the disturbance regime, differing strategies for ascending to the canopy strata may contribute to the coexistence of tree species. For shade-tolerant trees, Canham (1988b, 1989, 1990) describes two extremes in patterns for reaching the canopy strata. At one end of the continuum, trees reach the canopy strata through continuous slow growth in more shaded conditions. These trees can be considered gap independent, because by definition, they likely do not rely on gaps to reach the canopy. At the other end of the continuum, trees reach the canopy strata through multiple periods of suppression and release due to canopy gaps. These trees can be considered gap dependent, because they likely require gaps to reach the canopy.

In previous work on the influences of disturbance in old-growth stands within my study area, Daniels (2003) concluded that western redcedar was gap independent and western

hemlock and Pacific silver fir were gap dependent. My results do not support western redcedar as entirely gap independent, because a similar number of western redcedar, western hemlock, and Pacific silver fir released following gap formation. However, variation in the magnitude and duration of releases among the study species does suggest subtle, but biologically relevant, differences in how they respond to gaps and potentially grow into the canopy strata.

Western hemlock and Pacific silver fir were often extremely suppressed both in the canopy and subcanopy, which gave them tremendous potential to release (Black and Abrams 2003, 2004). For these species, the release magnitudes following the formation of a gap were high, with maximum values $> 1000\%$. The releases were also persistent, with durations slightly longer for western hemlock than for Pacific silver fir. These observations are consistent with independent research in old-growth stands on population size structures and growth histories in the understory. Specifically, western hemlock and Pacific silver fir produce a continuous seedling and sapling bank of individuals available to release if or when a gap forms (Lertzman 1992, Daniels 1994, Coates 2002, Parish and Antos 2004, 2006, Antos et al. 2005), and both species are able to undergo multiple episodes of suppression and release before reaching the canopy (Taylor 1990, Daniels and Klinka 1996, Wright et al. 2000, Passmore 2007). Taken together, these characteristics distinguish western hemlock and Pacific silver fir as gap-dependent species.

In contrast, western redcedar had high absolute growth rates both in the canopy and subcanopy, so had less potential to release as intensively as western hemlock or Pacific silver fir. Releases of low magnitude and short duration were most common for western redcedar, which partly reflected its large size in the stand. Low-intensity releases also indicate

physiological differences in growth rates and responses to gaps compared to western hemlock and Pacific silver fir. High growth rates for subcanopy western redcedar prior to gap formation and release suggest that gaps are less important for reaching the canopy strata. Yet, the high number of western redcedar that released following gap formation, even large, canopy dominants, implies complex tree interactions mediated by gaps, including competition for light and other limiting resources. To better understand the role of gaps for canopy ascendancy and growth of western redcedar will require additional research specifically focused on subcanopy individuals, which are lacking in this study because of the population size structures in these forests. Until more information is collected, it is difficult to place western redcedar along the continuum of gap independent to dependent.

Differing strategies for ascending to the canopy strata is one of several mechanisms that may contribute to tree species coexistence in old-growth forests of coastal British Columbia. Given the large discrepancy in potential adult lifespan of the study species, hypotheses related to longevity and canopy residence time also need to be considered. Specifically, western redcedar lives much longer than western hemlock or Pacific silver fir, and this life-history trait might play a crucial role in maintaining a seed source for when conditions are most favorable for its growth into the canopy strata (Lertzman 1992, 1995, Lusk and Smith 1998, Parish and Antos 2004, 2006, Mori et al. 2007). Competitive interactions among tree species might also be important. For forests of northern British Columbia, Canham et al. (2004) reported that crowding by western hemlock had a strong effect on the radial growth of western redcedar, but crowding by western redcedar had little effect on growth of western hemlock. Lack of equivalence of interspecific effects of

competition and any possible impacts on coexistence is worth exploring in coastal British Columbia.

3.6. Conclusions

Detailed information on growth release of trees following the formation of natural, extant canopy gaps can be useful for more accurately reconstructing past canopy disturbances. By first calibrating the radial-growth averaging method to detect release following gap formation, and then quantifying more detailed attributes of release, one can begin to understand processes of disturbance and tree response to these processes. In old-growth forests of coastal British Columbia, gap forming processes are complex and trees are sensitive to these processes. Understanding differences in modes of gap formation and growth release among western redcedar, western hemlock, and Pacific silver fir is crucial for precisely estimating past canopy disturbances. In these forests, as well as others, approaches for reconstructing stand disturbances that begin at the level of individual gaps and releases can lead to a better understanding of rates of gap formation, expansion, and closure.

Besides aiding in accurate stand reconstructions, a detailed understanding of growth release following gap formation permits assessing the importance of gaps for the coexistence of tree species. Western redcedar, western hemlock, and Pacific silver fir all showed measurable growth releases following the formation of fine-scale gaps. Differences in the magnitude and duration of releases were subtle among these species. However, these differences do suggest that gaps play important, but possibly different, roles in the population dynamics of each species.

3.7. Literature cited

- Acres International Limited. 1999. Annex to the Analysis Report, Watershed Management Plan #5, Volumes I-III. Greater Vancouver Regional District Watershed Ecological Inventory Program, Burnaby, British Columbia, Canada.
- Antos, J.A., H.J. Guest, and R. Parish. 2005. The tree seedling bank in an ancient montane forest: stress tolerators in a productive habitat. *Journal of Ecology* 93:536-543.
- Arsenault, A. 1995. Pattern and process in old-growth temperate rainforests of southern British Columbia. Ph.D. dissertation. University of British Columbia, Vancouver, British Columbia, Canada.
- Bartemucci, P., K.D. Coates, K.A. Harper, and E.F. Wright. 2002. Gap disturbances in northern old-growth forests of British Columbia, Canada. *Journal of Vegetation Science* 13:685-696.
- Beaudet, M., J. Brisson, D. Gravel, C. Messier. 2007. Effect of a major canopy disturbance on the coexistence of *Acer saccharum* and *Fagus grandifolia* in the understorey of an old-growth forest. *Journal of Ecology* 95:458-467.
- Beckage, B. and J.S. Clark. 2003. Seedling survival and growth of three forest tree species: the role of spatial heterogeneity. *Ecology* 84:1849-1861.
- Black B.A. and M.D. Abrams. 2003. Use of boundary-line growth patterns as a basis for dendroecological release criteria. *Ecological Applications* 13:1733-1749.
- Black B.A. and M.D. Abrams. 2004. Development and application of boundary-line release criteria. *Dendrochronologia* 22:31-42.

- Brokaw, N. and R.T. Busing. 2000. Niche versus chance and tree diversity in forest gaps. *Trends in Ecology and Evolution* 15:183-188.
- Canham, C.D. 1988a. An index for understory light levels in and around canopy gaps. *Ecology* 69:1634-1638.
- Canham, C.D. 1988b. Growth and canopy architecture of shade-tolerant trees: response to canopy gaps. *Ecology* 69:786-795.
- Canham, C.D. 1989. Different responses to gaps among shade-tolerant tree species. *Ecology* 70:548-550.
- Canham, C.D. 1990. Suppression and release during canopy recruitment in *Fagus grandifolia*. *Bulletin of the Torrey Botanical Club* 117:1-7.
- Canham, C.D., J.S. Denslow, W.J. Platt, J.R. Runkle, T.A. Spies, and P.S. White. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. *Canadian Journal of Forest Research* 20:620-631.
- Canham, C.D., P.T. LePage, and K.D. Coates. 2004. A neighborhood analysis of canopy tree competition: effects of shading versus crowding. *Canadian Journal of Forest Research* 34:778-787.
- Carter, R.E. and K. Klinka. 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.
- Chesson, P. 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* 31:343-366.

- Coates, K.D. 2002. Tree recruitment in gaps of various size, clearcuts and undisturbed mixed forest of interior British Columbia, Canada. *Forest Ecology and Management* 155:387-398.
- Collett, D. 2003. *Modelling survival data in medical research*. Chapman and Hall/CRC, Boca Raton, Florida, USA.
- Crawford, P.D. and C.D. Oliver. 1990. Pacific silver fir. *In* R.M. Burns and B.H. Honkala, technical coordinators. *Silvics of North America: Volume 1 Conifers*. USDA Forest Service, Agriculture Handbook 654.
- Daniels, L.D. 1994. Structure and regeneration of old-growth *Thuja plicata* stands near Vancouver, British Columbia. M.Sc. thesis. University of British Columbia, Vancouver, British Columbia, Canada.
- Daniels, L.D. 2003. Western redcedar population dynamics in old-growth forests: contrasting ecological paradigms using tree rings. *Forestry Chronicle* 79:517-530.
- Daniels, L.D., J. Dobry, K. Klinka, and M.C. Feller. 1997. Determining year of death of logs and snags of *Thuja plicata* in southwestern coastal British Columbia. *Canadian Journal of Forest Research* 27:1132-1141.
- Daniels, L.D. and R.W. Gray. 2006. Disturbance regimes in coastal British Columbia. *BC Journal of Ecosystems and Management* 7:44-56.
- Daniels, L.D. and K. Klinka. 1996. The dynamics of old-growth *Thuja-Tsuga* forests near Vancouver, British Columbia. Pages 379-393 *in* J.S. Dean, D.M. Meko, and T.W. Swetnam, editors. *Tree rings, environment, and humanity*.

- Denslow, J.S. 1980. Gap partitioning among tropical rainforest trees. *Biotropica* 12(Suppl):47-55.
- Dungan, R.J, R.P. Duncan, and D. Whitehead. 2003. Investigating leaf lifespans with interval-censored failure time analysis. *New Phytologist* 158:593-600.
- Dynesius, M. and B.G. Jonsson. 1991. Dating uprooted trees: comparison and application of eight methods in a boreal forest. *Canadian Journal of Forest Research* 21:655-665.
- Fox, G.A. 2001. Failure-time analysis: studying times to events and rates at which events occur. Pages 235-266 in S.M. Scheiner and J. Gurevitch, editors. *Design and analysis of ecological experiments*. Oxford University Press, New York, New York, USA.
- Franklin, J.F., H.H. Shugart, and M.E. Harmon. 1987. Tree death as an ecological process: the causes, consequences, and variability of tree mortality. *Bioscience* 37:550-556.
- Fraver, S. and A.S. White. 2005a. Identifying growth releases in dendrochronological studies of forest disturbance. *Canadian Journal of Forest Research* 35:1648-1656.
- Fraver, S. and A.S. White. 2005b. Disturbance dynamics of old-growth *Picea rubens* forests of northern Maine. *Journal of Vegetation Science* 16:597-610.
- Frazer, G.W., C.D. Canham, and K.P. Lertzman. 1999. Gap light analyzer (GLA), version 2.0: imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs. Simon Fraser University, Burnaby, British Columbia, Canada and the Institute of Ecosystem Studies, Millbrook, New York, USA.

- Frelich, L.E. 2002. Forest dynamics and disturbance regimes: studies from temperate evergreen-deciduous forests. Cambridge University Press, Cambridge, UK.
- Frelich, L.E. and C.G. Lorimer. 1991. Natural disturbance regimes in hemlock-hardwood forests of the upper Great Lakes region. *Ecological Monographs* 61:145-164.
- Fritts, H.C. 1976. Tree rings and climate. Academic Press, New York, New York, USA.
- Gavin, D.G, L.B. Brubaker, and K.P. Lertzman. 2003. Holocene fire history of a coastal temperate rain forest based on soil charcoal radiocarbon dates. *Ecology* 84:186-201.
- Gravel, D., C.D. Canham, M. Beaudet, C. Messier. 2006. Reconciling niche and neutrality: the continuum hypothesis. *Ecology Letters* 9:399-409.
- Grissino-Mayer H.D. 2001. Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. *Tree-Ring Research* 57:205-221.
- Gutiérrez, A.G., J.J. Armesto, and J. Aravena. 2004. Disturbance and regeneration dynamics of an old-growth North Patagonian rain forest in Chiloé Island, Chile. *Journal of Ecology* 92:598-608.
- He, F. and R.I. Alfaro. 2000. White pine weevil attack on white spruce: a survival time analysis. *Ecological Applications* 10:225-232.
- Hennon, P.E. and E.M. Loopstra. 1991. Persistence of western hemlock and western redcedar trees 38 years after girdling at Cat Island in southeast Alaska. USDA Forest Service, Research Note PNW-RN-507.
- Hennon, P.E. and M.H. McClellan. 2003. Tree mortality and forest structure in the temperate rain forests of southeast Alaska. *Canadian Journal of Forest Research* 33:1621-1634.

- Henry, J.D. and J.M.A. Swan. 1974. Reconstructing forest history from live and dead plant material - an approach to the study of forest succession in southwest New Hampshire. *Ecology* 55:772-783.
- Holmes, R.L. 1983. Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bulletin* 43:69-78.
- Hubbell, S.P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, New Jersey, USA.
- Ishikawa, Y., P.V. Krestov, K. Namikawa. 1999. Disturbance history and tree establishment in old-growth *Pinus koraiensis*-hardwood forests in the Russian Far East. *Journal of Vegetation Science* 10:439-448.
- Jin, L., B.J. van der Kamp, J. Wilson, and E.P. Swan. 1988. Biodegradation of thujaplicins in living western red cedar. *Canadian Journal of Forest Research* 18:782-786.
- Johnson, E.A. and S.L. Gutsell. 1994. Fire frequency models, methods and interpretations. *Advances in Ecological Research* 25:239-287.
- Kalbfleisch, J.D. and R.L. Prentice. 1980. The statistical analysis of failure time data. John Wiley and Sons, New York, New York, USA.
- Kaplan, E.L. and P. Meier. 1958. Nonparametric estimation from incomplete observations. *Journal of the American Statistical Association* 53:457-481.
- Kimmey, J.W. 1956. Cull factors for Sitka spruce, western hemlock, and western red-cedar in southeast Alaska. USDA Forest Service, Alaska Forest Research Center, Station Paper 6.

- Klein, J.P. and M.L. Moeschberger. 1997. Survival analysis: techniques for censored and truncated data. Springer-Verlag, New York, New York, USA.
- Klinka, K., R.E. Carter, and M.C. Feller. 1990. Cutting old-growth forests in British Columbia: ecological considerations for forest regeneration. Northwest Environmental Journal 6:221-242.
- Lafon, C.W. and J.H. Speer. 2002. Using dendrochronology to identify major ice storm events in oak forests of southwestern Virginia. Climate Research 20:41-54.
- Lee, E.T. and J.W. Wang. 2003. Statistical methods for survival data analysis. John Wiley and Sons, Hoboken, New Jersey, USA.
- Lertzman, K.P. 1992. Patterns of gap-phase replacement in a subalpine, old-growth forest. Ecology 73:657-669.
- Lertzman, K.P. 1995. Forest dynamics, differential mortality and variable recruitment probabilities. Journal of Vegetation Science 6:191-204.
- Lertzman, K., D. Gavin, D. Hallett, L. Brubaker, D. Lepofsky, and R. Mathewes. 2002. Long-term fire regime estimated from soil charcoal in coastal temperate rainforests. Conservation Ecology 6:5. [online] URL: <http://www.consecol.org/vol6/iss2/art5>.
- Lertzman, K.P. and C.J. Krebs. 1991. Gap-phase structure of a subalpine old-growth forest. Canadian Journal of Forest Research 21:1730-1741.
- Lertzman, K.P., G.D. Sutherland, A. Inselberg, and S.C. Saunders. 1996. Canopy gaps and the landscape mosaic in a coastal temperate rain forest. Ecology 77:1254-1270.
- Loehle, C. 2000. Strategy space and the disturbance spectrum: a life-history model for tree species coexistence. American Naturalist 156:14-33.

- Lorimer, C.G. 1980. Age structure and disturbance history of a southern Appalachian virgin forest. *Ecology* 61:1169-1184.
- 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 L.E. Frelich. 1989. A methodology for estimating canopy disturbance frequency and intensity in dense temperate forests. *Canadian Journal of Forest Research* 19:651-663.
- Lusk, C.H. and B. Smith. 1998. Life history differences and tree species coexistence in an old-growth New Zealand rain forest. *Ecology* 79:795-806.
- Maser, C., R.G. Anderson, K. Cromack, Jr., J.T. Williams, and R.E. Martin. 1979. Dead and down woody material. Pages 78-95 *in* J.W. Thomas, editor. *Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington*. USDA Forest Service, Agriculture Handbook 553.
- Mattheck, C., K. Bethge, and P.W. West. 1994. Breakage of hollow tree stems. *Trees – structure and function* 9:47-50.
- Meidinger, D.V. and J. Pojar, editors. 1991. *Ecosystems of British Columbia*. Special Report Series 6. British Columbia Ministry of Forests, Victoria, British Columbia, Canada.
- Merrens, E.J. and D.R. Peart. 1992. Effects of hurricane damage on individual growth and stand structure in a hardwood forest in New Hampshire, USA. *Journal of Ecology* 80:787-795.

- Monger, J.W.H. and J.M. Journeay. 1994. Guide to the geology and tectonic evolution of the southern Coast Mountains. Open File 2490. Geological Survey of Canada, Vancouver, British Columbia, Canada.
- Mori, A.S., E. Mizumachi, and A. Komiyama. 2007. Roles of disturbance and demographic non-equilibrium in species coexistence, inferred from 25-year dynamics of a late-successional old-growth subalpine forest. *Forest Ecology and Management* 241:74-83.
- Nakashizuka, T. 2001. Species coexistence in temperate, mixed deciduous forests. *Trends in Ecology and Evolution* 16:205-210.
- Nishimura, N., T. Hara, M. Kawatani, D. Hoshino, and S. Yamamoto. 2005. Promotion of species co-existence in old-growth coniferous forest through interplay of life-history strategy and tree competition. *Journal of Vegetation Science* 16:549-558.
- Norton, D.A., J.G. Palmer, and J. Ogden. 1987. Dendroecological studies in New Zealand 1. An evaluation of tree age estimates based on increment cores. *New Zealand Journal of Botany* 25:373-383.
- Nowacki, G.J. and M.D. Abrams. 1997. Radial-growth averaging criteria for reconstructing disturbance histories from presettlement-origin oaks. *Ecological Monographs* 67:225-249.
- Orwig, D.A. and M.D. Abrams. 1994. Contrasting radial growth and canopy recruitment patterns in *Liriodendron tulipifera* and *Nyssa sylvatica*: gap-obligate versus gap-facultative tree species. *Canadian Journal of forest Research* 24:2141-2149.

- Ott, R.A. and G.P. Juday. 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 J.A. Antos. 2004. Structure and dynamics of an ancient montane forest in coastal British Columbia. *Oecologia* 141:562-576.
- Parish, R. and J.A. Antos. 2006. Slow growth, long-lived trees, and minimal disturbance characterize the dynamics of an ancient, montane forest in coastal British Columbia. *Canadian Journal of Forest Research* 36:2826-2838.
- Passmore, J.A. 2007. Response of seedlings and saplings to canopy gaps in coastal old-growth forests. M.R.M. thesis, Simon Fraser University, Burnaby, British Columbia, Canada.
- Payette, S., L. Filion, and A. Delwaide. 1990. Disturbance regime of a cold temperate forest as deduced from tree-ring patterns: the Tantaré Ecological Reserve, Quebec. *Canadian Journal of Forest Research* 20:1228-1241.
- Rozas, V. 2003. Regeneration patterns, dendroecology, and forest-use history in an old-growth beech-oak lowland forest in Northern Spain. *Forest Ecology and Management* 182:175-194.
- Rubino, D.L. and B.C. McCarthy. 2004. Comparative analysis of dendroecological methods used to assess disturbance events. *Dendrochronologia* 21:97-115.
- Runkle, J.R. 1982. Patterns of disturbance in some old-growth mesic forests of eastern North America. *Ecology* 63:1533-1546.

- Ryder, J.M. 1981. Geomorphology of the southern part of the Coast Mountains of British Columbia. *Zeitschrift für Geomorphologie* 37:120-147.
- SAS Institute Inc. 2007. SAS OnlineDoc[®] 9.1.3, SAS Institute Inc., Cary, North Carolina, USA.
- Smith, K.T. and W.C. Shortle. 2002. Radial growth of hardwoods following the 1998 ice storm in New Hampshire and Maine. *Canadian Journal of Forest Research* 33:325-329.
- Sousa, W.P. 1984. The role of disturbance in natural communities. *Annual Review of Ecology and Systematics* 15:353-391.
- Spies, T.A., J.F. Franklin, and M. Klopsch. 1990. Canopy gaps in Douglas-fir forests of the Cascade Mountains. *Canadian Journal of Forest Research* 20:649-658.
- Stokes, M.A. and T.L. Smiley. 1968. An introduction to tree-ring dating. University of Chicago Press, Chicago, Illinois, USA.
- Taylor, A.H. 1990. Disturbance and persistence of sitka spruce (*Picea sitchensis* (Bong) Carr.) in coastal forests of the Pacific Northwest, North America. *Journal of Biogeography* 17:47-58.
- Taylor, A.H., S.W. Jang, L.J. Zhao, C.P. Liang, C.J. Miao, and J Huang. 2006. Regeneration patterns and tree species coexistence in old-growth *Abies-Picea* forests in southwestern China. *Forest Ecology and Management* 223:303-317.
- Thompson, R.D., L.D. Daniels, and K.J. Lewis. 2007. A new dendroecological method to differentiate growth responses to fine-scale disturbance from regional-scale environmental variation. *Canadian Journal of Forest Research* 37:1034-1043.

- Valentine, K.W.G., P.N. Sprout, T.E. Baker, and L.M. Lavkulich, editors. 1978. The soil landscapes of British Columbia. British Columbia Ministry of Environment, Victoria, British Columbia, Canada.
- van der Kamp, B.J. 1975. The distribution of microorganisms associated with decay of western red cedar. *Canadian Journal of Forest Research* 5:61-67.
- Van Pelt, R. 2001. Forest giants of the Pacific coast. University of Washington Press, Seattle, Washington, USA.
- Veblen, T.T. 1986. Treefalls and the coexistence of conifers in subalpine forests of the central Rockies. *Ecology* 67:644-649.
- Wang, T., A. Hamann, D.L. Spittlehouse, and S.N. Aitken. 2006. Development of scale-free climate data for western Canada for use in resource management. *International Journal of Climatology* 26:383-397.
- Wells, R.W., K.P. Lertzman, and S.C. Saunders. 1998. Old-growth definitions for the forests of British Columbia, Canada. *Natural Areas Journal* 18:279-292.
- White, P.S. and Pickett, S.T.A. 1985. Natural disturbance and patch dynamics: an introduction. Pages 3-13 *in* S.T.A. Pickett and P.S. White, editors. The ecology of natural disturbance and patch dynamics. Academic Press, New York, New York, USA.
- Wright, S.J. 2002. Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia* 130:1-14.

- Wright, E.F., C.D. Canham, and K.D. Coates. 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.
- Yamaguchi, D.K. 1991. A simple method for cross-dating increment cores from living trees. *Canadian Journal of Forest Research* 21:414-416.
- Ziegler, S.S. 2002. Disturbance regimes of hemlock-dominated old-growth forests in northern New York, U.S.A. *Canadian Journal of Forest Research* 32:2106-2115.

4. Growth release across a natural canopy gap-forest gradient in old-growth forests of coastal British Columbia¹

4.1. Introduction

In many forests, fine-scale tree death that creates gaps in the canopy is a dominant natural disturbance that affects the growth of nearby plants (White and Pickett 1985, Frelich 2002). The influence of a canopy gap on growth depends both on the changes in resources available to individual plants and the capacity of plants to respond to the changes in resources (Canham and Marks 1985).

At higher latitudes, changes in environmental conditions and resources available for plant growth following gap formation are often most pronounced along the north-south axis of canopy gaps (Canham et al. 1990). In the case of tree species, studies have assessed the establishment and/or growth of seedlings and saplings according to north-south position around or within natural (e.g. Runkle et al. 1995, Kneeshaw and Bergeron 1999) and artificial (e.g. Gray and Spies 1996, 1997, Van Pelt and Franklin 1999, Coates 2000, 2002, Collins and Battaglia 2002, York et al. 2003) canopy gaps. Fewer studies have considered the growth of canopy and subcanopy trees relative to north-south position (e.g. Jones and Thomas 2004, Pedersen and Howard 2004) or canopy gaps in general (e.g. Poage and Peart 1993). When a canopy gap forms, larger trees might not respond to the same degree as smaller trees, because larger trees are less likely to be limited by competition for resources or might not be as capable of increasing their growth due to physiological constraints. In

¹ A version of this chapter will be submitted for publication. Stan, A.B. and Daniels, L.D. Growth release across a natural canopy gap-forest gradient in old-growth forests of coastal British Columbia.

addition to tree size, other factors such as species, health, nearness to a canopy gap, and the spatial arrangements of nearby trees will likely influence the growth response of a tree following gap formation.

In recent decades, approaches to forest management have shifted towards better emulating natural disturbance regimes for the purpose of sustaining the structure and function of ecosystems (Christensen et al. 1996, Landres et al. 1999). Variable retention (Scientific Panel for Sustainable Forest Practices in Clayoquot Sound 1995, Franklin et al. 1997) is an approach to harvesting and silvicultural systems that has been incorporated into forestry operations throughout coastal British Columbia as a way to address objectives of ecosystem management (Mitchell and Beese 2002, Beese et al. 2003). Variable retention attempts to emulate the patchiness of natural disturbances by retaining structural and compositional attributes of mature or old forests, in varying amounts and spatial arrangements, within stands that are actively managed for timber and other values. High-retention harvesting is commonly applied in areas considered especially sensitive or difficult to harvest because of critical wildlife habitat, ecological or cultural values, or terrain features. In these areas, harvesting is often done at the scale of single trees or small groups of trees, using techniques such as “standing-stem harvesting” (see Beese et al. 2003). While the openings created by this technique may be structurally similar to the fine-scale canopy gaps that dominate the natural disturbance regime of the wetter forests of coastal British Columbia (Lertzman et al. 2002, Daniels and Gray 2006), uncertainty remains as to whether they mimic other important processes associated with natural gaps. For example, it is unknown whether the shade-tolerant trees that constitute the old-growth forests that developed at landscape scales

throughout coastal British Columbia over long periods of fine-scale gap processes show the same growth response following the formation of harvested versus natural gaps.

In a previous study (Chapter 3), I investigated growth releases (i.e. abrupt increases in radial growth) of canopy and subcanopy trees growing around the boundary of, or within, natural canopy gaps of known timing of origin in old-growth, western redcedar-western hemlock forests of coastal British Columbia. I found that the magnitude and duration of releases following gap formation were influenced by tree diameter, growth rate prior to release, and identity of the tree species, but patterns related to tree position relative to the gap were less clear. Therefore, the objectives of this study were to use additional data to determine attributes of growth releases along north-south transects that passed through the gaps and into the adjacent forest, and to evaluate this information for forest management. I addressed the study objectives by (1) quantifying the number of trees growing along the north-south transect that showed a release pattern following gap formation and quantifying the duration and magnitude of those releases, and (2) estimating the influence of tree position relative to the gap center, in addition to tree diameter, growth rate prior to release, and species, on duration and magnitude of releases along north-south transects. Detailed information on the growth release of trees of different size, species, and position following the formation of natural canopy gaps is important for developing and assessing variable retention approaches that aim to mimic natural range of variation.

4.2. Study area

I conducted this research in the Capilano, Seymour, and Coquitlam River watersheds in the Coast Mountains of southwestern British Columbia (Figure 4.1). These drainages encompass an area of approximately 58,500 ha that is managed by Metro Vancouver for

water supply to municipalities in the greater Vancouver area. In the past, processes of glacial erosion impacted the area and helped create the overall rugged topography and steep slopes that exist today (Ryder 1981). Relief in the watersheds ranges from 1300 to 1600 m, and slopes commonly exceed 35°, particularly at higher elevations. Across the terrain, several ecosystem types occur that are typical of those present throughout coastal British Columbia. Using the Biogeoclimatic Ecosystem Classification system of British Columbia, these include the Coastal Western Hemlock, Mountain Hemlock, and Alpine Tundra zones (Meidinger and Pojar 1991).

I restricted the study sites to mid-elevation (300-700 m a.s.l.), old-growth forests within the watersheds. The sites are located in the Very Wet Maritime subzone of the Coastal Western Hemlock zone, which has a wet, humid climate, with cool summers and mild winters (Meidinger and Pojar 1991). Based on spatially-interpolated monthly climate normals for the period 1961-1990 (Wang et al. 2006), mean annual temperature at all study sites ranged from 6.0 to 7.5°C, with a mean of 15 to 16°C in August and -1 to 1°C in December. Total annual precipitation was between 3000 to 4000 mm. Total growing season (May to September) precipitation ranged from 600 to 800 mm. At all study sites, soils are mostly Humo-Ferric Podzols derived from colluvium and glacial till (Valentine et al. 1978). Sites are located on Coast Plutonic Complex intrusions of Mid-Cretaceous quartz diorite in Capilano and Seymour and of Late-Jurassic to Early-Cretaceous quartz diorite in Coquitlam (Monger and Journeay 1994).

Historically, most low- and mid-elevation forests in the watersheds were old growth, as evidenced by an abundance of standing dead and downed trees, canopy gaps, and trees greater than 250 years of age (Acres International Limited 1999). These stands resulted from

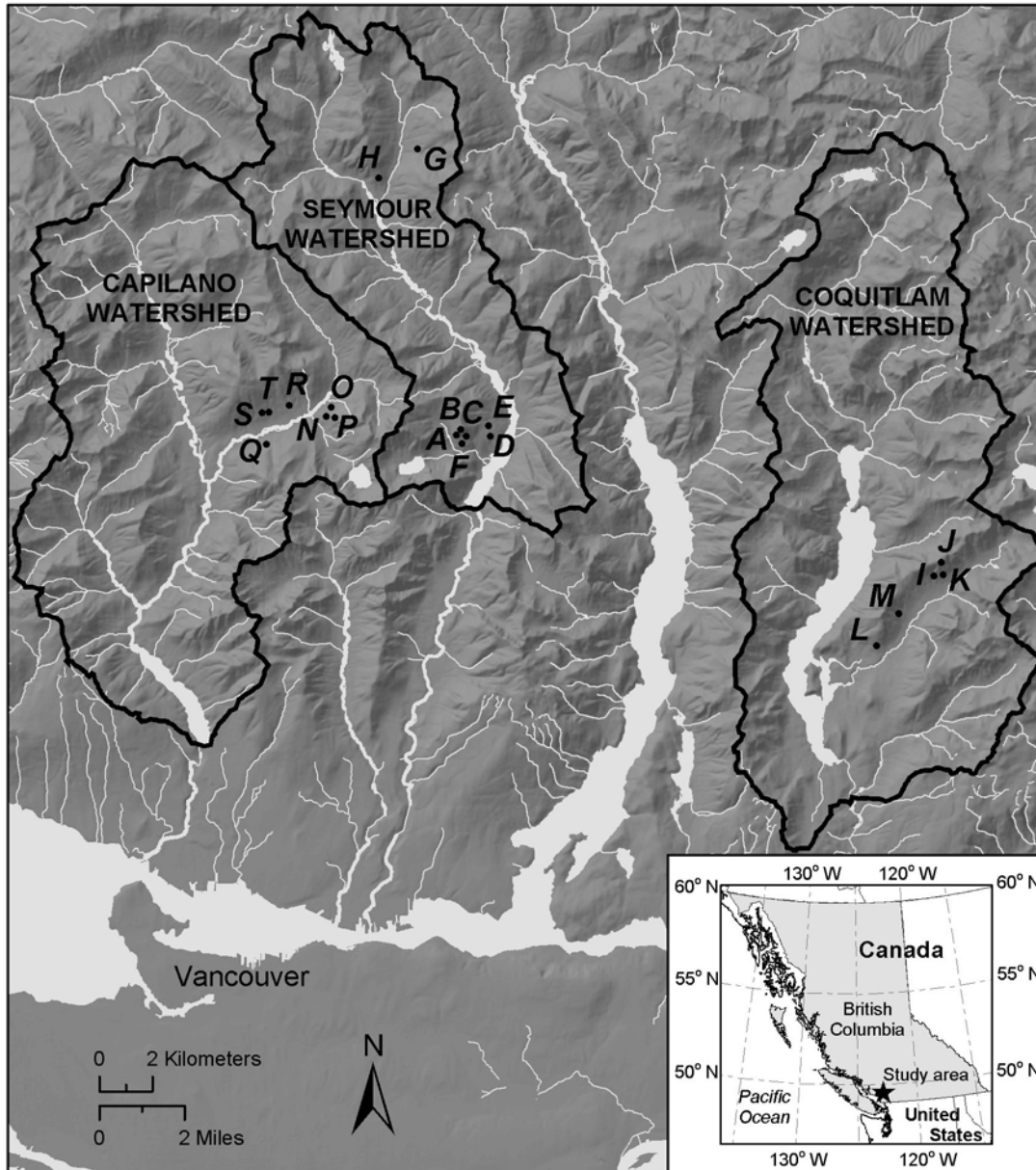


Figure 4.1. Location of the study area and sites in the Capilano, Seymour, and Coquitlam River watersheds, British Columbia, Canada.

long periods of fine-scale gap forming and filling processes occurring in the absence of catastrophic disturbances such as fire (Lertzman et al. 1996, Wells et al. 1998, Gavin et al. 2003). Until the early 1990s, many of these forests were impacted by harvesting (Acres International Limited 1999). Consequently, low- and mid-elevations in the watersheds are a mosaic of second-growth stands, interspersed with remnant patches of old-growth forest.

Shade-tolerant western redcedar (*Thuja plicata* Donn ex D. Don), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and Pacific silver fir (*Abies amabilis* Dougl. ex J. Forbes), and a small number of shade-intolerant Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) constitute mid-elevation, old-growth stands in the watersheds (Meidinger and Pojar 1991). Life spans are ≥ 360 years for Pacific silver fir, ≥ 450 years for western hemlock, and ≥ 1000 for western redcedar and Douglas-fir (Daniels 1994). Trees grow to massive sizes, with Pacific silver fir reaching ≥ 100 cm diameter at breast height (dbh), western hemlock ≥ 120 cm dbh, and western redcedar and Douglas-fir ≥ 250 cm dbh (Daniels 1994).

4.3. Methods

4.3.1. Selecting study sites

I used a combination of watershed ecological inventory data and field reconnaissance to locate canopy gaps. From forest cover maps of the watersheds (Acres International Limited 1999), I identified remnant patches of old-growth, western redcedar-western hemlock forest situated on slopes $\leq 30^\circ$ between 300 and 700 m a.s.l. All stands $\geq 20\%$ western redcedar and $\leq 20\%$ Douglas-fir by volume were considered appropriate for this study. In coastal British Columbia, Douglas-fir establishes primarily after stand-destroying disturbances and therefore can be a minor component of very old stands. Approximately 3000 ha of forest stands met the above criteria. I randomly selected stands and inspected them to verify old-growth structural and compositional characteristics, along with site features and accessibility. Stands that were poorly drained, difficult to access because of topographic features (e.g. stream crossing), or too small to contain canopy gaps not influenced by edge effects from roads or major streams were omitted from further sampling.

Stands confirmed appropriate through field reconnaissance were systematically searched for gaps that were (1) created by one or two uprooted canopy dominant(s) and (2) likely formed within the last 50 years. I focused on gaps that were created by uprooted trees in order to maintain consistency in terms of their mode of formation. While modes of gap-forming mortality in coastal British Columbia include standing death, snapping, and uprooting (Lertzman and Krebs 1991, Arsenault 1995, Lertzman et al. 1996), the last has the greatest potential to offer the most information for determining the timing of gap formation using dendroecological methods. In addition, “recently” formed gaps were best suited for determining the timing of gap formation using dendroecological methods. Over time, information such as outer-ring dates of gapmakers can become less accurate due to loss of bark and decay, and in addition, secondary gap expansion or formation of adjacent gaps can result in complex growth patterns of trees growing around and within gaps, making older gaps less desirable for use in this study. I used the five-class system of log decomposition described by Maser et al. (1979) to facilitate identification of gaps that met the appropriate age criterion. Based on this system, gaps were marked for more rigorous assessment of timing of formation only if the gapmakers were in decay classes I, II, or III. Logs in the first three decay classes correspond to the least decayed individuals and therefore should represent the most recently created gaps (Daniels et al. 1997).

For each marked gap, I attempted to determine the year of death and year of fall of the gapmaker(s). To determine year of death, I took multiple increment cores from the least decayed sections of each bole to ensure that (1) enough intact rings, including the outermost rings, were available for crossdating and (2) when possible, samples included the bark and sapwood (Dynesius and Jonsson 1991, Daniels et al. 1997). Cores were mounted and sanded

following the procedures of Stokes and Smiley (1968). I measured ring widths to the nearest 0.001 mm with a stereozoom microscope and Velmex sliding-stage micrometer interfaced with MeasureJ2X software. The program COFECHA (Holmes 1983, Grissino-Mayer 2001) was used to statistically crossdate ring-width series from gapmakers against preliminary master-dating series developed from cores collected from nearby living trees; crossdating was later verified against regional-scale, species-specific final master-dating series (Chapter 2). By crossdating cores, I was able to assign a calendar year to each tree ring and thus estimate the last year of growth of the gapmakers. To determine year of fall, I collected partial or whole-stem cross sections from any live trees scarred or crushed by the gapmaker. In addition, I sampled cross sections from seedlings or saplings growing on the gapmaker. Cross sections were sanded (Stokes and Smiley 1968) and visually crossdated (Yamaguchi 1991) to determine year of establishment of seedlings and saplings (an estimate of maximum year of fall) along with year of scar or reaction wood formation in injured trees. Gapmakers that could not be successfully dated to year of death or fall were rejected and no further sampling was conducted at those sites. A total of 20 gaps were dated with confidence. Data collected to determine the timing of gap formation were presented in Chapter 3. Gaps ranged in age from 4 to 48 years old. Gaps ranged in size from 118 to 560 m², with a median of 317 m², as defined by the boles of the trees whose crowns delineated each opening in the canopy (i.e. expanded gap, Runkle 1982).

4.3.2. Sampling and crossdating trees

I established belt transects along the north-south axis of the 20 dated canopy gaps. Starting at the center of each gap, I extended transects north and south towards and into the adjacent forest until another recent gap was encountered. Transects were 10 m wide. Any

small openings in the canopy caused by spaces between tree crowns were not considered canopy gaps. I extracted two increment cores from all trees ($\text{dbh} \geq 10 \text{ cm}$) located within each transect. Trees were cored at approximately 30 cm above the ground on the side facing the center of the gap. Cores were mounted and sanded according to Stokes and Smiley (1968).

I took a rigorous approach to crossdating because the frequent occurrence of modest to severe suppression within western hemlock and Pacific silver fir that grow in these stands made it difficult to match their ring patterns. First, the two cores collected from each tree were visually crossdated (Yamaguchi 1991) relative to each other to identify locally absent rings, i.e. those that were missing along one or more radii of the tree (Fritts 1976, Norton et al. 1987). Then, ring widths of all cores were measured to the nearest 0.001 mm using a stereozoom microscope and Velmex sliding-stage micrometer interfaced with MeasureJ2X software and statistically crossdated (Holmes 1983, Grissino-Mayer 2001) both within individual trees and among all trees of a single species. In general, cores with the greatest number of suppressions and/or releases were difficult to statistically crossdate, and at best, could only be visually crossdated using narrow and wide marker rings.

4.3.3. Identifying release of trees

I assessed all trees growing along the north-south axis of the 20 dated gaps for growth release. I converted ring width into basal area increment and used a species- and ecosystem-specific version of the radial-growth averaging method (Chapter 2) to determine if individual trees showed a release pattern following the formation of a canopy gap of known timing of origin. As formalized by Nowacki and Abrams (1997), this method is expressed using the equation:

$$\%GC = (M_2 - M_1) / M_1 \times 100,$$

where %GC is percent-growth change for a single year, M_1 is the mean basal area increment preceding that year, and M_2 is the mean basal area increment following that year. I applied the percent-growth change equation with a 5-year moving average (i.e. M_1 and M_2) to basal area increment values of individual trees (i.e. mean of two cores per tree) and identified a release as the highest peak growth-change value $\geq 25\%$, within the 10-year window that surrounded the year of death of the gapmaker (Figure 4.2). The peak percent-growth-change value represented the year prior to the onset of a release (Nowacki and Abrams 1997). If a peak $\geq 25\%$ did not occur, I then assessed whether the last calculated growth-change value within the window was $\geq 25\%$. This subsequent inspection was particularly useful for the younger gaps for which it was not always possible to determine if a tree released using a peak value. An adjustment was made for trees from gaps with information on only the year of fall of the gapmaker. For those trees, I established the window relative to the year of fall and shortened the portion after fall to five years because it was unlikely that any associated releases occurred beyond that time (Figure 4.2). I used all the releases detected in these analyses in later analyses of duration and magnitude.

I used the CATMOD procedure (SAS Institute Inc. 2007) to conduct a log-linear analysis of a three-way contingency table of species, canopy position, and release. In addition to the number of trees that showed a release pattern, this procedure allowed me to assess the association of western redcedar, western hemlock, and Pacific silver fir in canopy (co-dominant and dominant trees) and subcanopy (suppressed and intermediate trees) positions.

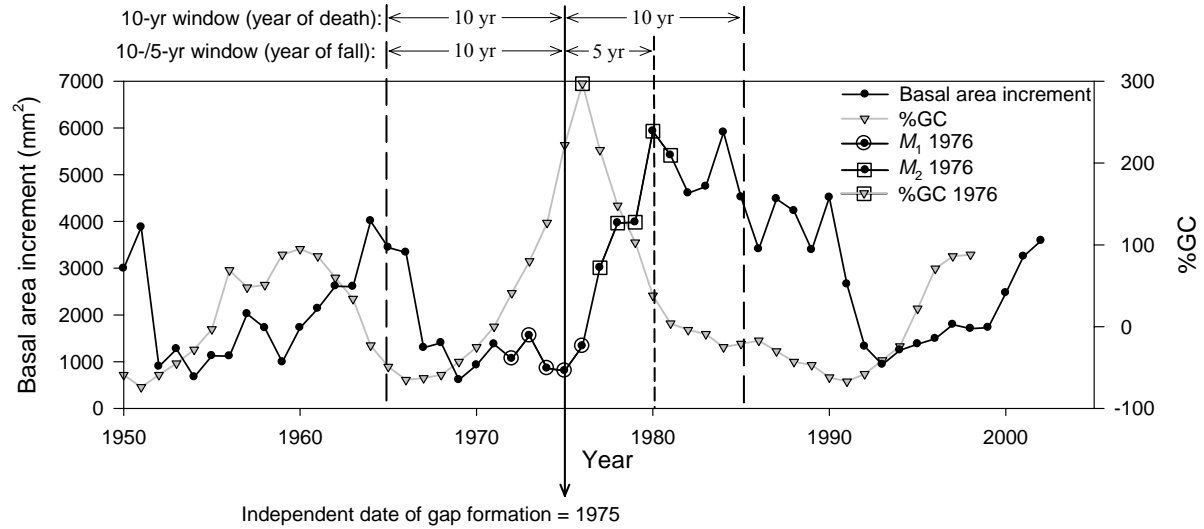


Figure 4.2. Schematic depicting the detection of a release for a tree growing along the north-south axis of a canopy gap of known timing of origin using the radial-growth averaging method with a 5-year moving average. Percent-growth change (%GC) for a single year is equal to $(M_2 - M_1)/M_1 \times 100$, where M_1 is the mean basal area increment for the five years preceding that year, and M_2 is the mean basal area increment for the five years following that year (adapted from Nowacki and Abrams 1997). %GC is highlighted for a release detected within windows surrounding 1975, the year of gap formation (i.e. year of death or fall).

4.3.4. Duration of releases

Duration is the number of years from the onset to the end of a release. To determine the duration of a release, M_1 for the year of peak percent-growth change was held constant as M_2 was shifted successively one year at a time (Figure 4.2). A release was considered to have ended when percent-growth change decreased below the 25% threshold. Thus, the end of a release was defined as the last calendar year in M_2 when percent-growth change was still $\geq 25\%$ (Figure 4.2). Some releases were sustained, i.e. percent-growth change was $\geq 25\%$ at the time of sampling and thus the end of the release was not observed.

I assessed the duration of releases using survival analysis. This class of statistical procedures is concerned with studying the time until a specific event occurs (Kalbfleish and Prentice 1980, Klein and Moeschberger 1997, Fox 2001, Lee and Wang 2003). Besides

accommodating strongly skewed distributions, survival analysis allows for the inclusion of censored observations, i.e. those in which the event of interest is not observed.

I calculated both nonparametric and parametric survival functions. The survival function $S(t)$ is the probability that a release survives beyond time t , i.e. $\Pr(T > t)$, where T is a continuous random variable that represents the number of years from the onset to the end of a release (i.e. duration). Nonparametric survival functions do not require any assumptions of distribution. Parametric survival functions require selecting a distribution, thus allowing for a regression analysis with explanatory variables.

I estimated nonparametric survival functions using the product-limit (Kaplan-Meier) estimate of the survival function (Kaplan and Meier 1958). The product-limit estimate accounts for censored observations. In this study, observations were right censored because a release could continue beyond the date of sampling. This method estimates the survival function $S(t)$ as a product of t conditional observed survival probabilities:

$$S(t) = p_1 \times p_2 \times \dots \times p_t$$

where $1, 2, \dots, t$ are distinct times at which releases end, $p_i = (n_i - d_i)/n_i$ is the proportion of releases surviving the i th year after they have survived $i - 1$ years, where n_i is the number of releases at risk of ending at t_i (i.e. the number of uncensored releases just prior to t_i), and d_i is the number of releases ending at t_i . Analysis was done using the LIFETEST procedure (SAS Institute Inc. 2007).

I fit a parametric survival model to duration of releases. The model was an accelerated failure time model in which the explanatory variables multiplicatively affected failure time of a release, or linearly affected the natural logarithm of a failure time, $\ln(T)$

(Kalbfleish and Prentice 1980, Klein and Moeschberger 1997, Fox 2001). The model is of the form:

$$\ln(T) = \mathbf{X}\boldsymbol{\beta} + \sigma\epsilon,$$

where \mathbf{X} is an $n \times p$ matrix of explanatory variables for n observations and p variables, $\boldsymbol{\beta}$ is a $p \times 1$ vector of unknown parameters, σ is a scale parameter, and ϵ is a $n \times 1$ vector of random errors from a specified survival distribution that is independent of \mathbf{X} . In this study, I used a model in which T was defined as a Weibull distribution. This distribution is commonly used in survival analysis because it is flexible and appropriate for a range of monotonic survival functions (Kalbfleish and Prentice 1980, Klein and Moeschberger 1997, Fox 2001).

I started with a model developed for trees growing around the boundary of, or within, the gaps (Chapter 3). The variables for this base model were: species as a dummy variable, the natural logarithm of diameter in the year of release (cm), and the interaction of these variables. To this model, I added two variables that described tree position relative to the center of the gap. The variables were: north-south position as a dummy variable and distance from the gap center (m). After entry of a variable, I subsequently tested its interaction with species. In addition, I tested the interaction of north-south position and distance from the gap center. All significant ($P \leq 0.05$) terms were kept in the model, where the dummy variables or dummy variables by continuous variables were considered a single term. All analyses were done using the LIFEREG procedure (SAS Institute Inc. 2007).

4.3.5. *Magnitude of releases*

I assessed the magnitude of releases according to the peak percent-growth-change value associated with the onset of each release. Similar to the duration analysis, I started

with a base model developed for trees growing around the boundary of, or within, the gaps (Chapter 3). However, for this analysis, the base model was a general linear model. The variables for the base model were: species as a dummy variable, the natural logarithm of diameter in the year of release (cm), the natural logarithm of prior growth (cm²), and the interaction of the latter two variables with each other and species. To this model, I added the variables for tree north-south position and distance from the gap center in the same manner as done for the duration of releases. In addition to diameter in the year of release and prior growth, percent-growth change was transformed using the natural logarithm to improve model fit and normality of residuals. Analysis was done using the GLM procedure (SAS Institute Inc. 2007).

4.4. Results

4.4.1. Number of trees and releases

There were 323 trees growing along the north-south axis of the 20 study gaps. Trees were not evenly distributed among species and canopy positions (Table 4.1; $P < 0.001$). There were 64 western redcedar, 185 western hemlock, and 74 Pacific silver fir. Western redcedar and western hemlock occurred in the greatest numbers in the canopy, while the subcanopy was composed mostly of western hemlock and Pacific silver fir (Figure 4.3). Mean dbh was 140 ± 6.28 , 61 ± 2.47 , and 52 ± 6.71 cm for canopy western redcedar, western hemlock, and Pacific silver fir, respectively. Mean dbh was 47 ± 3.13 , 22 ± 0.89 , and 17 ± 0.75 cm for subcanopy western redcedar, western hemlock, and Pacific silver fir, respectively.

A high number of western redcedar, western hemlock, and Pacific silver fir showed a release pattern following gap formation (Figure 4.3). In total, 89% (288 of 323) of all

Table 4.1. Partial associations for the saturated log-linear model of species, canopy position, and release. Values in bold are significant at $P < 0.05$.

Variable	df	Wald χ^2	P
species	2	34.93	<0.001
canopy position	1	0.04	0.844
release	1	43.19	<0.001
species \times canopy position	2	27.31	<0.001
species \times release	2	1.40	0.496
canopy position \times release	1	2.40	0.121
species \times canopy position \times release	2	3.02	0.221

Note: species = western redcedar, western hemlock, or Pacific silver fir; canopy position = canopy or subcanopy; release = detected or not detected.

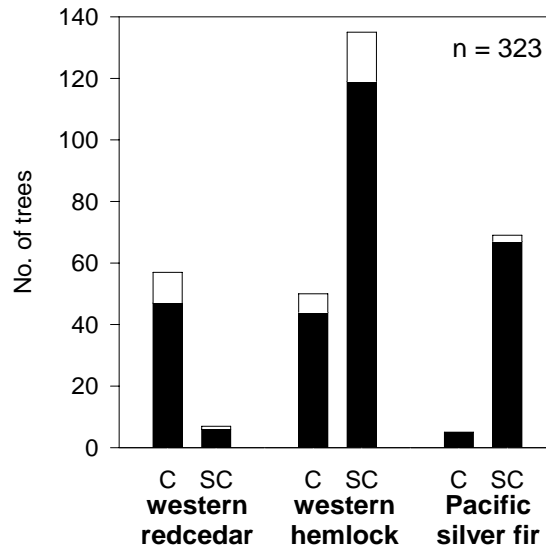


Figure 4.3. Frequency distribution of canopy (C) and subcanopy (SC) western redcedar, western hemlock, and Pacific silver fir growing along the north-south axis of 20 gaps of known timing of origin. The number of trees that showed a release pattern following gap formation is depicted in black; trees that did not are in white.

individuals had an increase in growth $\geq 25\%$ within 10 years of gap formation, a proportion that was significantly different from random (Table 4.1; $P < 0.001$). However, there was no evidence for a more complex interaction among the number of trees that released, species, or canopy position (Table 4.1; $P = 0.221$).

4.4.2. Duration of releases

For western hemlock, Pacific silver fir, and western redcedar, the median duration of releases was approximately 30, 27, and 21 years, respectively (Figure 4.4). There was a significant species \times \log diameter the year of release interaction (Table 4.2; $P = 0.011$), indicating that there were differences in the duration of releases among species. For western hemlock, increasing diameter resulted in decreasing duration of releases (Table 4.3; slope = -0.482). This pattern was opposite for western redcedar, as increasing diameter resulted in increasing duration of releases (Table 4.3; slope = 0.466). Pacific silver fir showed a pattern similar to western hemlock (Table 4.3; slope = -0.582).

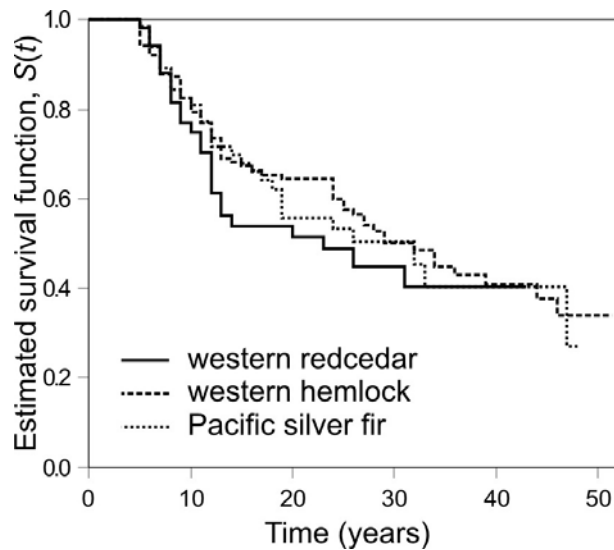


Figure 4.4. Survival functions $S(t)$ for duration of releases of western redcedar, western hemlock, and Pacific silver fir. $S(t)$ is the probability that a release will survive beyond time t , having survived to time t . The survival functions are nonparametric product-limit (Kaplan-Meier) estimates.

The north-south position \times distance interaction was significant for duration of releases for all three species (Table 4.2; $P = 0.011$). For all trees, there was a pattern of decreasing duration of releases with increasing distance from the gap center (Table 4.3; $P =$

Table 4.2. Analysis of variance results for the Weibull survival model of duration of releases. Values in bold are significant at $P < 0.05$.

Variable	df	Deviance	Pr(Chi)
species	2	0.83	0.661
<i>logdiameter</i> the year of release	1	20.03	<0.001
species \times <i>logdiameter</i> the year of release	2	10.21	0.011
distance	1	5.63	0.022
north-south position	1	0.33	0.572
north-south position \times distance	1	6.63	0.011

Note: Variables were added sequentially and are order dependent (see Methods). Species are western redcedar, western hemlock, and Pacific silver fir; *logdiameter* the year of release is the diameter of the tree at coring height (i.e. approximately 30 cm above the ground) in the year the release began; distance is the tree distance from the gap center; north-south position is the tree location relative to the gap center (north = 1, south = 0).

Table 4.3. Parameter estimates for the Weibull survival model of duration of releases. Estimates are for levels of a given variable included in the model. Note: P-values for species or for species by continuous variable interactions should be interpreted for all species combined and were given in Table 4.2.

Variable	Coefficient	Standard error	<i>z</i>	<i>P</i>
intercept [§]	3.610	0.107	33.72	<0.001
species (Pacific silver fir)	-0.065	0.156	-0.42	0.675
species (western redcedar)	-0.120	0.163	-0.74	0.462
<i>logdiameter</i> the year of release ^{§†}	-0.482	0.106	-4.53	<0.001
Pacific silver fir \times <i>logdiameter</i> the year of release	-0.100	0.190	-0.52	0.601
western redcedar \times <i>logdiameter</i> the year of release	0.948	0.284	3.34	<0.001
distance [‡]	-0.003	0.011	-0.26	0.794
north-south position	0.073	0.129	0.57	0.571
north-south position \times distance	-0.045	0.017	-2.67	0.008

[§]Results with respect to western hemlock.

[†]Variable is centered at the corresponding species-specific mean.

[‡]Variable is centered at the mean for all trees.

Note: Species are western redcedar, western hemlock, and Pacific silver fir; *logdiameter* the year of release is the diameter of the tree at coring height (i.e. approximately 30 cm above the ground) in the year the release began; distance is the tree distance from the gap center; north-south position is the tree location relative to the gap center (north = 1, south = 0).

0.008). However, this distance effect on duration of releases was greater for trees north of the gap center. None of the other interaction terms tested were significant and were not kept in the model.

4.4.3. Magnitude of releases

The magnitude of releases was greatest for western hemlock and Pacific silver fir (Figure 4.5a, b). For canopy trees, mean growth change was 133% for western hemlock and 107% for Pacific silver fir. For subcanopy trees, mean growth change was 187% for western hemlock and 172% for Pacific silver fir. Maximum growth change was > 700% for western hemlock and > 1000% for Pacific silver fir. These findings differ from those for western redcedar, for which maximum growth change was > 300%, and mean growth change was 76% and 64% for canopy and subcanopy trees, respectively (Figure 4.5a, b). While relative-growth change was lower for western redcedar, this species grew at an overall faster rate both before and after release compared to western hemlock and Pacific silver fir (Figure 4.5a, b). All three species had variable growth rates (Figure 4.5a, b).

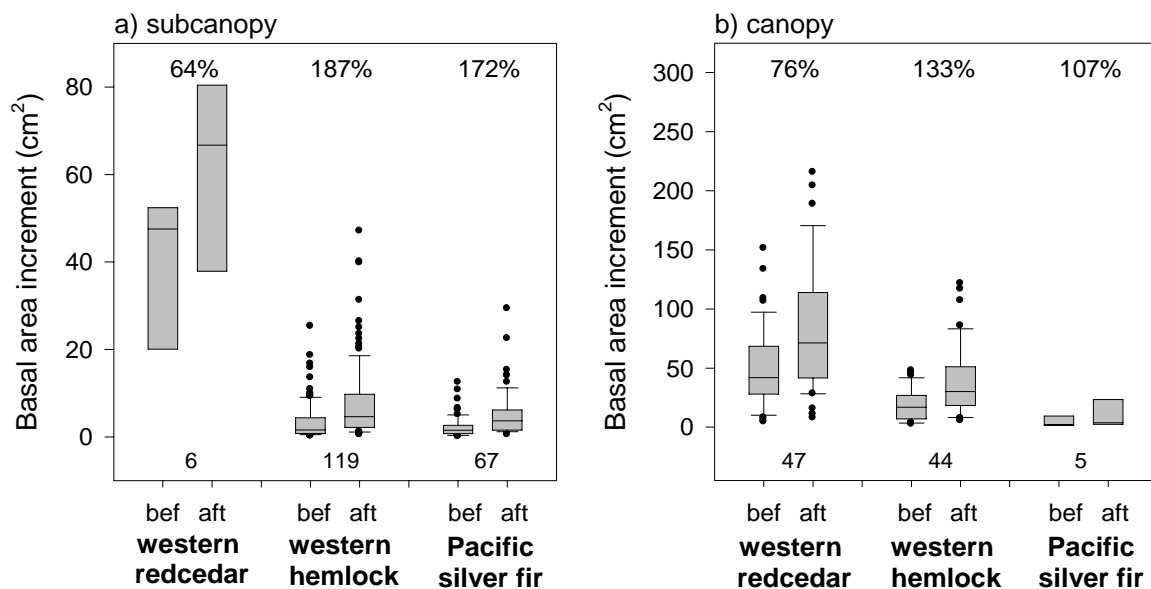


Figure 4.5. Box plots of mean basal area increment five years before (bef) and after (aft) release for (a) subcanopy and (b) canopy trees. Values at the top and bottom of the plots are mean percent-growth change and sample size, respectively. The horizontal line in each box is the median, the lower and upper limits of each box are the 25th and 75th percentiles, the lines are the 5th and 95th percentiles, and the circles are outliers.

Based on the general linear model, species, *log*prior growth, and distance from the gap center explained a significant amount of variation in magnitude of release (Table 4.4; $P = 0.010$ to < 0.001). The *log*diameter the year of release \times *log*prior growth interaction was also significant (Table 4.4; $P = 0.008$). None of the other variables tested were significant and were not kept in the model.

Table 4.4. Analysis of variance results for the general linear model of magnitude of releases. Values in bold are significant at $P < 0.05$.

Variable	df	SS [†]	F	Pr(F)
species	2	14.16	18.75	<0.001
<i>log</i> diameter the year of release	1	0.50	1.33	0.249
<i>log</i> prior growth	1	2.53	6.71	0.010
species \times <i>log</i> diameter the year of release	2	1.06	1.40	0.249
species \times <i>log</i> prior growth	2	0.72	0.95	0.389
<i>log</i> diameter the year of release \times <i>log</i> prior growth	1	2.74	7.24	0.008
distance	1	6.55	17.33	<0.001

[†]Type III sums of squares.

Note: Variables were added sequentially and are order dependent (see Methods). Species are western redcedar, western hemlock, and Pacific silver fir; *log*diameter the year of release is the diameter of the tree at coring height (i.e. approximately 30 cm above the ground) in the year the release began; *log*prior growth is mean basal area increment for the five years prior to the year of the peak-percent-growth change value associated with the onset of the release; distance is the tree distance from the gap center.

There was a pattern of decreasing percent-growth change with increasing diameter in the year of release and prior growth (Figure 4.6a, b). In addition, the effect of prior growth varied significantly among trees of different diameters (Table 4.4 and 4.5; $P = 0.008$). For the largest diameter hemlock trees, prior growth had a minimal effect on percent-growth change. However, for the largest diameter Pacific silver fir and western redcedar trees, prior growth had a moderate effect, with higher values of prior growth resulting in lower values of percent-growth change. For the smallest diameter trees of all species, prior growth had a

more substantial effect, with higher values of prior growth resulting in lower values of percent-growth change, particularly for Pacific silver fir.

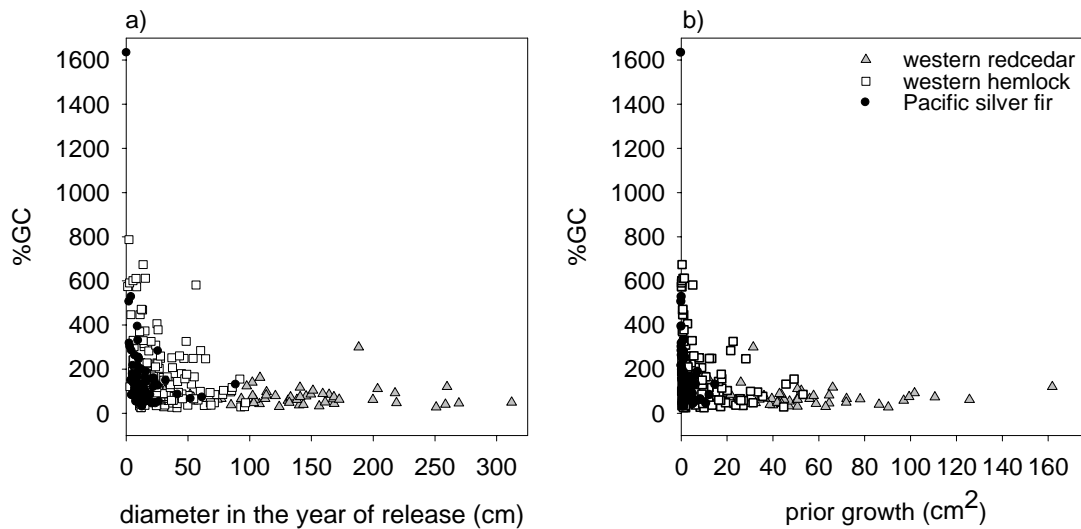


Figure 4.6. Plots of percent-growth change (%GC) with respect to (a) diameter in the year of release and (b) prior growth for western redcedar, western hemlock, and Pacific silver fir growing along the north-south axis of 20 gaps of known timing of origin.

There was a pattern of decreasing release magnitudes with increasing distance from the gap center for all three tree species (Table 4.4 and 4.5; $P < 0.001$, Figure 4.7).

4.5. Discussion

4.5.1. Number, duration, and magnitude of releases

A high number of western redcedar, western hemlock, and Pacific silver fir growing along the north-south axis of canopy gaps showed a release pattern following gap formation. The duration and magnitude of releases varied according to diameter, growth rate prior to release, and species. In addition, distance from the gap center had an effect on duration and magnitude of releases.

Table 4.5. Parameter estimates for the general linear model of magnitude of releases. Estimates are for levels of a given variable included in the model. Note: P-values for species or for species by continuous variable interactions should be interpreted for all species combined and were given in Table 4.4.

Variable	Coefficient	Standard error	<i>t</i>	<i>P</i>
intercept [§]	4.779	0.056	86.10	<0.001
species (Pacific sliver fir)	-0.022	0.089	-0.27	0.791
species (western redcedar)	-0.591	0.100	-5.91	<0.001
<i>logdiameter</i> the year of release ^{§†}	-0.226	0.096	-2.36	0.019
<i>logprior</i> growth ^{§†}	-0.098	0.054	-1.82	0.070
Pacific sliver fir × <i>logdiameter</i> the year of release	0.071	0.165	0.43	0.667
western redcedar × <i>logdiameter</i> the year of release	0.350	0.209	1.67	0.096
Pacific sliver fir × <i>logprior</i> growth	-0.143	0.107	-1.33	0.183
western redcedar × <i>logprior</i> growth	-0.082	0.140	-0.59	0.556
<i>logdiameter</i> the year of release × <i>logprior</i> growth	0.079	0.029	2.69	0.008
distance [*]	-0.020	0.005	-4.16	<0.001

[§]Results with respect to western hemlock.

[†]Variable is centered at the corresponding species-specific mean.

^{*}Variable is centered at the mean for all trees.

Note: $R^2 = 0.34$ and Akaike's information criterion (AIC) = 536.3; the base model has an $R^2 = 0.30$ and an AIC = 550.3. Species are western redcedar, western hemlock, and Pacific silver fir; *logdiameter* the year of release is the diameter of the tree at coring height (i.e. approximately 30 cm above the ground) in the year the release began; *logprior* growth is mean basal area increment for the five years prior to the year of the peak-percent-growth change value associated with the onset of the release; distance is the tree distance from the gap center.

Diameter and growth rate prior to release were the most important predictors of duration and magnitude of release. In most cases, the smallest and most suppressed trees had the longest duration and most intensive magnitude release following gap formation. Compared to larger trees, smaller trees have a greater ability to increase their growth following canopy disturbance (Merrens and Peart 1992, Black and Abrams 2003, 2004). Smaller trees often have slow, suppressed growth because of shading or competition for below-ground resources. Therefore, when a gap forms, smaller, more limited trees will experience a relatively greater increase in resources and growth than larger trees. While the smallest and most suppressed trees had the most intensive magnitude release following gap formation, absolute growth remained lower in smaller versus larger trees. Other studies have

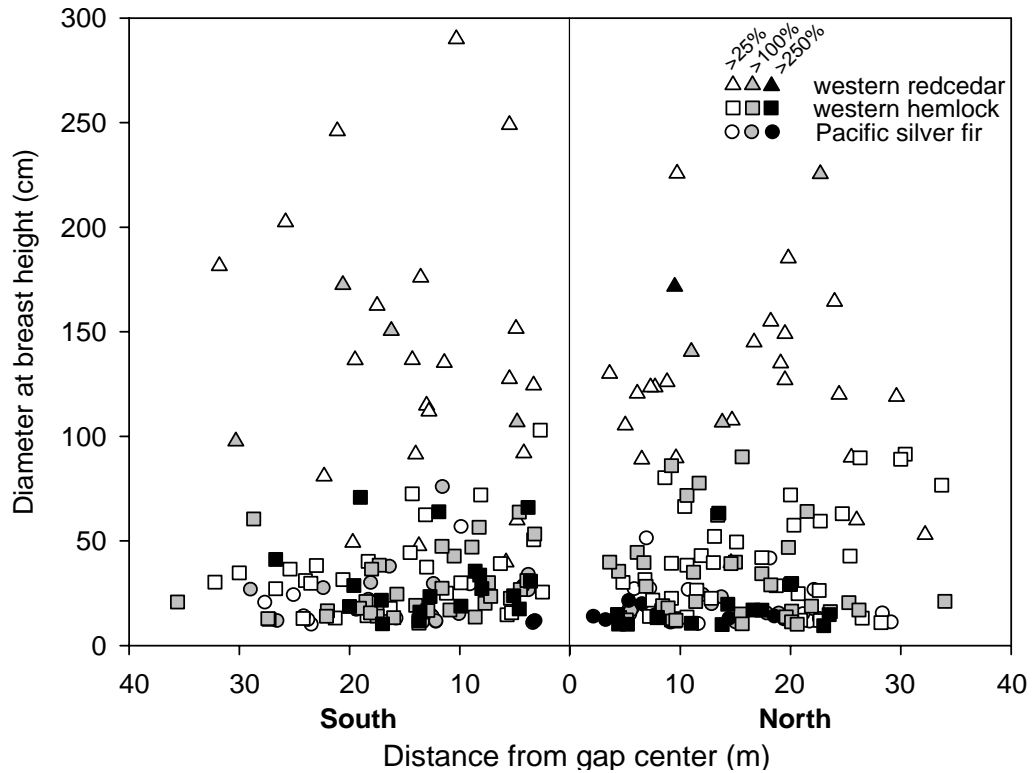


Figure 4.7. Plot of magnitude of releases relative to distance along the north-south axis of canopy gaps for all trees that released ($n = 288$). Diameter is shown to indicate the influence of tree size on magnitude of release.

reported similar patterns for the influence of diameter on growth response following gap formation (DiGregorio et al. 1999, Jones and Thomas 2004, Pedersen and Howard 2004), or release from competition in general (Canham et al. 2004).

The effect of distance from the gap center on the duration and magnitude of releases might be related to the variability in light and below-ground resources around and within gaps. Several factors including latitude, size of opening, as well as height, type, and arrangement of nearby trees influence light around and within a canopy gap. At high latitudes the angle of incoming sunlight is low, so peak light availability is displaced from the center of a gap such that in the Northern Hemisphere, the north edge of an opening receives direct-beam light, while the south edge receives only diffuse light (Canham 1988, Canham et

al. 1990, Lieffers et al. 1999). In addition, as the size of a gap decreases, so does the amount of diffuse and direct-beam light reaching its center. Taller trees with denser canopies further decrease the amount of light to lower parts of the canopy and understory (Canham et al. 1990, Lieffers et al. 1999, Parker et al. 2002). These patterns of light can operate together with reduced root competition following the death of a canopy tree to affect soil moisture and/or nutrients around and within gaps (Coomes and Grubb 2000).

Although not measured in this study, any greater increase in light north versus south of the gap center following gap formation was not enough to cause the magnitude of releases to differ between these two locations. Because of the small size of the study gaps and great height of the neighboring trees, some of which exceeded 60 m, only the tallest trees on the north edge of the gaps would have been exposed to increased levels of uninterrupted, direct-beam light. These canopy dominant trees had high growth rates prior to release and therefore less potential to increase their growth.

However, an increase in diffuse light following gap formation might be a reason for the effect of distance from gap center on magnitude of release. In structurally similar coastal Douglas-fir forests, Gray et al. (2002) reported that diffuse light was slightly greater in experimental gaps equivalent in size to single-tree openings than in closed-canopy forest, and diffuse light decreased symmetrically from the center of those gaps to and beyond their edges. Growth of seedlings in the same experimental gaps was 50% greater than in closed-canopy forest (Gray and Spies 1996). In the present study, a similar pattern of diffuse light in gaps could have caused trees closer to the center of gaps to release more intensively. For highly shade-tolerant western redcedar, western hemlock, and Pacific silver fir, even minor increases in radiation can equate to relatively large increases in growth (Carter and Klinka

1992, Wright et al. 1998). In a simulation study, Ménard et al. (2002) also observed decreasing magnitude of releases with increasing distance from the center of gaps, with releases occurring up to 20 m beyond gap edges. These release patterns corroborate those observed in the present study and provide evidence that the effects of gaps can extend well beyond their physical edges (Runkle 1982, Canham et al. 1990).

The effect of distance from gap center on magnitude of release might also be related to decreased competition for moisture or other below-ground resources following gap formation. Previous studies have reported a general pattern of decreasing soil moisture along the gradient from gap center towards the adjacent forest (Gray et al. 2002, Gálhidy et al. 2006, Walters et al. 2006). This pattern of soil moisture is usually attributed to decreased uptake and transpiration following reduced root density after tree removal (Wilczynski and Pickett 1993). In this study, reduced root competition following gap formation could have caused trees closer to the center of gaps to release more intensively. Any immediate increase in moisture following gap formation has been shown, however, to decrease over time, as plants around and within gaps increase in size and/or density (Gray et al. 2002, Kranabetter and Coates 2004, Walters et al. 2006). For harvested gaps in western redcedar-western hemlock forests of northern British Columbia, soil nitrogen decreased over time in the same manner as moisture (Kranabetter and Coates 2004, Walters et al. 2006). In the present study, a similar trend of decreasing moisture and/or nutrients over time could have occurred and acted together with light to cause the complex pattern observed for duration of releases. For example, greater light north versus south of the gap center could have facilitated an increase in the rate of uptake of below-ground resources, causing releases to end more quickly with increasing distance north versus south of the gap center. The presence of overlapping and

intermingled tree roots in western redcedar-western hemlock stands of coastal British Columbia certainly suggests intense competition for available soil resources (Wang et al. 2002). Because of the retrospective nature of the present study, it was not possible to measure light and below-ground resources before and after gap formation. An experimental approach looking at these resources together with the growth release of trees following gap formation in coastal, old-growth stands would be helpful for clarifying the mechanisms behind the release patterns observed in this study.

4.5.2. Implications for management

To scientifically demonstrate that variable retention is an ecologically sustainable approach to forest management, we must be able to understand its impacts on forest structure and composition. Acquiring detailed information on spatial and temporal aspects of natural disturbance regimes gives us the tools to manage forests according to principles of ecosystem management and natural range of variation (Scientific Panel for Sustainable Forest Practices in Clayoquot Sound 1995, Christensen et al. 1996, Landres et al. 1999). For the forests of coastal British Columbia, growth release of trees following the formation of natural, fine-scale canopy gaps represents important, and previously unknown, information for understanding the impacts of variable retention. Directly, such information provides a benchmark against which to compare growth release following the formation of harvested gaps. Indirectly, results from this study can be used to calibrate forest models to better anticipate the growth release of residual canopy and subcanopy trees following high-retention harvesting. Together, these applications represent important steps toward better management of uneven-aged stands in coastal British Columbia.

Results of this study appear promising for management regimes that apply high-retention harvesting in old-growth, western redcedar-western hemlock forests of coastal British Columbia. From a timber perspective, harvesting single trees or small groups of trees creates gaps that may cause enough of a change in environmental conditions and resources to initiate an increase in growth of nearby trees of varying sizes and species. In this study, even large, canopy dominant western redcedar released following the formation of fine-scale gaps. Furthermore, release of western redcedar showed a pattern of increasing duration with increasing diameter. These release patterns of western redcedar, combined with its high growth rate, are beneficial for the timber value of a post-harvest stand where fine-scale gaps are created. From an ecological or non-timber perspective, harvesting single trees or small groups of trees creates gaps with a spatial scale similar to that which occurs naturally in coastal British Columbia (Lertzman and Krebs 1991, Lertzman et al. 1996, Wells et al. 1998). This harvesting approach also protects conditions and resources that span a wide range of values, such as forest structure, soil integrity, and individual trees of high ecological or cultural significance.

High-retention harvesting does have its limitations. Removing trees using techniques such as standing-stem harvesting does not allow for processes of soil disturbance associated with natural tree death and fall. This technique also affects the input of woody biomass into the ecosystem, which is important for the functioning of forest organisms and regeneration of coastal tree species (Christy and Mack 1984, Harmon et al. 1986). Furthermore, a recent review of the sustainability of timber in high-retention cutblocks in coastal British Columbia (Forest Practices Board 2008) reported a concern for this approach to provide economically viable harvests in the future. For many of the stands examined in the review, prescriptions

for harvesting failed to account for site-specific conditions, or in the case where the prescriptions were site-specific, they often were not followed. This lack of proper planning and/or implementation was usually associated with the harvesting of only commercially valuable cedar and spruce. Practices such as these not only fail to meet objectives of sustainable timber, but they also fail to meet any additional ecological, social, or cultural objectives of ecosystem management.

These recent findings suggest a need to call to mind how variable retention fits into managing under principles of ecosystem management. An important aspect of ecosystem management is its multi-scale nature (Scientific Panel for Sustainable Forest Practices in Clayoquot Sound 1995, Christensen et al. 1996, Franklin et al. 1997, Landres et al. 1999). Planning must start at the landscape level and be for long time frames, with conservation and biological diversity as primary management objectives. Starting at these spatial and temporal scales will permit a better understanding of which areas within a watershed are available for harvest and how they link with other parts of the landscape identified for reserves or other resource values. Then, site-specific approaches can be planned for harvesting areas. This planning approach will permit a more realistic approximation of what resources, from timber to non timber, are currently available on the landscape and how they might be expected to vary in the long term. Only when applied within the broader context of landscape-level planning for biological diversity will variable retention offer a way to meet the range of objectives that constitute ecosystem-based management.

4.6. Literature cited

Acres International Limited. 1999. Annex to the Analysis Report, Watershed Management Plan #5, Volumes I-III. Greater Vancouver Regional District Watershed Ecological Inventory Program, Burnaby, British Columbia, Canada.

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

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

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

Black, B.A. and M.D. Abrams. 2004. Development and application of boundary-line release criteria. *Dendrochronologia* 22:31-42.

Canham, C.D. 1988. An index for understory light levels in and around canopy gaps. *Ecology* 69:1634-1638.

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

Canham, C.D., P.T. LePage, and K.D. Coates. 2004. A neighborhood analysis of canopy tree competition: effects of shading versus crowding. *Canadian Journal of Forest Research* 34:778-787.

- Canham, C.D. and P.L. Marks. 1985. The response of woody plants to disturbance: patterns of establishment and growth. Pages 197-216 in S.T.A. Pickett and P.S. White, editors. The ecology of natural disturbance and patch dynamics. Academic Press, New York, New York, USA.
- Carter, R.E. and K. Klinka. 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.
- Christensen, N.L., A.M. Bartuska, J.H. Brown, S. Carpenter, C. D'Antonio, R. Francis, J.F. Franklin, J.A. MacMahon, R.F. Noss, D.J. Parsons, C.H. Peterson, M.G. Turner, and R.G. Woodmansee. 1996. The report of the Ecological Society of America Committee on the scientific basis for ecosystem management. Ecological Applications 6:665-691.
- Christy, E.J. and R.N. Mack. 1984. Variation in demography of juvenile *Tsuga heterophylla* across the substratum mosaic. Journal of Ecology 72:75-91.
- Coates, K.D. 2000. Conifer seedling response to northern temperate forest gaps. Forest Ecology and Management 127:249-269.
- Coates, K.D. 2002. Tree recruitment in gaps of various size, clearcuts and undisturbed mixed forest of interior British Columbia, Canada. Forest Ecology and Management 155:387-398.
- Collins, B.S. and L.L. Battaglia. 2002. Microenvironmental heterogeneity and *Quercus michauxii* regeneration in experimental gaps. Forest Ecology and Management 155:279-290.

- Coomes, D.A. and P.J. Grubb. 2000. Impacts of root competition in forests and woodlands: a theoretical framework and review of experiments. *Ecological Monographs* 70:171-207.
- Daniels, L.D. 1994. Structure and regeneration of old-growth *Thuja plicata* stands near Vancouver, British Columbia. M.Sc. thesis. University of British Columbia, Vancouver, British Columbia, Canada.
- Daniels, L.D., J. Dobry, K. Klinka, and M.C. Feller. 1997. Determining year of death of logs and snags of *Thuja plicata* in southwestern coastal British Columbia. *Canadian Journal of Forest Research* 27:1132-1141.
- Daniels, L.D. and R.W. Gray. 2006. Disturbance regimes in coastal British Columbia. *BC Journal of Ecosystems and Management* 7:44-56.
- DiGregorio, L.M., M.E. Krasny, and T.J. Fahey. 1999. Radial growth trends of sugar maple (*Acer saccharum*) in an Allegheny northern hardwood forest affected by beech bark disease. *Journal of the Torrey Botanical Society* 126:245-254.
- Dynesius, M. and B.G. Jonsson. 1991. Dating uprooted trees: comparison and application of eight methods in a boreal forest. *Canadian Journal of Forest Research* 21:655-665.
- Forest Practices Board. 2008. High retention harvesting and timber sustainability on the British Columbia coast. Special Investigation Report 20. Forest Practices Board, Victoria, British Columbia, Canada.

- Fox, G.A. 2001. Failure-time analysis: studying times to events and rates at which events occur. Pages 235-266 *in* S.M. Scheiner and J. Gurevitch, editors. Design and analysis of ecological experiments. Oxford University Press, New York, New York, USA.
- Franklin, J.F., D.R. Berg, D.A. Thornburgh, and J.C. Tappeiner. 1997. Alternative silvicultural approaches to timber harvesting: variable retention harvest systems. Pages 111-139 *in* K.A. Kohm and J.F. Franklin, editors. Creating a forestry for the 21st century: the science of ecosystem management. Island Press, Washington, DC, USA.
- Frelich, L.E. 2002. Forest dynamics and disturbance regimes: studies from temperate evergreen-deciduous forests. Cambridge University Press, Cambridge, UK.
- Fritts, H.C. 1976. Tree rings and climate. Academic Press, New York, New York, USA.
- Gálhidy, L., B. Mihók, A. Hagyó, K. Rajkai, and T. Standovár. 2006. Effects of gap size and associated changes in light and soil moisture on the understory vegetation of a Hungarian beech forest. *Plant Ecology* 183:133-145.
- Gavin, D.G, L.B. Brubaker, and K.P. Lertzman. 2003. Holocene fire history of a coastal temperate rain forest based on soil charcoal radiocarbon dates. *Ecology* 84:186-201.
- Gray, A.N. and T.A. Spies. 1996. Gap size, within-gap position and canopy structure effects on conifer seedling establishment. *Journal of Ecology* 84:635-645.
- Gray, A.N. and T.A. Spies. 1997. Microsite controls on tree seedling establishment in conifer forest canopy gaps. *Ecology* 78:2458-2473.

- Gray, A.N., T.A. Spies, and M.J. Easter. 2002. Microclimatic and soil moisture responses to gap formation in coastal Douglas-fir forests. *Canadian Journal of Forest Research* 32:332-343.
- Grissino-Mayer H.D. 2001. Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. *Tree-Ring Research* 57:205-221.
- Harmon, M.E., J.F. Franklin, F.J. Swanson, P. Sollins, S.V. Gregory, J.D. Lattin, N.H. Anderson, S.P. Cline, N.G. Aumen, J.R. Sedell, G.W. Lienkaemper, K. Cromack, and K.W. Cummins. 1986. Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research* 15:133-302.
- Holmes, R.L. 1983. Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bulletin* 43:69-78.
- Jones, T.A. and S.C. Thomas. 2004. The time course of diameter increment responses to selection harvests in *Acer Saccharum*. *Canadian Journal of Forest Research* 34:1525-1533.
- Kalbfleisch, J.D. and R.L. Prentice. 1980. The statistical analysis of failure time data. John Wiley and Sons, New York, New York, USA.
- Kaplan, E.L. and P. Meier. 1958. Nonparametric estimation from incomplete observations. *Journal of the American Statistical Association* 53:457-481.
- Klein, J.P. and M.L. Moeschberger. 1997. Survival analysis: techniques for censored and truncated data. Springer-Verlag, New York, New York, USA.

- Kneeshaw, D.D. and Y. Bergeron. 1999. Spatial and temporal patterns of seedling and sapling recruitment within canopy gaps caused by spruce budworm. *Ecoscience* 6:214-222.
- Kranabetter, J.M. and K.D. Coates. 2004. Ten-year postharvest effects of silviculture systems on soil-resource availability and conifer nutrition in a northern temperate forest. *Canadian Journal of Forest Research* 34:800-809.
- Landres, P.B., P. Morgan, and F.J. Swanson. 1999. Overview of the use of natural variability concepts in managing ecological systems. *Ecological Applications* 9:1179-1188.
- Lee, E.T. and J.W. Wang. 2003. Statistical methods for survival data analysis. John Wiley and Sons, Hoboken, New Jersey, USA.
- Lertzman, K., D. Gavin, D. Hallett, L. Brubaker, D. Lepofsky, and R. Mathewes. 2002. Long-term fire regime estimated from soil charcoal in coastal temperate rainforests. *Conservation Ecology* 6:5. [online] URL: <http://www.consecol.org/vol6/iss2/art5>.
- Lertzman, K.P. and C.J. Krebs. 1991. Gap-phase structure of a subalpine old-growth forest. *Canadian Journal of Forest Research* 21:1730-1741.
- Lertzman, K.P., G.D. Sutherland, A. Inselberg, and S.C. Saunders. 1996. Canopy gaps and the landscape mosaic in a coastal temperate rain forest. *Ecology* 77:1254-1270.
- Lieffers, V.J., C. Messier, K.J. Stadt, F. Gendron, and P.G. Comeau. 1999. Predicting and managing light in the understory of boreal forests. *Canadian Journal of Forest Research* 29:796-811.

- Maser, C., R.G. Anderson, K. Cromack, Jr., J.T. Williams, and R.E. Martin. 1979. Dead and down woody material. Pages 78-95 in J.W. Thomas, editor. Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington. USDA Forest Service, Agriculture Handbook 553.
- Meidinger, D.V. and J. Pojar, editors. 1991. Ecosystems of British Columbia. Special Report Series 6. British Columbia Ministry of Forests, Victoria, British Columbia, Canada.
- Ménard, A., P. Dubé, A. Bouchard, and D.J. Marceau. 2002. Release episodes at the periphery of gaps: a modeling assessment of gap impact extent. *Canadian Journal of Forest Research* 32:1651-1661.
- Merrens, E.J. and D.R. Peart. 1992. Effects of hurricane damage on individual growth and stand structure in a hardwood forest in New Hampshire, USA. *Journal of Ecology* 80:787-795.
- Mitchell, S.J. and W.J. Beese. 2002. The retention system: reconciling variable retention with the principles of silvicultural systems. *Forestry Chronicle* 78:397-403.
- Monger, J.W.H. and J.M. Journeay. 1994. Guide to the geology and tectonic evolution of the southern Coast Mountains. Open File 2490. Geological Survey of Canada, Vancouver, British Columbia, Canada.
- Norton, D.A., J.G. Palmer, and J. Ogden. 1987. Dendroecological studies in New Zealand 1. An evaluation of tree age estimates based on increment cores. *New Zealand Journal of Botany* 25:373-383.

- Nowacki, G.J. and M.D. Abrams. 1997. Radial-growth averaging criteria for reconstructing disturbance histories from presettlement-origin oaks. *Ecological Monographs* 67:225-249.
- Parker, G.G., M.M. Davis, and S.M. Chapotin. 2002. Canopy light transmittance in Douglas-fir–western hemlock stands. *Tree Physiology* 22:147-157.
- Pedersen, B.S. and J.L. Howard. 2004. The influence of canopy gaps on overstory tree and forest growth rates in a mature mixed-age, mixed-species forest. *Forest Ecology and Management* 196:351-366.
- Poage, N.J. and D.R. Peart. 1993. The radial growth response of American beech (*Fagus grandifolia*) to small canopy gaps in a northern hardwood forest. *Bulletin of the Torrey Botanical Club* 120:45-48.
- Runkle, J.R. 1982. Patterns of disturbance in some old-growth mesic forests of eastern North America. *Ecology* 63:1533-1546.
- Runkle, J.R., G.H. Stewart, and T.T. Veblen. 1995. Sapling diameter growth in gaps for two *Nothofagus* species in New Zealand. *Ecology* 76:2107-2117.
- Ryder, J.M. 1981. Geomorphology of the southern part of the Coast Mountains of British Columbia. *Zeitschrift für Geomorphologie* 37:120-147.
- SAS Institute Inc. 2007. SAS OnlineDoc[®] 9.1.3, SAS Institute Inc., Cary, North Carolina, USA.

- Scientific Panel for Sustainable Forest Practices in Clayoquot Sound. 1995. Sustainable ecosystem management in Clayoquot Sound: planning and practices. Scientific Panel for Sustainable Forest Practices in Clayoquot Sound, Victoria, British Columbia, Canada.
- Stokes, M.A. and T.L. Smiley. 1968. An introduction to tree-ring dating. University of Chicago Press, Chicago, Illinois, USA.
- Walters, M.B., C.C. Lajzerowicz, and K.D. Coates. 2006. Soil resources and the growth and nutrition of tree seedlings near harvest gap-forest edges in interior cedar-hemlock forests of British Columbia. *Canadian Journal of Forest Research* 36:62-76.
- Wang, T., A. Hamann, D.L. Spittlehouse, and S.N. Aitken. 2006. Development of scale-free climate data for western Canada for use in resource management. *International Journal of Climatology* 26:383-397.
- Wang, X.L., K. Klinka, H.Y.H. Chen, and L. de Montigny. 2002. Root structure of western hemlock and western redcedar in single- and mixed-species stands. *Canadian Journal of Forest Research* 32:997-1004.
- Wells, R.W., K.P. Lertzman, and S.C. Saunders. 1998. Old-growth definitions for the forests of British Columbia, Canada. *Natural Areas Journal* 18:279-292.
- White, P.S. and Pickett, S.T.A. 1985. Natural disturbance and patch dynamics: an introduction. Pages 3-13 *in* S.T.A. Pickett and P.S. White, editors. The ecology of natural disturbance and patch dynamics. Academic Press, New York, New York, USA.

- Wilczynski, C.J. and S.T.A. Pickett. 1993. Fine root biomass within experimental canopy gaps: evidence for a below-ground gap. *Journal of Vegetation Science* 4:571-574.
- Wright, E.F, K.D. Coates, C.D. Canham, and P. Bartemucci. 1998. Species variability in growth response to light across climatic regions in northwestern British Columbia. *Canadian Journal of Forest Research* 28:871-886.
- Valentine, K.W.G., P.N. Sprout, T.E. Baker, and L.M. Lavkulich, editors. 1978. The soil landscapes of British Columbia. British Columbia Ministry of Environment, Victoria, British Columbia, Canada.
- Van Pelt, R. and J.F. Franklin. 1999. Response of understory trees to experimental gaps in old-growth Douglas-fir forests. *Ecological Applications* 9:504-512.
- Yamaguchi, D.K. 1991. A simple method for cross-dating increment cores from living trees. *Canadian Journal of Forest Research* 21:414-416.
- York, R.A., J.J. Battles, R.C. Heald. 2003. Edge effects in mixed conifer group selection openings: tree height response to resource gradients. *Forest Ecology and Management* 179:107-121.

5. Summary and conclusions

This research provides detailed information on growth release of canopy and subcanopy trees following the formation of natural, fine-scale canopy gaps of known timing of origin in old-growth, western redcedar-western hemlock forests of coastal British Columbia. Differences in the magnitude and duration of releases were subtle among shade-tolerant western redcedar, western hemlock, and Pacific silver fir in these stands. However, documenting even subtle differences in growth release of trees is useful for reconstructing the history of past canopy disturbances, elucidating mechanisms of species coexistence, and assessing and predicting stand changes due to forest management in coastal British Columbia.

A 25% threshold, 5-year moving average, and 10-year window emerged as appropriate parameters for detecting releases using radial-growth averaging in old-growth, western redcedar-western hemlock forests of coastal British Columbia. These parameters minimized growth increases occurring as a result of regional-scale factors, such as climate, and yet maximized those following fine-scale canopy disturbances. In addition, basal area increment was found to be the growth index best suited for detecting releases in these stands. Using radial-growth averaging, the size-related trend in original ring-width values leads to errors when size structures are complex within and among populations, as is the case for western redcedar, western hemlock, and Pacific silver fir in old-growth stands. Establishing these empirically-based criteria for detecting growth releases due to canopy disturbances was an important first step towards quantifying the magnitude and duration of releases.

The magnitude and duration of releases varied according to tree species, distance from the gap center, growth rate prior to release, and diameter, the latter two of which were

the best predictors. Western hemlock and Pacific silver fir were often growing slowly both in the canopy and subcanopy, giving them tremendous potential to release. For these species, release magnitudes were generally high. In contrast, western redcedar were often growing quickly both in the canopy and subcanopy, giving them less potential to release as intensively as western hemlock or Pacific silver fir. For western redcedar, release magnitudes were generally low. Western hemlock and Pacific silver fir releases were not only more intensive than western redcedar releases, they were also more persistent. Patterns related to tree position relative to gap center emerged for trees growing along the north-south axis of gaps. Regardless of species, increasing distance from the gap center resulted in decreasing magnitude and duration of releases. However, patterns for duration were complex, as the distance effect on duration of releases was greater for trees north of the gap center.

These patterns of release can help with reconstructing the history of past canopy disturbances in coastal British Columbia. Stand reconstructions that begin with measuring tree response to natural, extant canopy gaps are powerful. By starting at this level, one can generate species- and ecosystem-specific criteria on tree release following gap formation that take into account the complex processes associated with gap formation in natural stands. Future studies involving stand reconstructions can apply the criteria from this study to more precisely estimate past canopy disturbances and historic gap boundaries over time scales of centuries. Given that coastal tree species are so long lived, and gap dynamics have been occurring for long periods in many stands, it is possible to establish long-term records of canopy disturbance history. Long-term records of past canopy disturbances can lead to better inferences of rates of gap formation, expansion, and closure in coastal forests.

Patterns of release are also helpful for better understanding tree species coexistence in western redcedar-western hemlock forests. Variation in the magnitude and duration of releases among western redcedar, western hemlock, and Pacific silver fir suggests subtle, but biologically relevant, differences in how these species grow, respond to gaps, and potentially ascend to the canopy. Compared to western hemlock and Pacific silver, western redcedar released less intensively and for shorter periods following gap formation. Subcanopy and canopy western redcedar had higher growth rates than the other two species both before and after release. These release and growth patterns imply that western redcedar relies less on gaps for growing into the canopy strata. Yet, release of large, canopy dominant western redcedar following gap formation implies complex tree interactions mediated by gaps, including competition for light and other limiting resources. Fine-scale gaps might be less important for western redcedar to recruit to the canopy, but still may play an important role in the persistence of this species in old-growth stands. Processes of gap dynamics, along with differences in life-history traits across life-stages, may explain the population structures of western redcedar, western hemlock, and Pacific silver fir in old-growth forests and the coexistence of these species through time.

Growth release of trees following the formation of natural, fine-scale canopy gaps represents important, and previously unknown, information for understanding the impacts of variable retention. Directly, such information provides a benchmark against which to compare growth release following the formation of harvested gaps. Indirectly, results from this study can be used to calibrate forest-growth models to better predict the growth release of residual canopy and subcanopy trees following high-retention harvesting. Together, these

applications represent important steps toward better management of uneven-aged stands in coastal British Columbia.