First American Dendrochronology Conference
Vancouver, British Columbia

2008 AmeriDendro

Temperate Rainforest Dynamics in Coastal British Columbia

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TREE RING LAB at UBC

Welcome to the North Shore Mountains and Old-Growth Forests

We will travel by bus to the field trip stops. If needed, sunscreen, insect repellent, first aid supplies, snacks and drinking water are available.

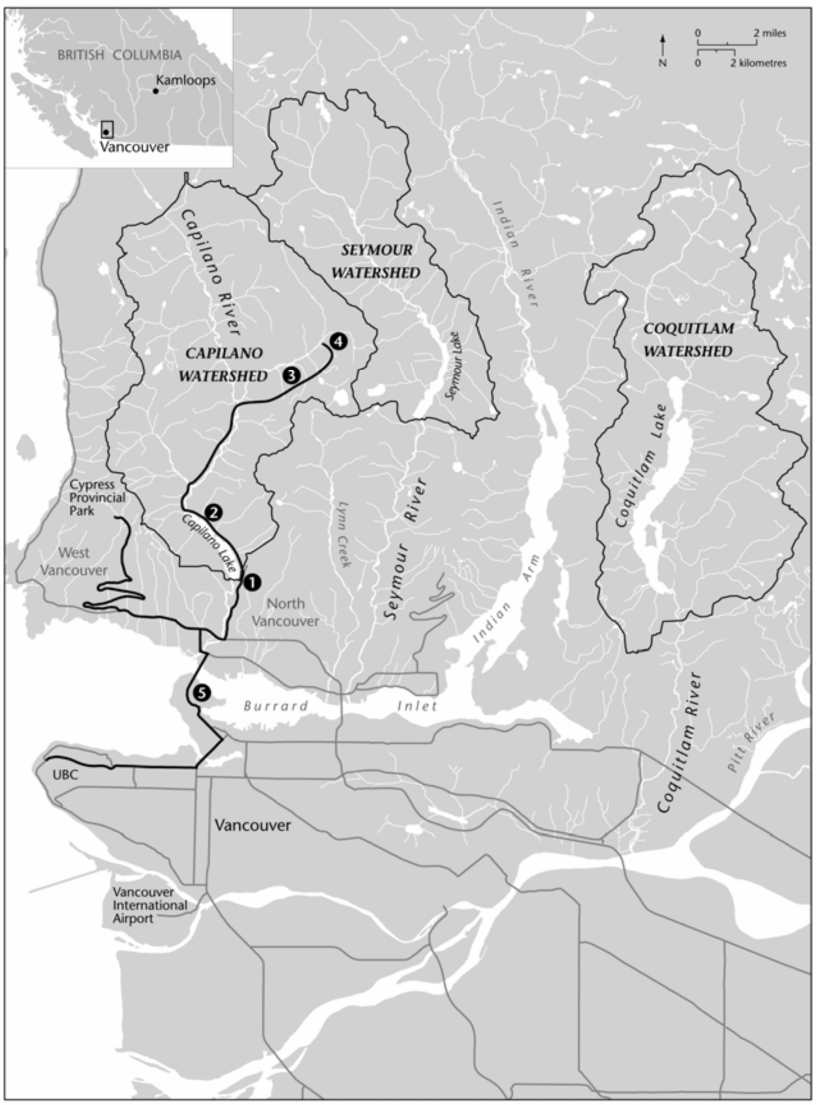
Please keep in mind the following words of caution…

	We have been given special permission to enter the Capilano River watershed, the drinking water supply for Metro Vancouver. It is essential that we follow the instructions of the Watershed Personnel and use sanitary facilities provided for the protection of the water supply. And, no smoking!
	Be cautious when walking off trail in the old-growth forest - we are steep slopes, sometimes with unstable substrates. Take your time and allow at least a meter between people as you walk. Coarse woody debris provides great opportunities for pictures but can be slippery even when dry.
	Devil's club (*Oplopanax horridus*) is aptly named. The stems and leaves of this tall, deciduous shrub are armed with yellow spines that are 5-10 mm long. The spines easily embed in your hands, but are difficult to remove!
	We are in black bear habitat. With such a large group we do not anticipate problems, but please be aware and have your camera ready!

Feel free to ask questions at any time!

Field Trip Itinerary

8:00 am		Meet at UBC - Introductions
8:15 am		Depart for Capilano River Watershed
9:00 am	1	Welcome to Capilano River Watershed at Cleveland Dam
10:00 am	2	Western hemlock looper populations and their impacts on coastal forests
10:45 am	3	Structure and dynamics of submontane western redcedar-hemlock old growth forests
12:00 pm		Lunch at Roger's Lake (box lunches provided)
1:00 pm	4	Radial growth release & responses of seedlings and saplings following the creation of canopy gaps in old-growth forests
3:00 pm	5	Depart for UBC via Stanley Park (time permitting)
5:00 pm		Return to Gage Towers at UBC



TREE RING LAB at UBC

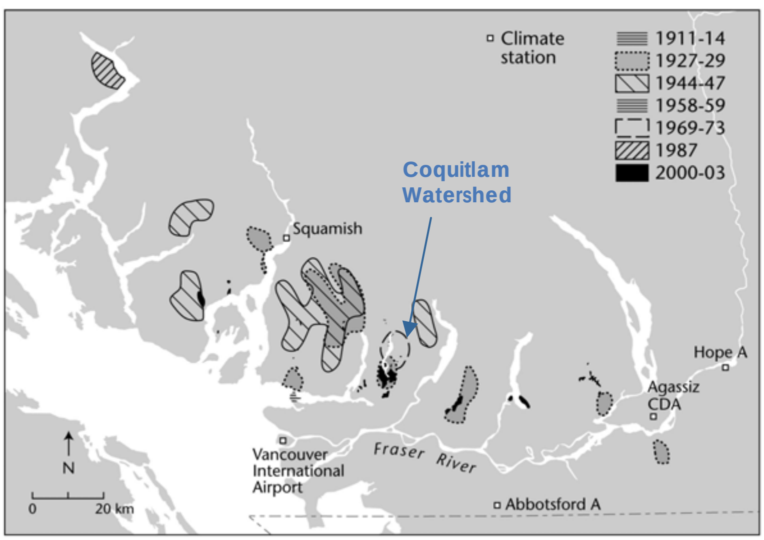
Western Hemlock Looper Populations and their Impacts on Coastal BC Forests

S.P.J. McCloskey and L.D. Daniels

Background

The western hemlock looper, (*Lambdina fiscellaria lugubrosa* (Hulst)), is an indigenous defoliator of coniferous and broadleaved tree species in British Columbia (BC). Defoliating insects are a natural disturbance agent responsible for alterations in forest composition and succession and have impacts on overall forest health. However, in coastal BC, it is unknown how forest stands change following western hemlock looper (WHL) defoliations. How are tree growth rates affected? Are there changes in crown closure? What rates of tree mortality can be expected? How does snag frequency change? What is the response of the understory vegetation? This report addresses these questions by summarizing three studies:

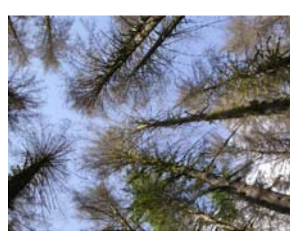
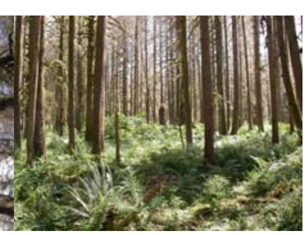
(a) comparative analysis of the effects of the 2000-3 western hemlock looper outbreak,
(b) a test for linkages between outbreaks and antecedent climatic conditions, and
(c) historical reconstruction of past outbreaks.



Study Locations

To study the impacts of the 2000-3 western hemlock looper outbreak, we established 15 study plots representing three severities of defoliation, light (5-25% visible defoliation, n=5), medium (26-65%, n=5), or severe (>65%, n=5) in the Coquitlam River watershed, 40 km northeast of Vancouver. For our investigation of the links between climate and western hemlock looper outbreaks, we assessed a wider area consisting of the south coast of mainland BC.


Examples of forest change ▸ due to defoliation by looper

Forest Impacts

Although the most recent outbreak began in 2000, reductions in basal area increments were not apparent until 2001 at which point many trees ceased growth and died, especially at the severely-defoliated sites (Figure 1). Tree mortality continued in the years following the outbreak, as severely defoliated trees succumbed (Figure 2).

The loss of needles through herbivory and the death of large numbers of canopy trees directly altered the physical structure of the forest stands in our study area by significantly increasing canopy openness. Using hemispherical photography, we measured average canopy openness to be 5% at lightly-, 13% at moderately- and 24% at severely-defoliated sites. Following three years of continuously severe defoliation by western hemlock looper, the five severely-defoliated sites that recorded the highest levels of canopy openness also had the greatest vascular plant understory richness and groundcover (Figure 3). Few tree seedlings or saplings survived at these sites leading to the establishment of a diverse understory that lacked a seedling bank.

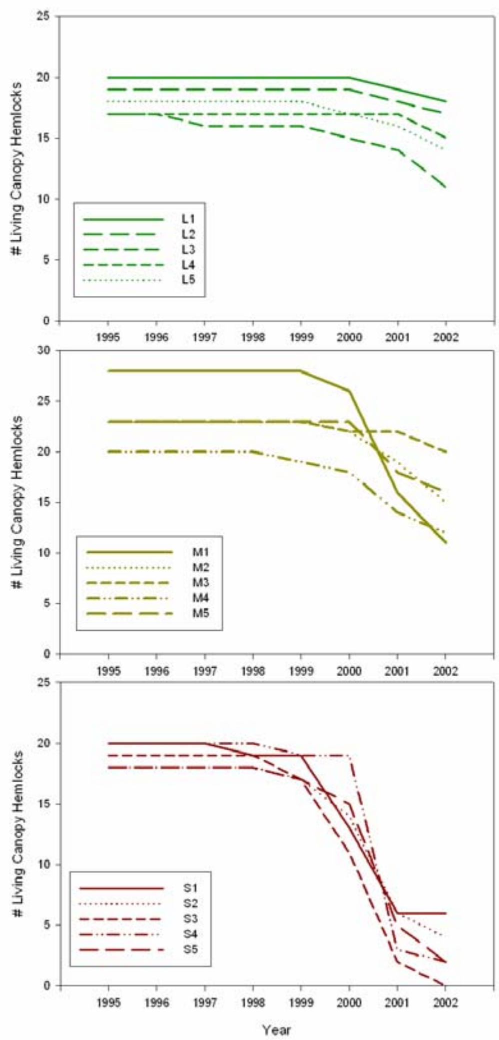


Figure 1. Number of living western hemlock canopy trees by year for a) lightly, b) moderately and c) severely defoliated sites during the 2000-2003 western hemlock looper outbreak in the Coquitlam River watershed. Trees and recent snags were cored in 2003 and years of last radial growth were reconstructed using crossdated, species- and site-specific ring-width chronologies.

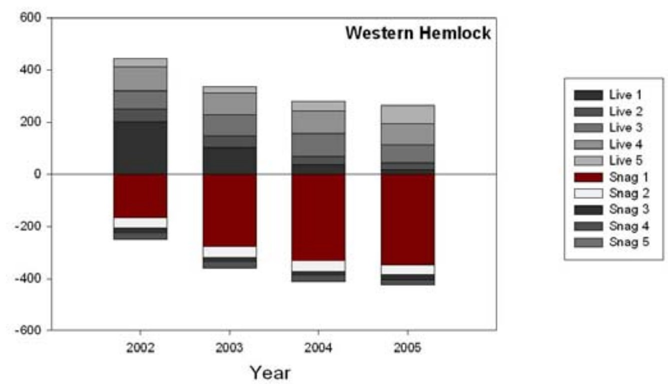


Figure 2. Number of western hemlock trees by health class (1=1-19% live canopy, 2=20-39%, 3=40-59%, 4=60-79%, 5=80-100%) and snags by decay class (1=newly dead coincident with the 2000-3 western hemlock looper outbreak, 2-5= advanced decay, death prior to the 2000-3 outbreak) in all lightly, moderately and severely defoliated sites.

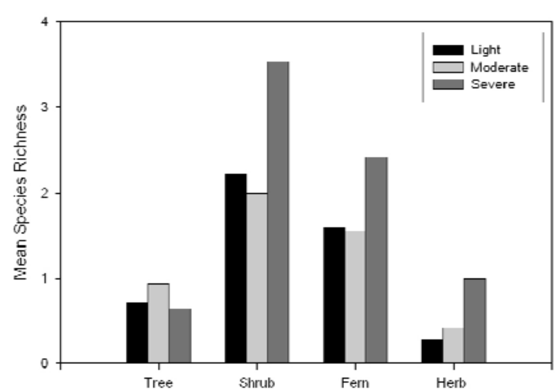


Figure 3. Mean understory species richness by life form for lightly-, moderately- and severely-defoliated sites

Climatic Driver

Western hemlock looper populations along coastal British Columbia have undergone seven episodes of outbreak from 1911 to 2004, leading to visible defoliation of western hemlock-dominated forests. We analyzed local meteorological records to develop a moisture stress index of combined temperature and precipitation data that identified periods of warm, dry climate between 1895 and 2004. A high moisture stress index in June was associated with the onset of visible defoliation by western hemlock looper populations later that year (Figure 4a). A high moisture stress index over the entire growing season (May to September) was associated with conditions 2 years before visible defoliation events (Figure 4b), providing a trigger for populations to increase to outbreak levels in subsequent years. We hypothesized that warm, dry conditions during these periods improve the survival of western hemlock looper larvae and facilitate population increases.

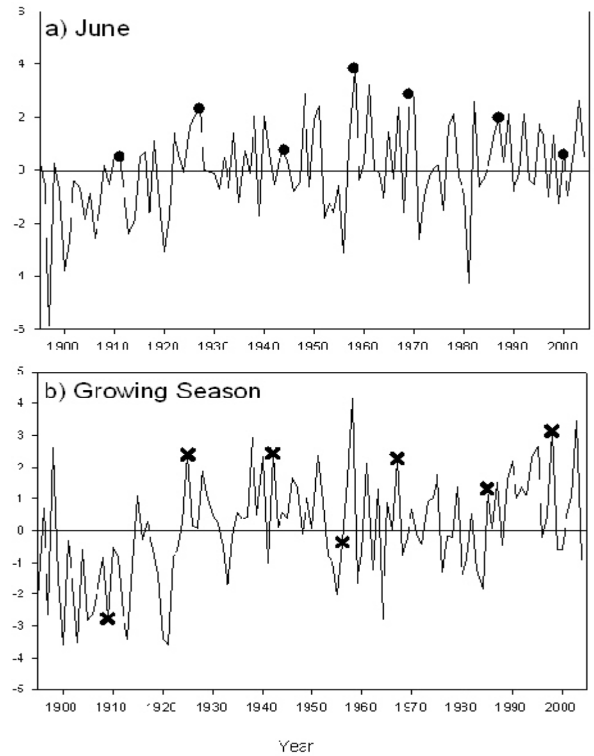


Figure 4. Moisture stress indices for a) June, and b) May-September growing season. Dots in a) indicate significant correlation with the initial year of western hemlock looper outbreaks. X's in b) indicate significant correlation with conditions 2 year antecedent to western hemlock looper outbreaks.

Reconstructing Past Outbreaks

We identified a "tree-ring signature" for trees that had experienced past western hemlock looper defoliations by quantifying the radial growth patterns of trees that survived known defoliations on Coquitlam Island during the 20th century. To do this, we compared the tree-ring series of western hemlock and western redcedar trees. Both species of tree responded similarly to historical climate conditions, yet differed in their growth rates following known western hemlock looper defoliations on the island. Immediately following each of the four documented periods of western hemlock looper outbreaks on Coquitlam Island, the growth of western hemlock trees was much slower or suppressed relative to their western redcedar neighbours (Figure 5). By assessing tree growth following known outbreaks, we verified that tree rings can be used to reconstruct historic outbreaks.

To reconstruct historic outbreaks prior to the first documented western hemlock looper outbreak in 1911, we compared long tree-ring series of western hemlock *versus* western redcedar. We identify four periods of suppressed growth that were unique to western hemlock, which provided evidence that several western hemlock looper outbreaks had occurred on Coquitlam Island during the 19th century (Figure 5). Our results extended the historical record of western hemlock looper outbreaks by over 100 years and provided evidence of outbreaks in 1803-9, 1829-1831, 1865-9 and 1901-6.

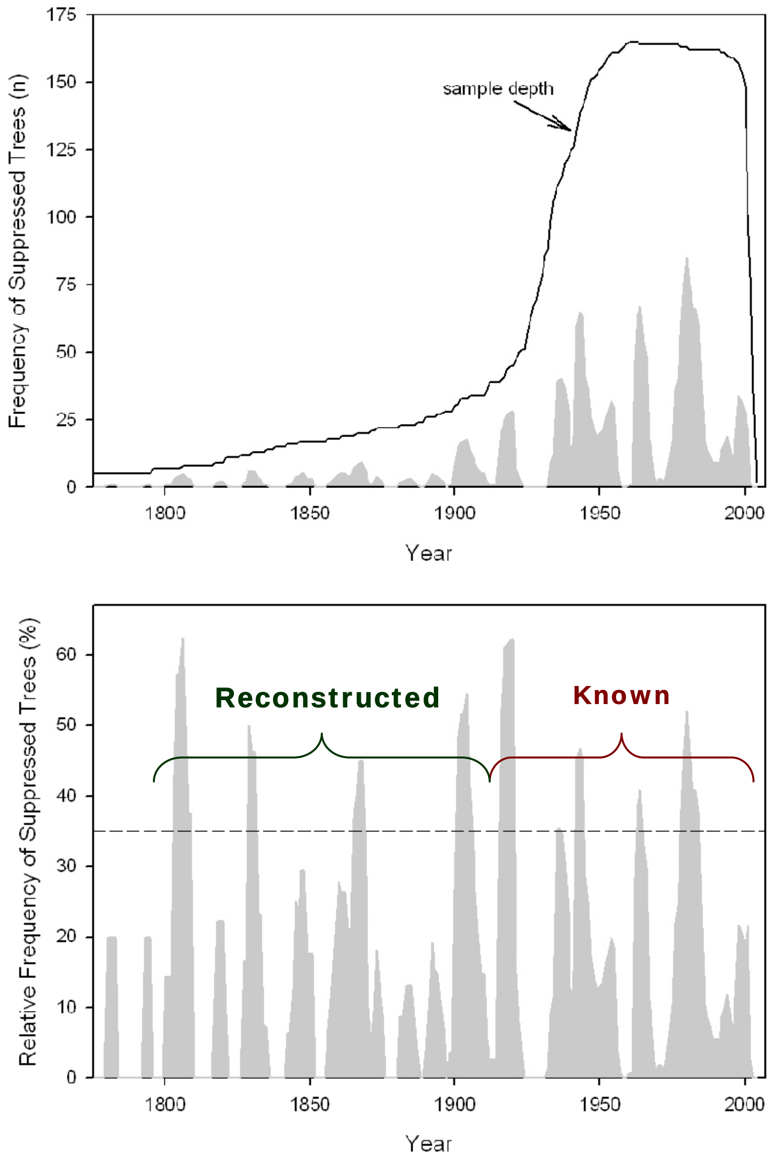


Figure 5 The absolute frequency (upper graph) and relative frequency (lower graph) of western hemlock trees sampled on Coquitlam Island showing significant radial growth suppression compared to neighbouring western redcedar trees (grey bars). Radial growth suppressions were considered significant when the ring-width index was ≥1.28 standard deviations below the average. The upper graph shows the sample depth line as the number of western hemlock trees in the dataset in each year. The lower graph shows a dashed line at 35% indicating the threshold percentage of suppressed trees used to identify known and reconstructed outbreaks of western hemlock looper.

Funding Acknowledgments

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TREE RING LAB at UBC

Western redcedar population dynamics in old-growth forests

Lori D. Daniels

Background

In coastal British Columbia, western redcedar-dominated, late-successional forests are structurally complex with deep multi-layered canopies, large trees that are >250 years old, and abundant coarse woody debris. These forests are presumed to be "old-growth" forests in which fine-scale gaps are the dominant disturbance regime, accounting for their structural diversity.

I have used tree-ring analyses to investigate western redcedar regeneration dynamics in old-growth forests. Western redcedar dominates canopies of many stands, but is rare in the understory, although it tolerates shade. The traditional interpretation is that western rededar depends on catastrophic disturbance to regenerate and that it is replaced through succession by western hemlock and Pacific silver fir, which are abundant in the understory. Canopy-dominant redcedars were perceived as even-aged, post-disturbance cohorts and it was assumed populations were declining in absence of catastrophic disturbances, given low abundance of regeneration.

Assumptions of the Traditional Paradigm

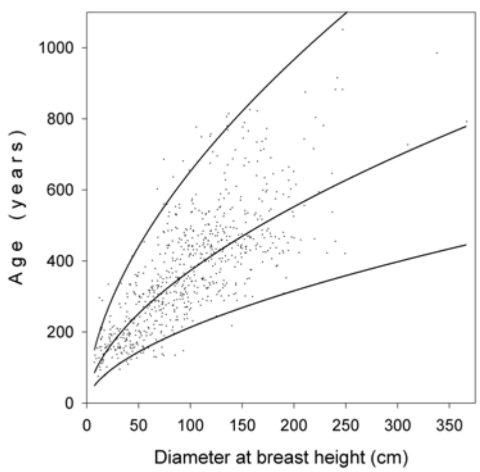
In my research in the Capilano watershed, I have investigated four assumptions underlying the tradition interpretation of western redcedar dynamics:

(1) Tree size indicates age.
(2) Populations establish as even-aged, post-disturbance cohorts.
(3) Abundant coarse woody debris represents recent tree mortality.
(4) Regeneration is insufficient to maintain canopy dominance.

Testing Assumptions

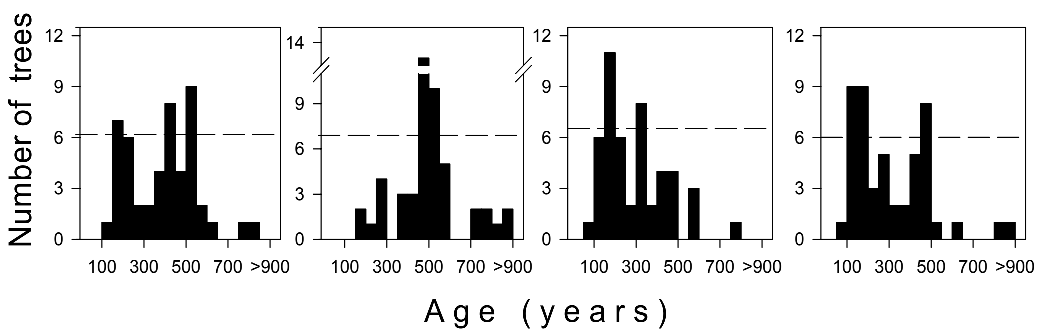
Using tree-ring evidence, I show that population dynamics of western redcedar are a combination of gap-phase establishment and a continuous mode of recruitment from the subcanopy to the canopy. Although western redcedar can regenerate following catastrophic disturbances such as fire or logging, stand-level disturbances are not necessary to sustain redcedar in old-growth forests. The four assumptions underlying the catastrophic paradigm of redcedar regeneration in old-growth stands were not supported by age and growth data derived from dendroecological analyses.

Assumption 1. Tree size indicates age. Tree size proved to be a poor surrogate for age. The largest trees in a stand are not necessarily the oldest trees and dominant trees do not necessarily represent a single age cohort.



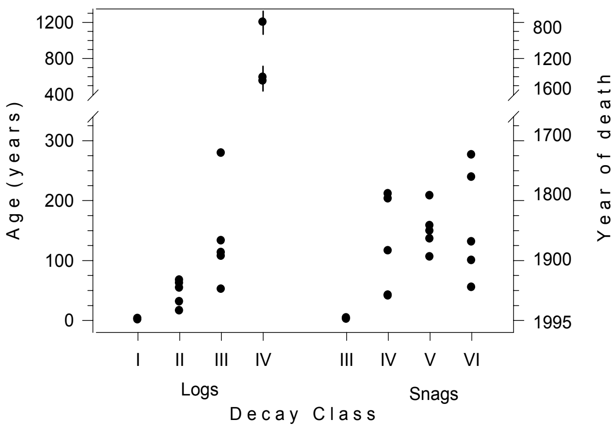
Relationship between age and dbh for western redcedar with dbh > 7.5 cm. The middle curve marks the regression of age on dbh [log10 (age) = 1.435 + 0.568 log10(dbh)].Upper and lower curves mare the regression line +/-1.96 SEE, including 95% of observations (n = 720) (from Daniels et al. 1995).

Assumption 2. Populations establish as even-aged, post-disturbance cohorts. Uneven age-structures and low initial growth rates suggest that regeneration following catastrophic disturbance is not necessarily the dominant mode of regeneration of western redcedar. Rather, regeneration following fine-scale, gap-phase disturbances more common than previously thought.



Age frequency distributions of western redcedar in the tree layer (dbh >7.5cm) of four sites along the East Capilano Creek. The x-axis labels show the upper limits of 50-year classes, except the oldest class which includes all trees with age > 850 years. The broken lines mark the mean class frequencies + 1 standard deviation of the mean; classes with frequencies above the line are "peak" classes (after Daniels et al. 1995).

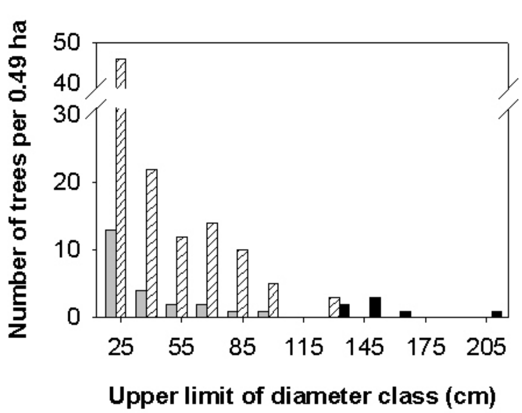
Assumption 3. Abundant coarse woody debris represents recent mortality. Western redcedar snags and logs have accumulated over several centuries. This coarse woody debris is persistent and represents centuries of accumulated tree mortality rather than recent tree deaths.



Age and year of death for 15 logs and 17 snags of western redcedar. Age was calculated as 1995 minus the year of death. For logs in classes I to III, year of death was determined using dendrochronological methods including statistical crossdating. Class IV logs were aged by radiocarbon-dating; the vertical lines show 95% confidence intervals around the age estimates. The year of death of all snags determined by statistical crossdating (from Daniels et al. 1997).

Assumption 4. Regeneration is insufficient to maintain canopy dominance. Based on preliminary evidence, I hypothesized that western redcedar recruitment from the subcanopy to the canopy may be independent of gaps. Thus, western redcedar populations may be maintained in old-growth forests in spite of low density of seedlings and saplings in the understory. In contrast, western hemlock and Pacific silver fir depend on canopy gaps to recruit to the canopy and thus require an abundance of seedlings, saplings and subcanopy trees that are able to respond rapidly and exploit resources that become available in a gap. Out current research tests this hypothesis using three lines of evidence:

(1) Monitoring of permanent research plots to compare rates survivorship, mortality and recruitment between canopy strata;
(2) Analysis of regeneration dynamics in canopy gaps, including seedling ages, growth rates and responses to canopy gaps; and,
(3) Comparative analysis of western redcedar, western hemlock and Pacific silver fir radial growth responses to canopy gaps.



Diameter distribution of subcanopy and canopy trees (dbh > 10 cm) in the forest at field trip stop 3. Tree species are western redcedar (black), western hemlock (hatched) and Pacific silver fir (grey). Trees are grouped in 15 cm diameter classes from 10 cm (after Daniels 1994).

When this plot was established in 1992, there were 255 western redcedar seedlings and saplings in the understory, compared to c. 10,600 western hemlock and 2,450 Pacific silver fir.

Management Implications

The traditional and contemporary interpretations of old-growth forest dynamics imply different strategies for managing western redcedar. According to the traditional paradigm, catastrophic, stand-level disturbances are needed to establish dominant populations of western redcedar. Thus, harvesting at relatively coarse scales was perceived as necessary to manage and sustain the species. In contrast, this study showed that western redcedar successfully regenerates in association with disturbances of a range of spatio-temporal scales, including fine-scale canopy gaps. These results provide an ecological precedent for use of a range of silvicultural systems, including clearcuts through single-tree harvesting and protection forest, when managing western redcedar in coastal British Columbia.

Ecosystem management aims to conserve biodiversity and maintain ecosystem function while sustaining renewable resources. To achieve these goals, patterns of natural variation can be used to guide management activities. It is now recognized that traditional even-aged approaches to forest management substantially alter the structural characteristics of coastal old-growth forests of British Columbia and these changes have significant consequences for the forest biota. Variable retention (VR) silviculture aims to maintain trees of a range of ages and structural diversity within stands and distributes cutting over periods of decades to centuries, emulating both partial stand disturbances and canopy gap disturbance regimes more closely than clearcut harvesting does. VR has been proposed as one method toward a sustainable approach for timber management of coastal old-growth forests.

From an ecological perspective, successful VR needs to maintain structural attributes in the managed forest while sustaining a diverse species composition. To achieve these goals requires a comprehensive understanding of the regeneration dynamics of individual species in the context of the multiple disturbance regimes, including harvesting, that influence old-growth forests. Such knowledge provides both ecologically-based guidelines for management decisions as well as criteria for evaluating and monitoring outcomes and success. As this study has illustrated, many questions remain unanswered about the dynamics, processes, and mechanisms that allow tree populations to be sustained and to coexist in old-growth forests. The contemporary ecological paradigm provides a framework for addressing these types of questions. The answers are needed to guide management decisions and to ensure future successful management and protection of the coastal old-growth forests of British Columbia.

Funding Acknowledgements

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Growth release of trees following fine-scale canopy disturbances in old-growth forests of coastal British Columbia

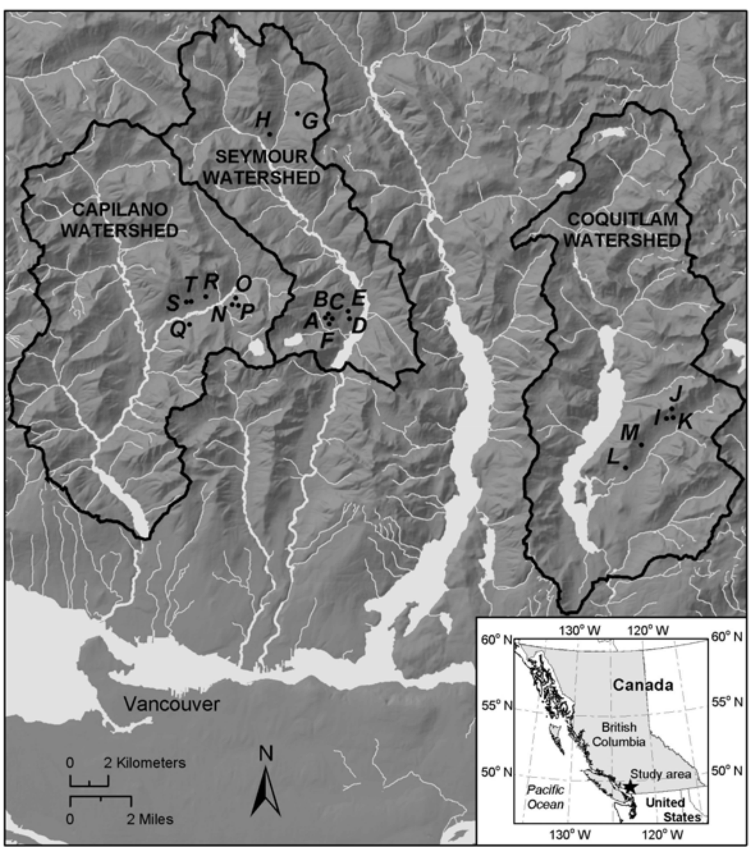
A.B. Stan and L.D. Daniels

Background

Fire and other stand-destroying disturbances are rare throughout the wetter parts of the coastal temperate rainforest of British Columbia. As a result, forests here are mostly late successional, formed and maintained through fine-scale canopy disturbance and recovery processes. The overall objective of our research was to examine growth release of trees following the formation of natural, fine-scale canopy gaps in old-growth forests of coastal British Columbia. To address this objective we (1) estimated the timing of origin of natural canopy gaps, (2) quantified the number of trees that showed a release pattern following the formation of these gaps, (3) quantified the duration and magnitude of releases in response to gap formation, and (4) estimated the influence of different tree- and gap-level variables on the duration and magnitude of releases.

Study Area

We conducted this research in the Capilano, Seymour, and Coquitlam River watersheds in the Coast Mountains of southwestern British Columbia (Figure 1). All study sites are located in stands of old-growth forest between 300 and 700 m a.s.l. In these stands, western redcedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*), and Pacific silver fir (*Abies amabilis*) dominate the canopy.



Methods

We used dendroecological methods to determine the timing of formation of 20 natural canopy gaps in old-growth stands. All gaps were dated according to the year of death and/or fall of the one or two uprooted trees responsible for the opening in the canopy. We extracted two increment cores from trees (dbh ≥ 10 cm) growing around the boundary of, within, or in the forest adjacent to each gap. A subset of these cores was used to calibrate a radial-growth averaging technique to differentiate growth increases caused by fine-scale canopy disturbance from those related to climate or other regional-scale factors. We then applied the calibrated release-detection method to quantify the number, duration, and magnitude of releases following gap formation.

Figure 1. Location of the study area and sites.

Number of Releases

In total, 87% (304 of 348) of all individuals growing around or within 20 gaps had an increase in growth ≥ 25% within 10 years of gap formation (Figure 2). Releases were evenly distributed between the study species in canopy and subcanopy positions. However, trees were not evenly distributed among species and size classes (Figure 2). Western redcedar and western hemlock occurred in the greatest numbers in the canopy, while most trees in the subcanopy were western hemlock and Pacific silver fir.

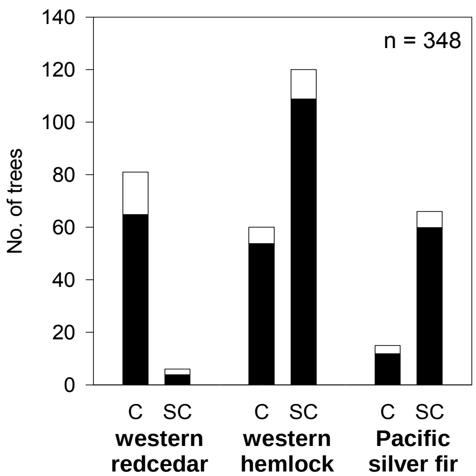


Figure 2. Frequency distribution of canopy (C) and subcanopy (SC) western redcedar, western hemlock, and Pacific silver fir growing around or within 20 gaps of known timing of origin. The number of trees that showed a release pattern following gap formation is depicted in black; trees that did not are in white.

Duration of Releases

The median duration of releases was approximately 37, 26, and 21 years for western hemlock, Pacific silver fir, and western redcedar, respectively (Figure 3). For western hemlock and Pacific silver fir, increasing diameter resulted in decreasing duration of releases. This pattern was opposite for western redcedar, as increasing diameter resulted in increasing duration of releases.

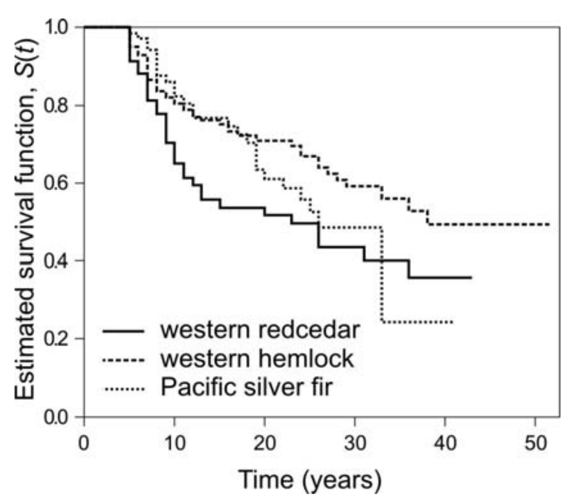


Figure 3. Survival functions, $S(t)$, for duration of releases of western redcedar, western hemlock, and Pacific silver fir. $S(t)$ is the probability that a release will survive beyond time t, having to survived to time t. The survival functions are nonparametric, product-limit (Kaplan-Meier) estimates.

Magnitude of Releases

The magnitude of releases was highest for western hemlock and Pacific silver fir and lowest for western redcedar (Figure 4). For all species, there was a pattern of decreasing percent-growth change with increasing diameter the year of release and growth prior to release. In addition, the effect of prior growth varied significantly among trees of different diameters. For the largest diameter trees, prior growth had a minimal effect on percent-growth change. However, for the smallest diameter trees, prior growth had a more substantial effect, with higher values of prior growth resulting in lower values of percent-growth change.

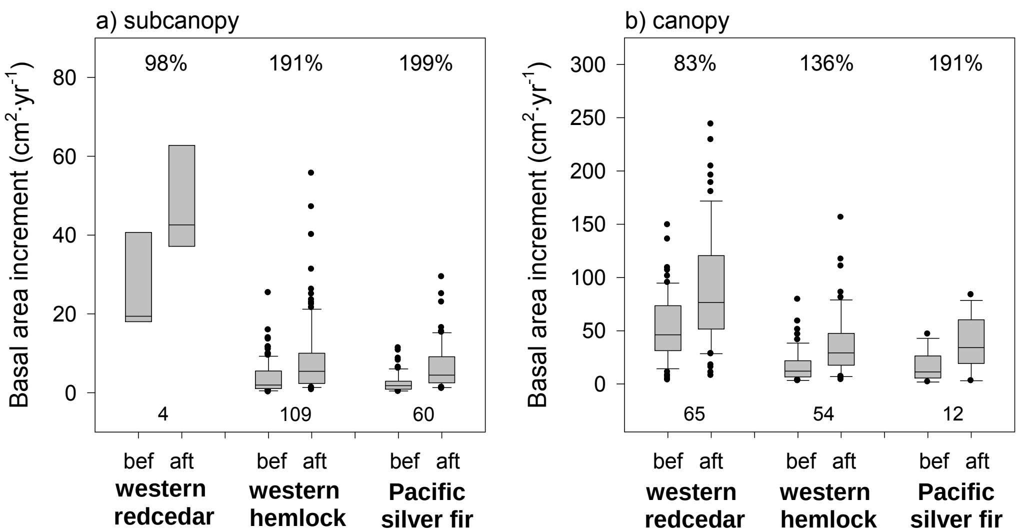


Figure 4. Box plots of mean basal area increment five years before (bef) and after (aft) the onset of release for (a) subcanopy and (b) canopy trees. Values at the top and bottom of the plots are mean percent-growth change and sample size, respectively. The horizontal line in each box is the median, 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.

Why quantify Releases?

Reconstructing canopy disturbances

Release attributes such as magnitude and duration are 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 at the level of the individual tree goes beyond the traditional binary classification of release or no release and allows for inferences about the type of gap and location of tree relative to the gap.

Tree species coexistence in coastal, old-growth forests

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, western hemlock, and Pacific silver fir in old-growth forests of coastal British Columbia. Variation in the magnitude and duration of releases among the study species suggests subtle, but biologically relevant, differences in how they respond to gaps and potentially grow into the canopy.

Management implications

Growth release of trees following the formation of natural, fine-scale canopy gaps represents important 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.

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School of Resource and Environmental Management, SFU

Department of Geography, UBC

Responses of Seedlings and Saplings to Canopy Gaps in Coastal Old-Growth Forests.

J. Passmore, L. Daniels, K. Lertzman, and A. Stan

Background

In forests where large, stand-replacing disturbances are rare, fine-scale disturbances forming small gaps in the canopy provide new opportunities for recruitment and regeneration and have a dominant influence on community and population dynamics. To better understand the response of seedlings and saplings to fine-scale disturbances in the Coastal Western Hemlock Zone of British Columbia, we examined patterns of regeneration and recruitment within and adjacent-to canopy gaps of known date of origin in three watersheds near Vancouver, BC. We sought to answer the following questions:

(1) Do gaps affect the abundance of seedlings and saplings?
(2) Do gaps affect establishment of new recruits?
(3) Do gaps affect patterns of radial growth by initiating releases?

Study Locations

We sampled within and adjacent-to 20 gaps of known date of origin. The gaps were located in stands of old growth forest within the Coquitlam, Capilano, and Seymour river watersheds, currently managed by the GVRD to supply Vancouver's drinking water. All stands fell within the Very Wet Maritime Coastal Western Hemlock (CWHvm) biogeoclimatic subzone.

Field and Laboratory Methods

At each of the 20 gaps, we established four two-by-two meter plots within the boundary of the expanded gap (gap plots), and four two-by-two meter plots in the adjacent closed-canopy forest (forest plots). In each plot we measured the abundances of western hemlock, Pacific silver fir and western redcedar seedlings and saplings across five height classes. From a subset of six gaps, we destructively sampled seedlings and saplings of each species from the gap and forest plots for tree-ring analyses. These samples were processed in the lab according to standard dendroecological techniques. We determined the age of each sample as the year attributed to the pith, and identified periods of suppression and release using a radial-growth averaging technique.

Analysis and Results

Abundance

The abundances of Pacific silver fir seedlings and saplings in height classes 1-5 did not vary significantly between gap and forest sites (Figure 1). However, western hemlock and western redcedar seedlings in height class 1 were significantly more abundant in gap versus forest sites. These results suggest that gaps increase the recruitment and/or survival of newly established hemlock and cedar seedlings, but do not have a large influence on patterns of recruitment and/or survival in Pacific silver fir seedlings and saplings. Across height classes and locations, western hemlocks were also significantly more abundant than western redcedar and/or Pacific silver fir.

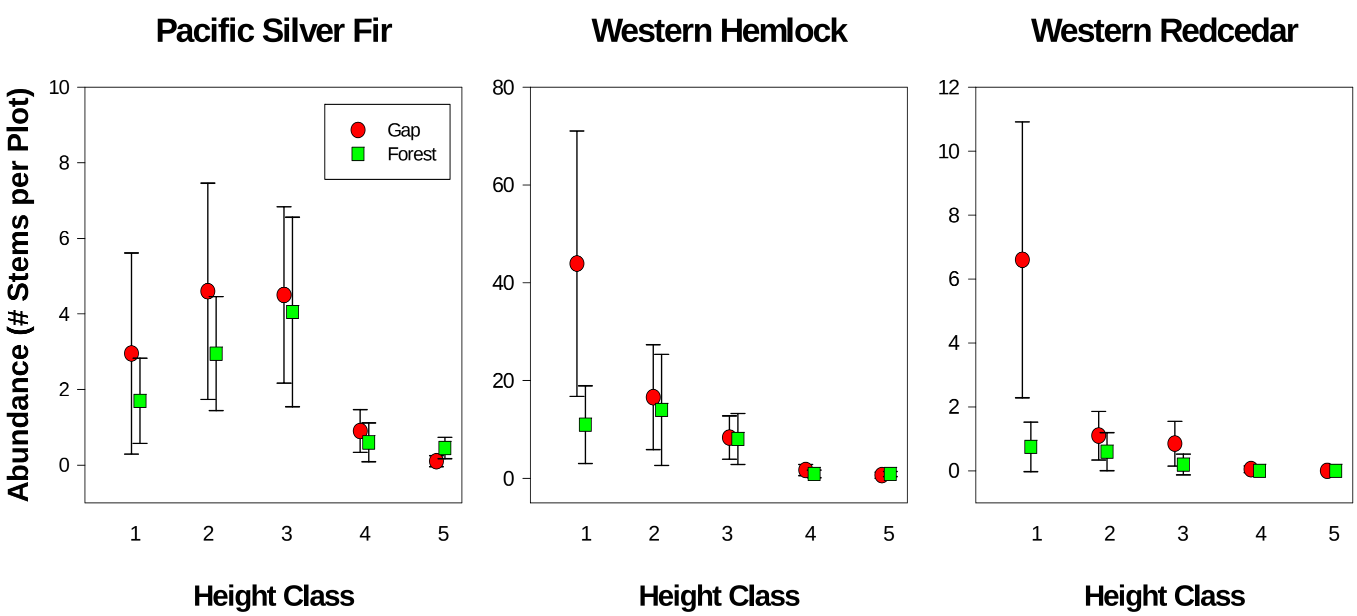


Figure 1. Abundances (+/- 95% CI's) of Pacific silver fir, western hemlock, and western redcedar regeneration in gap (circle) and forest (square) sites. Height Class 1 includes seedlings less than 10 cm tall, but greater than one-year in age; Height Class 2 includes seedlings between 10 and 30 cm tall; Height Class 3 includes seedlings between 30 and 130 cm tall; Height Class 4 includes saplings between 130 and 300 cm tall; and Height Class 5 includes saplings greater than 300 cm tall, but less than 10 cm in diameter at breast height.

Age and Establishment

Saplings collected from forest sites were significantly older than saplings collected from gap sites (Table 1). Seedlings, in contrast, did not vary significantly in age between locations. The advanced age of saplings from forest plots suggests that gaps increase rates of vertical growth in saplings, speeding the rate at which saplings ascend into the sub-canopy and lowering their average age. Similarities in the ages of seedlings collected from gap and forest plots suggest that gaps do not have a large influence on patterns of establishment or recruitment out of the seedling layer. However, the proportions of seedlings and saplings that established within 10-years of the gap-formation dates were higher in gap versus forest sites (Figure 2). Although this trend was significant only in Pacific silver fir, it was observed across all three species and suggests that gaps improve conditions for the establishment and/or survival of new recruits. Nevertheless, our results also indicate that most seedlings and saplings established at least 10-years prior to gap-formation, regardless of location. This finding draws attention to the importance of seedling and sapling banks (advanced regeneration) in these stands.

Table 1. Ages (+/- SE) of seedlings and saplings collected from gap and forest sites.

Species	Size Class	Gap	Forest
Pacific Silver fir	Seedling	47.0 +/- 6.2	48.2 +/- 7.0
Western hemlock	Seedling	23.8 +/- 6.2	25.7 +/- 7.0
Western redcedar	Seedling	17.8 +/- 6.4	19.4 +/- 7.0
Pacific Silver Fir	Sapling	74.8 +/- 19.2	102.2 +/- 20.0
Western hemlock	Sapling	66.8 +/- 19.2	72.3 +/- 20.0

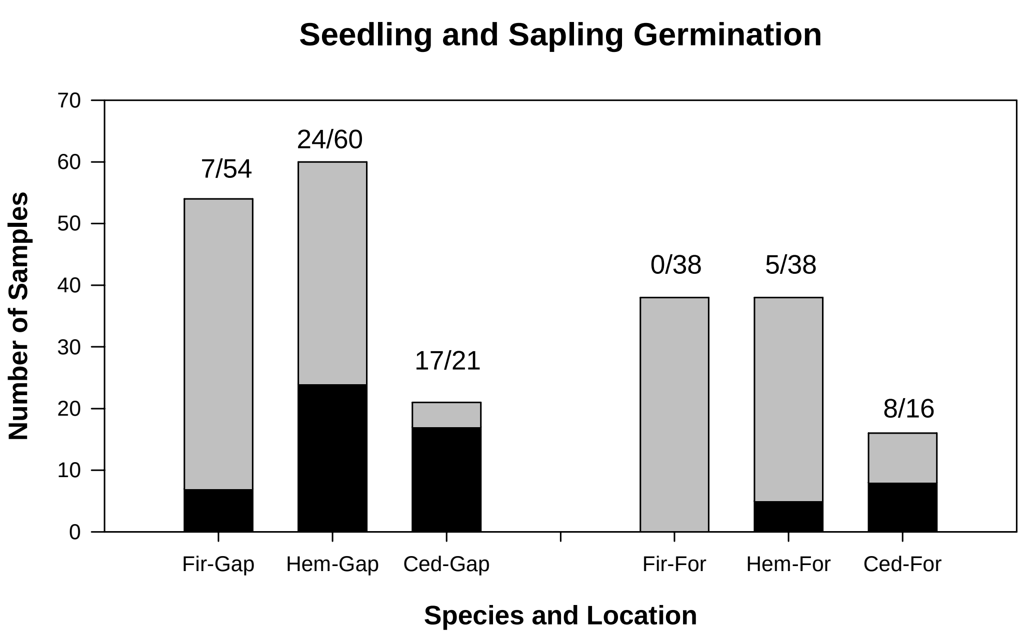
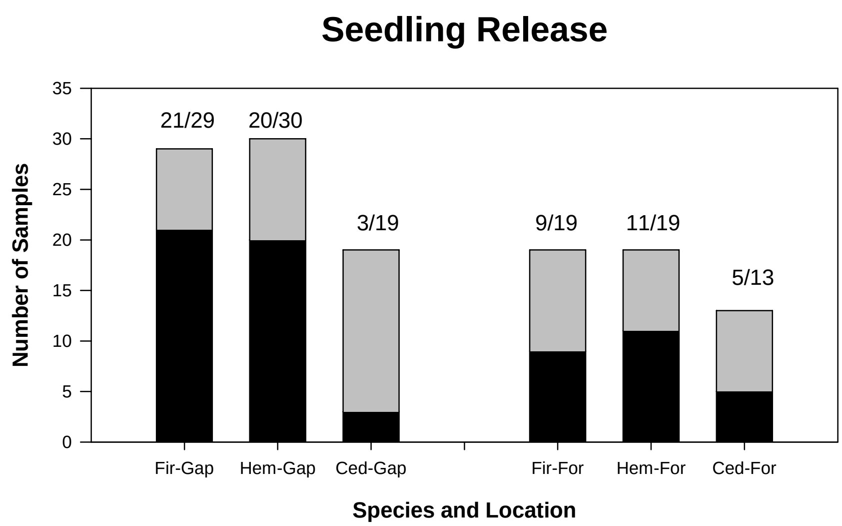


Figure 2. Number of seedlings and saplings that did (black bar) and did not (grey bar). establish within 10-years of the gap-formation dates, separated by species (Pacific silver fir, western hemlock, and western redcedar) and location (gap and forest sites).

Release

The proportions of seedlings and saplings that released within 10-years of the gap-formation dates were greater in gap versus forest sites (Figure 3). This trend was observed across species with the exception of cedar seedlings. Although differences between gap and forest sites with respect to the proportion of samples experiencing a release within 10-years of the gap-formation dates were significant only for Pacific Silver fir, the finding that releases were more common in gap versus forest sites suggests that gaps improve conditions for growth in seedlings and saplings. Moreover, Irrespective of release criteria, average growth rates during the period 10-years following gap-formation were significantly higher than average growth rates during the period 10 years prior to gap-formation. These differences suggest that gaps improve conditions for radial growth in both saplings and seedlings.



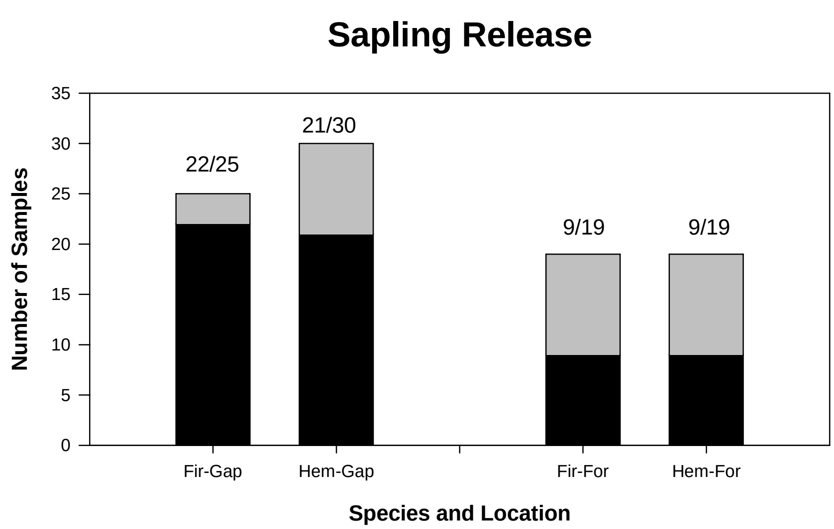


Figure 2. Number of seedlings and saplings that did (black bars) and did not (grey bars) exhibit radial growth release within +/- 10 years of the gap-formation dates, separated by species and location (gap and forest sites).

Management Implications

Our results have direct applications to forest management. Knowledge of patterns of regeneration and recruitment in natural gaps can be used to predict future growth and forest composition following the creation of human-made gaps. For example the abundance, composition, and growth rates of seedlings and saplings in natural gaps suggest possible patterns of recruitment and regeneration in similar human-made gaps. This research also provides valuable baseline ecological information that enables future studies to compare the effects of natural versus human-made gaps, and to assess the degree to which human-made gaps emulate natural disturbance processes. For example, the abundance, composition and radial growth of natural regeneration in human-made gaps can be compared to the corresponding values observed in this study.

Conclusions

Our results support the paradigm of gap-phase replacement. Gaps supported higher densities of seedlings and saplings, promoted the establishment of new recruits, and initiated radial growth releases in pre-existing seedlings and saplings. Our results also suggest that most seedlings and saplings in gaps established and persisted under closed-canopy conditions prior to gap-formation. These findings provide insight into the natural dynamics of coastal old-growth forests and supply valuable baseline ecological information relevant to ecosystem-based management.

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