Western redcedar population dynamics in old-growth forests: Contrasting ecological paradigms using tree rings¹

by Lori D. Daniels²

In coastal British Columbia, late-successional forests dominated by western redcedar (*Thuja plicata* Donn ex D. Don) are structurally complex, with deep multi-layered canopies, large trees that are > 250 years old, and abundant coarse woody debris (CWD). These forests are presumed to be "old-growth" forests in which fine-scale gaps are the dominant disturbance regime, accounting for their structural diversity. In this study, I have used tree-ring analyses to investigate western redcedar regeneration dynamics in these old-growth forests. Western redcedar dominates canopies of many stands, but is rare in the understorey although it tolerates shade. The traditional interpretation is that western redcedar depends on catastrophic disturbance to regenerate and that it is replaced through succession by western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and Pacific silver fir (*Abies amabilis* (Dougl. ex Loud.) Dougl. ex J. Forbes), which are abundant in the understorey. Dominant trees are perceived to represent an even-aged, post-disturbance cohort and the lack of regeneration indicates a population decline in the absence of catastrophic disturbances. In this paper, I investigate four assumptions underlying this interpretation: (1) Tree size indicates age. (2) Populations establish as even-aged, post-disturbance cohorts. (3) Abundant CWD represents recent mortality. (4) Regeneration is insufficient to maintain canopy dominance. 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. Specifically, size is a poor surrogate for tree age. Age distributions from 15 sites revealed uneven-aged populations, rather than single post-disturbance cohorts. Both logs and snags of western redcedar may persist more than 270 years; they do not represent recent mortality that is disproportionate to the number of live western redcedar in canopy. The regeneration niches of western redcedar and western hemlock overlap. For both species, gap-phase disturbances result in substrate suitable for successful seedling establishment. Preliminary results from dendroecological analysis of radial growth rates of trees in the subcanopy and canopy strata suggest that western hemlock and Pacific silver fir depend on gaps to recruit to the upper canopy, but recruitment of western redcedar may be independent of canopy gaps. I propose that differences in mode of recruitment to the canopy may explain the differences in population structures between western redcedar, western hemlock, and Pacific silver fir in the old-growth forest. These results provide an ecological precedent for use of a range of silvicultural systems, including clearcuts through single-tree harvesting and protection forests, when managing western redcedar in coastal British Columbia.

Key words: Coastal British Columbia, disturbance regimes, regeneration dynamics, *Thuja plicata*, variable retention silviculture

Dans la région côtière de la Colombie-Britannique, les forêts de fin de succession dominées par le thuya géant (*Thuja plicata* Donn ex D. Don) possèdent une structure très complexe qui comprend un couvert forestier à strates multiples, de gros arbres âgés de plus de 250 ans et une abondance de débris ligneux grossiers. On présume qu'il s'agit de forêts anciennes dans lesquelles les trouées à petite échelle constituent le principal régime de perturbation, qui serait à l'origine de leur diversité structurale. Dans cette étude, j'ai effectué des analyses des cernes pour examiner la dynamique de régénération du thuya géant dans ces forêts anciennes. Cette essence domine l'étage supérieur de nombreux peuplements, mais elle est rare dans le sous-étage, bien que tolérante à l'ombre. L'explication traditionnelle est que le thuya géant dépend des perturbations catastrophiques pour se régénérer et que, dans le processus de succession, il est remplacé par la pruche de l'Ouest (*Tsuga heterophylla* (Raf.) Sarg.) et le sapin gracieux (*Abies amabilis* (Dougl. ex Loud.) Dougl. ex J. Forbes) qui sont abondants dans le sous-étage. On considère que les arbres dominants représentent une cohorte équienne établie après une perturbation, et que l'absence de régénération indique un déclin de la population en l'absence de perturbation catastrophique. Dans cette étude, je vérifie quatre hypothèses à la base de cette explication : 1) la taille des arbres est un indicateur de l'âge; 2) les populations sont constituées de cohortes équiennes établies après une perturbation; 3) l'abondance de débris ligneux grossiers témoigne d'une mortalité récente; 4) la régénération est insuffisante pour assurer le maintien de la dominance du couvert par le thuya géant. À l'aide de données sur les cernes, je montre que la dynamique des populations de thuya géant est une combinaison de la régénération par trouées et d'un mode de recrutement continu à partir de la strate inférieure du couvert. La taille d'un arbre est un mauvais indicateur de son âge. Les distributions d'âges déterminées pour 15 sites révèlent des populations inéquiennes plutôt que des cohortes uniques issues d'une perturbation. Le bois mort et les chicots de thuya géant peuvent persister plus de 270 ans et ils ne représentent pas une mortalité récente disproportionnée par rapport au nombre d'arbres vivants présents dans le couvert forestier. Les niches de régénération du thuya géant et de la pruche de l'Ouest se chevauchent. Les perturbations produisant des trouées créent un substrat approprié à l'établissement des semis des deux espèces. D'après les résultats préliminaires d'une analyse dendroécologique de la croissance radiale des arbres des strates inférieure et supérieure du couvert, la pruche de l'Ouest et le sapin gracieux dépendraient des trouées pour leur recrutement à la strate supérieure du couvert, tandis que le recrutement du thuya géant en serait indépendant. Je propose que les différences dans le mode de recrutement à la strate supérieure peuvent expliquer les différences dans la structure des populations du thuya géant, de la pruche de l'Ouest et du sapin gracieux dans la forêt ancienne. Ces résultats constituent un précédent écologique pour l'utilisation d'un ensemble de régimes sylvicoles (notamment coupes à blanc, récolte d'arbres individuels et forêts de protection) dans le cadre de la gestion du thuya géant dans la région côtière de la Colombie-Britannique.

Mot clés : Côte de la Colombie-Britannique, *Thuja plicata*, rétention variable

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Introduction

Succession and disturbance regimes

In the latter part of the 20th century, ecological theory underwent a major revolution that has influenced our understanding of vegetation dynamics, biodiversity conservation, and management of biological resources (Glenn-Lewin *et al.* 1992, Pickett *et al.* 1992). Three major trends in our understanding of vegetation dynamics emerged as part of the new, contemporary paradigm. (1) Non-equilibrium dynamics. Contemporary successional theory states that vegetation change is the outcome of populations interacting with one another within a fluctuating environment (Glenn-Lewin *et al.* 1992). Disturbance at a range of spatio-temporal scales is frequent and integral to vegetation change (White 1979, Sousa 1984, Pickett and White 1985). Deterministic trajectories, long-term environmental stability, and an endpoint to succession are no longer assumed (Glenn-Lewin *et al.* 1992). (2) Multiple-scale approach. A reductionist approach has focused on mechanisms and proximate causes of vegetation change. Such research investigates process rather than endpoints or outcomes of change (Glenn-Lewin *et al.* 1992). The importance of multi-scalar processes is now widely acknowledged, resulting in new approaches and disciplines such as landscape ecology (Pickett *et al.* 1987, Pickett and Kolasa 1989, Glenn-Lewin *et al.* 1992). (3) Human impacts. Humans are now explicitly recognized as agents of disturbance and an important source of variation in vegetation dynamics (Pickett *et al.* 1992).

This paradigm shift has profoundly changed our understanding of late-successional or old-growth forest communities. According to the classical paradigm, old-growth or “climax” forests develop under stable conditions and in the absence of disturbance. In contrast, contemporary models of forest development acknowledge the ubiquitous influence of fine-scale canopy-gap disturbances in late-successional forests (Oliver 1981, Oliver and Larson 1990, Franklin *et al.* 2002). In this context, Wells *et al.* (1998) have defined “old growth” as a forest in which processes of gap dynamics predominate. Old-growth forests develop as trees recruit from the understorey to the canopy under the influence of frequent, fine-scale canopy-gap disturbances. According to this contemporary definition, “old-growth” is a dynamic ecological process driven by disturbance, rather than a stable endpoint or outcome of change. This definition is particularly powerful as it acknowledges that developmental processes are the proximate cause of structural attributes such as large range of tree sizes, horizontal and vertical structural complexity in the canopy, and accumulation of coarse woody debris (CWD) (Wells *et al.* 1998). In turn, these structural attributes can be used as surrogates to identify old-growth forests when detailed knowledge of ecological process is not available for a specific location. In this study, I demonstrate how this contemporary definition of old growth can be used to improve our understanding of the western redcedar-dominated forests of coastal British Columbia.

Old-growth forests of coastal British Columbia

Old-growth forests exist where stand-replacing disturbances are sufficiently rare that an uneven-aged forest develops under the influence of fine-scale canopy gaps. As stand-level disturbances are common in many forest types (White 1979, Sousa 1984), landscapes dominated by old-growth forests are relatively rare. Under the influence of a cool, wet climate, catastrophic

disturbance (i.e., fire) is infrequent in coastal British Columbia, thus old-growth forests dominate many landscapes (Lertzman *et al.* 1996, Pojar *et al.* 1999). These landscapes afford a unique opportunity to examine canopy gap disturbance regimes at a range of spatial scales and to study the mechanisms that underlie community structure and composition.

Linked to our understanding of disturbances as agents of temporal change in coastal old-growth forests are questions pertaining to population dynamics and successional trajectories. In submontane forests of the very wet maritime Coastal Western Hemlock subzone of British Columbia, old-growth stands are often composed of western redcedar (*Thuja plicata* Donn ex D. Don), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and Pacific silver fir (*Abies amabilis* (Dougl. ex Loud.) Dougl. ex J. Forbes), and sometimes Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) (Pojar *et al.* 1991). Canopy trees grow to heights exceeding 60 m and diameters of up to 350 cm, and live more than 1000 years. Canopy structure is complex vertically and horizontally, with canopy gaps related to snags and downed trees.

In the wet coastal environment, Douglas-fir is shade-intolerant, thus it establishes following catastrophic stand-level disturbances (Klinka *et al.* 1990, Carter and Klinka 1992) and dominates late-successional stands by virtue of its longevity (Munger 1940, Franklin and Hemstrom 1981, Kuiper 1988). Western redcedar, western hemlock, and Pacific silver fir are exposure-tolerant, with vigorous growth in full sunlight, and yet shade-tolerant and able to grow beneath old-growth canopies (Klinka *et al.* 1990, Carter and Klinka 1992). Western redcedar dominates many old-growth forest canopies but is rare in the understorey, although it tolerates shade (Schmidt 1955, Gregory 1957, Franklin and Dyrness 1973, Keenan 1993, Daniels 1994). The traditional successional paradigm for these forests is based on equilibrium concepts. In the absence of catastrophic disturbance, western redcedar is replaced by western hemlock and Pacific silver fir, which are abundant in the understorey and subcanopy strata of the forest. Western hemlock and Pacific silver fir are considered the “climatic climax” species, and western redcedar is a “seral” species, with its populations sustained only on edaphically unique sites (Krajina 1969). The interpretation that western redcedar populations are replaced through succession implies that this species, like Douglas-fir, relies on catastrophic, stand-level disturbance to regenerate (Krajina 1969, Pojar *et al.* 1991).

Several field observations appear consistent with the interpretation that western redcedar exhibits a “catastrophic mode of regeneration” (*sensu* Veblen 1992). Large, dominant trees may represent even-aged, post-disturbance cohorts of western redcedar. Abundant western redcedar CWD may indicate senescence and recent mortality of an even-aged post-disturbance cohort. The low density of seedlings and saplings appears insufficient to replace canopy trees and maintain canopy dominance. Thus, the scarcity of regeneration indicates a population decline in absence of coarse-scale disturbance. How-

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Fig. 1. The 26 study sites are located in the Capilano, Seymour and Coquitlam River watersheds, located north of Vancouver, British Columbia. Sites A to R were in clearcuts of former old-growth forests and sites S to Z were in extant old-growth forests.

ever, there are four assumptions implicit to this interpretation:

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

The new ecological paradigm provides an alternative perspective and research framework from which to consider western redcedar population dynamics. This paper summarizes a series of studies in which I have used a dendroecological approach to document the influences of disturbance at three spatial scales—individuals, populations, and stands—in order to test these four assumptions.

Study area

This research was conducted in the Capilano, Coquitlam, and Seymour watersheds, an area of 57 791 ha managed by the Greater Vancouver Water District (GVWD) for water supply to the greater Vancouver municipalities (Fig. 1). The study area was located within the Very Wet Maritime Coastal Western Hemlock (CWHvm) biogeoclimatic subzone, which delineates the influence of a very wet, cool mesothermal climate (Klinka *et al.* 1991). Mean annual temperature of the region is 8.2°C, with a mean temperature in the warmest month of 16.0°C and in the cold-

est month of 0.3°C. Annual precipitation averages 2787 mm, 752 mm of which falls during the summer growing season (Canadian Climate Program 1993). Soils are predominantly steep-slope, coarse-skeletal, Ferro-Humic Podzols (Agriculture Canada Expert Committee on Soil Survey 1987) derived from colluvium and glacial till, and underlain by granite bedrock.

Stands in which western redcedar, western hemlock, Pacific silver fir and Douglas-fir compose the tree layer are prevalent on submontane sites in the watersheds where logging has not disturbed the forest cover. Most extant stands are considered old growth due to their structural complexity and the dominance of trees greater than 250 years of age (Acres International 1999). In these old-growth stands, Pacific silver fir grows to diameters of 100 cm at breast height, western hemlock to 120 cm, and western redcedar and Douglas-fir to 250 cm (Daniels 1994). Life spans are 360 years for Pacific silver fir, 450 western hemlock and > 1000 for western redcedar and Douglas-fir (Daniels 1994).

Eight extant old-growth stands and 18 clearcuts of former old-growth stands were sampled to acquire data for the four studies summarized in this paper (Fig. 1). The clearcut sites range from 4 to 13 ha in area. According to forest inventory, each clearcut had been dominated by western redcedar > 250 years old and

included western hemlock and Pacific silver fir. Douglas-fir had been present at sites E, F, G, H, M, and N.

Assumption 1: Tree Size Indicates Age

Where large western redcedar and Douglas-fir co-dominate old-growth stands, western redcedar may be interpreted as a cohort that established concurrently with the shade-intolerant Douglas-fir following a catastrophic disturbance. Even in the absence of Douglas-fir, large western redcedar may be assumed to be among the oldest trees in old-growth stands given their long lifespan. Underlying these two interpretations is the assumption that tree size indicates age. The first of the four studies outlined in this paper was designed to test this assumption and to answer the question: Are dominant western redcedar the oldest trees in a stand?

Methods

To assess the relation between tree size and age, data were collected from 720 western redcedar (Daniels *et al.* 1995). Accurate age data are difficult to collect from western redcedar for several reasons. Trees with dbh exceeding about 160 cm are common but cannot be aged using increment cores because increment borers have a maximum length of 80 cm and are not long enough to sample a complete radius from the bark to the pith of the tree. Second, it is difficult to extract a core that includes the pith for large trees (dbh > approximately 100 cm), especially when growth is asymmetrical. Third, it is not possible to extract a complete core from many western redcedar because of the high incidence of heartwood decay in this species. To overcome these limitations, age and size data were collected from 720 stumps in 15 clearcut sites (Daniels *et al.* 1995).

Fifteen clearcut sites, five in each of the three watersheds that comprise the study area, were located on mid-slope positions of various aspects at elevations from 400 to 825 m a.s.l. (A to O in Fig. 1). At each site, 48 western redcedar stumps with diameter ≥ 10 cm at stump height and with sound wood from the pith to the bark were located using random and systematic methods (Daniels *et al.* 1995). A minimum diameter of 10 cm was arbitrarily used to differentiate understorey seedlings and saplings from the tree layer that included subcanopy and canopy trees. Moreover, stumps with a diameter < 10 cm were difficult to locate in the cutovers as small trees were likely destroyed during harvesting. The diameter and height of stumps were measured and converted to diameter at breast height (dbh) using conversion tables (Demaerschalk and Omule 1978); all but four trees had a dbh ≥ 10 cm. Field counts of annual rings were corrected for age at stump height to estimate tree ages (Daniels *et al.* 1995). Correction factors ranged from 17 to 33 years (Daniels *et al.* 1995).

Results and discussion

Western redcedar examined in this study included trees with dbh from 8 to 367 cm. Ages ranged from 75 to 1051 years. For western redcedar comprising the tree layer of old-growth stands, larger trees were generally older than smaller trees (Fig. 2). The regression of age on size was statistically significant ($r^2 = 0.65$, $p < 0.001$); however, the standard error of estimated age was 109 years. The curvilinear relationship indicates that variance is not homogeneous over the range of diameters. Age predictions within the 95% confidence limits for trees with dbh of 100 cm are 150 to 600 years, and predictions for trees with dbh of 150 cm are 200 to 800 years.

Fig. 2. Relationship between age and dbh for western redcedar with dbh > 7.5 cm. The middle curve marks the regression of age on dbh [$\log_{10}(\text{age}) = 1.435 + 0.568 \log_{10}(\text{dbh})$]. Upper and lower curves are the regression line ± 1.96 SEE, including 95% of observations ($n = 720$) (from Daniels *et al.* 1995)

At all diameters, size was neither accurate nor a precise indicator of the age of western redcedar trees. Large tree size may indicate relatively old trees, but the largest trees in a stand are not necessarily the oldest trees. At the population level, dominant trees do not necessarily represent a single age cohort. Size data are an inappropriate substitute for age data when interpreting the dynamics of these old-growth stands (Daniels *et al.* 1995).

Assumption 2: Populations Establish as Even-aged, Post-Disturbance Cohorts

The second study is a two-part study that addressed the question: What is the dominant mode of regeneration of western redcedar in old-growth forests? Populations that establish over relatively short periods of time following stand-devastating disturbance and sudden release of resources exhibit a “catastrophic regeneration mode” (Veblen 1992). Experimental studies and regeneration of western redcedar in managed stands show that regeneration of western redcedar can follow a catastrophic mode. For example, western redcedar germinates successfully on exposed mineral soil following fire (Klinka and Feller 1993). Preliminary data collected from a post-fire stand in the Seymour watershed that originated around 1895 showed that, following stand-level fires, western redcedar can form relatively even-aged cohorts (Daniels 1996). At this site, individual western redcedar were open-grown, meaning that radial growth pattern includes wide tree rings close to the pith and a geometric decline in ring width with age and size. Based on these contemporary observations, I predicted that if old-growth stands regenerated after catastrophic disturbances in past centuries, then western redcedar populations would include post-disturbance cohorts of old trees that exhibit an open-grown radial growth pattern.

Methods

To test Assumption 2, age frequency distributions were prepared using the age data from the 15 study sites used to test Assumption 1 (Daniels *et al.* 1995). Age classes were 50 years with all trees > 850 years included in the oldest class. The mean class frequency and its standard deviation were calculated for each distribution. Peak age classes were defined as those with a frequency greater than the mean frequency plus one standard deviation. Peak age classes were compared among study sites.

In the second part of this study, the radial growth patterns of western redcedar and Douglas-fir were assessed using supplementary data collected from sites F to J plus three additional cutovers in the Seymour watershed (Sites P, Q and R in Fig. 1) (Daniels 1996). Canopy tree composition, presence of charcoal, and age structures suggested that these eight sites had likely burned in the past. At sites F, G, and H the old-growth stands had been dominated by western redcedar and Douglas-fir prior to logging, and direct physical evidence of past fire at the sites included charcoal in the soil and root mounds of windthrown trees and burnt snags. Sites I and J were dominated by western redcedar but did not include Douglas-fir and showed no direct physical evidence of past fire. However, the age structures of sites H and I showed distinct age class peaks and included few trees older than 500 years (Fig. 3), possibly due to a stand-replacing disturbance at that time (Daniels *et al.* 1995).

Fifty-five western redcedar and 19 Douglas-fir stumps were located within the eight clearcut sites. Radial sections were cut from the surface of stumps and prepared following standard dendrochronological procedures (Stokes and Smiley 1968). To determine the calendar year of the pith, ring-width series were visually (Yamaguchi 1991) and statistically cross-dated using the program COFECHA (Holmes 1986). Pith dates were corrected for age at stump height to estimate tree ages. Correction factors for western redcedar ranged from 17 to 33 years (Daniels *et al.* 1995) and for Douglas-fir were 10 years (Agee 1993). The initial growth rates of trees (mm per year) were determined by counting the number of rings along a 5-cm radius from the pith. The starting years of growth releases were noted. A release was defined as an increase in radial growth of $\geq 50\%$ that was sustained for at least 10 years, so that a comparison of consecutive 10-year periods showed that mean ring width had increased by a factor of at least 1.5 (Lorimer and Frelich 1989).

Results and discussion

At the spatial scale of a patch on the landscape (e.g., the cutovers), western redcedar populations were uneven-aged (Fig. 3). The range in age at individual sites was at least 457 years and up to 891 years. All age distributions included peak age classes and most included multiple peaks or cohorts. Many peaks were concurrent in the 200 (e.g., 200 = upper limit of the class from 151 to 200 years), 350, 450, and 500 classes, although the study sites were distributed throughout three different watersheds. At all sites there were at least three western redcedar of an age greater than the oldest cohort peak.

The age structures suggest disturbances of a range of magnitudes have influenced the stands. Peak age classes often indicate relatively severe disturbances that facilitated a pulse of regeneration (Veblen 1992). However, even at the sites dominated by individual cohorts, where stand-level disturbance most likely occurred, veteran western redcedar were present

(Fig. 3). Western redcedar has relatively thin bark that is very flammable, making it susceptible to fire rather than resistant to it (Agee 1993). The presence of veteran western redcedar suggests a need to carefully define a "catastrophic" disturbance in these forest systems and to better understand regional fire regimes. Also, climate variation influencing the success of western redcedar establishment or interactions between climate and fire cannot be eliminated as possible explanations for the peaks in the age histograms (Daniels *et al.* 1995).

The ring widths of the Douglas-fir were typical of trees establishing in large openings where competition is low and growth is relatively unrestricted. Initial radial growth averaged 3.68 mm per year (s.d. = 1.28, $n = 19$) and ranged from 1.16 to 6.25 mm per year (Fig. 4). For 16 Douglas-fir, ring widths became progressively narrower as the tree grew, with no radial growth release. Two Douglas-fir released once during their 360-year lifespan and one tree released twice in 600 years.

In contrast with the Douglas-fir, the ring widths of 53 of 55 western redcedar showed suppressed growth at the time of establishment. Initial radial growth averaged 0.85 mm per year (s.d. = 0.43, $n = 55$, Fig. 4), which is significantly lower than the initial growth rate of Douglas-fir (Mann-Whitney rank sum test, $p < 0.001$). The initial growth of only two western redcedar was > 2 mm per year, one of which released once while the other showed no substantive, sustained radial growth release. Of the 53 western redcedar that were initially suppressed, four trees showed no release. The remaining 49 trees had released at least once, including two trees that had released four times during their 460- and 550-year life spans. Following release, high growth rates typically were sustained for one to several centuries.

The growth rates of western redcedar did not show open-growth ring-width patterns as predicted if the populations established following catastrophic disturbance. Initial growth patterns of western redcedar were similar at sites with and without physical evidence of fire. There was agreement between the age of Douglas-fir trees and ages and/or releases of western redcedar at sites F and G; however, the western redcedar did not exhibit an open-grown ring-width pattern. The initial growth rates of western redcedar that established during peak age classes (Fig. 3) were not different from growth rates of western redcedar that established at other times (Mann-Whitney rank sum test, $p = 0.54$).

I propose two possible interpretations of western redcedar growth rates. First, western redcedar may rarely produce wide initial growth rings even when it establishes in large openings. It is possible that my preliminary observation that western redcedar exhibits an open-grown ring-width pattern was not indicative of this species in the study area. To test this possibility, I have initiated an investigation of radial growth rates and allometric growth relations of relatively young (≤ 120 years) trees within even-aged stands of mixed species composition, including western redcedar. Alternatively, slow initial radial growth may indicate that the trees were suppressed because they established beneath an existing canopy (Lorimer and Frelich 1989, Canham 1990, Payette *et al.* 1990, Orwig and Abrams 1994). Dominant western redcedar in the old-growth forest may have established after partial stand disturbances, in canopy gaps, or independently of disturbance.

In contrast to severe stand-level disturbances, fine-scale canopy-gap disturbances facilitate regeneration through time and result in a spread of ages among trees (Veblen 1992). Given

Fig. 3. Age frequency distributions of western redcedar in the tree layer (dbh > 7.5 cm) of sites A to O. 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 “7 peak” classes (after Daniels *et al.* 1995).

Fig. 4. Comparison of initial radial growth rates of western redcedar (left) and Douglas-fir (right). The median growth rates, represented by the horizontal lines inside the boxes, were significantly different (Mann-Whitney rank sum test, $p < 0.001$). The upper and lower limits of each box represent 25th percentiles of age; the bars above and below each box represent 75th percentiles; and, the dots represent the 90th percentiles.

the new ecological paradigm and understanding of disturbance in old-growth forests, it is now recognized that fine-scale disturbance is ubiquitous in coastal forests of British Columbia (Lertzman and Krebs 1991, Lertzman 1992, Beese and Sandford 1992, Lertzman *et al.* 1996). The uneven-age structures of western redcedar suggest that regeneration following catastrophic disturbance is not necessarily the dominant mode of regeneration in these forests. The age structures, combined with low initial radial growth rates, suggest that either gap-phase or continuous modes of regeneration of western redcedar may be more common than previously thought under the pretext of the traditional successional paradigm.

Assumption 3: Abundant CWD Represents Recent Mortality

The third study investigated snags and logs of western redcedar to determine whether this CWD resulted from recent mortality or had accumulated over time. Where live western redcedar dominate the canopy, CWD is often abundant. Logs in decay class 3, with detached or missing bark but boles that are structurally intact (Thomas *et al.* 1979), are often particularly abundant (e.g., Keenan *et al.* 1993). Early reports of western redcedar wood decay in coastal forests suggested that logs in decay class 3 had been dead about 30 years and that by about 85 years, logs would advance to stage 4 of decay (Sollins *et al.* 1987). The same study indicated that logs of western redcedar, western hemlock, and Douglas-fir decay at comparable rates (Sollins *et al.* 1987). Given these similarities, one interpretation of the abundant CWD in decay class 3 is that it represents relatively high mortality of western redcedar during the last century. Specifically, it may represent the synchronous death of an overstorey cohort that established following a catastrophic disturbance and is now senescent and dying. Alternatively, it may represent mortality of western redcedar over

several centuries and the accumulation of CWD due to very slow decomposition.

Methods

To differentiate recent mortality from accumulated mortality, Daniels *et al.* (1997) determined the year of death of 15 western redcedar logs and 17 snags that were at various stages of decay (Thomas *et al.* 1979). Using a range of historical reconstruction methods, including dendrochronological cross-dating of ring-width patterns and radiocarbon analysis of logs in advanced stages of decay, we determined the year of death of the trees and the “age” of the CWD (Daniels *et al.* 1997). The mean ages of the log and snag classes were compared by analysis of variance and the Tukey HSD method for multiple comparisons of the mean that accounted for unequal sample sizes (Norusis 1994).

Results and discussion

For snags in classes 4 to 6, ages range from 41 to 276 years with overlap among all three classes (Fig. 5). Generally, the age of the logs increased with decay class, however the overlap in age of logs of classes 2 and 3 was sufficient that they could not be differentiated statistically (Fig. 5). Class 2 and 3 logs had been dead for 17 to 293 years; they ranged in diameter from 79 to 250 cm but remained relatively sound and will likely persist on the sites for decades to centuries. Class 4 logs were losing their structural integrity, having been dead at least 500 years (Fig. 5). The slow decay of western redcedar indicated by these results is consistent with its wood chemistry and resistance to decay (Barton and MacDonald 1971, Nault 1988, Kelsey and Harmon 1989, van der Kamp 1986). Recent results from a long-term experiment tracking CWD decay in coastal Oregon corroborate these observations (Harmon 1992).

The slow decay of western redcedar wood has resulted in an accumulation of logs and snags in old-growth stands over time. I concluded that the abundant CWD of western redcedar does not represent a pulse of recent mortality or synchronous death of an overstorey cohort. Nor does it represent a mortality rate that is disproportionate to the number of live trees in the canopy and subcanopy. Rather, tree deaths have occurred over a period of hundreds of years.

Assumption 4: Regeneration Is Insufficient To Maintain Canopy Dominance

Following the test of Assumption 2, I asserted that (1) the uneven-age structures and radial growth rates of dominant trees suggested that western redcedar is capable of successful regeneration in old-growth forests and (2) western redcedar may coexist with western hemlock and Pacific silver fir in late-successional forests, rather than being replaced by them. The fourth study considers mechanisms of western redcedar establishment and recruitment to the canopy as possible explanations for the relatively low density of western redcedar in the understorey of old-growth stands.

In coastal British Columbia, western redcedar, western hemlock, and Pacific silver fir tolerate shade, although none of the three species requires shade (Klinka *et al.* 1990, Carter and Klinka 1992). Theoretically, all three species can establish following both fine- and coarse-scale disturbances. Despite these similarities, the population size structures of the three species

Fig. 5. 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).

Table 1. Tree density by species and canopy stratum in eight study stands (0.49 ha) (after Daniels 1994). Mean values for the eight stands are followed by the standard deviation in parentheses

Species Canopy stratum	Study stand								Mean (s.d.)
	S	T	U	V	W	X	Y	Z	
Western redcedar									
Seedlings	59	249	179	148	638	808	1344	209	454 (444)
Saplings	0	5	1	4	24	31	35	0	13 (15)
Subcanopy trees	1	0	0	2	3	7	26	2	5 (9)
Canopy trees	8	8	2	23	26	15	16	13	14 (8)
Western hemlock									
Seedlings	5 782	10 241	13 132	5 880	12 495	7 252	3 553	10 486	8 603 (3 476)
Saplings	561	404	806	380	523	588	493	257	502 (164)
Subcanopy trees	68	72	71	36	107	136	111	45	81 (34)
Canopy trees	31	43	20	18	21	20	28	54	29 (13)
Pacific silver fir									
Seedlings	6 909	2 107	5 929	4 018	147	147	98	5194	3 069 (2 807)
Saplings	40	338	383	784	68	7	16	637	284 (303)
Subcanopy trees	2	21	170	61	17	6	12	109	50 (60)

differ substantially (Keenan 1993, Daniels 1994). The abundance of western hemlock and Pacific silver fir in the understorey of old-growth stands suggests that opportunities for regeneration of these two species are not limited. In contrast, the intermittent establishment of western redcedar at fine spatial scales (Gregory 1957, Keenan 1993, Daniels 1994) suggests that opportunities for its successful regeneration may be limited either spatially or temporally. In this last study, I have used stand structure analysis and historical reconstruction techniques to examine regeneration niches and recruitment modes as possible mechanisms of co-existence of western redcedar, western hemlock, and Pacific silver fir in old-growth stands.

Methods

In 1992, I established eight plots in western redcedar-dominated old-growth stands (Sites S to Z in Fig. 1; Daniels 1994). The plots measured 70 × 70 m (0.49 ha). In each plot, I recorded the species, location, dbh (cm), height (m), and canopy position (subcanopy versus canopy) of all trees (dbh > 10 cm). Seedlings (height ≤ 130 cm) and saplings (height > 13 cm, dbh ≤ 10 cm) of western redcedar were censused and their location, rooting substrate (CWD, exposed mineral soil, or undisturbed forest floor), and height were recorded. The same attributes were measured for western hemlock and Pacific silver fir seedlings

and saplings within systematically located 2 × 2 m and 10 × 10 m quadrats, respectively. Morisita's index of dispersion (I_d) was used to test the spatial distributions of western redcedar seedlings and saplings within nested quadrats ranging from 16 to 576 m². It was calculated for western hemlock and Pacific silver fir seedlings in 4-m² quadrats and saplings in 100-m² quadrats. Within each plot, ground cover was estimated along four 70-m line transects. The extent along each line of CWD, exposed mineral soil, undisturbed forest floor, water and bedrock was measured and average percent cover of each type was calculated.

Daniels and Klinka (1996) conducted a dendroecological reconstruction of historic canopy gaps within 0.23-ha subplots nested within plots V and Z. Increment cores were extracted from the base (about 20–50 cm above ground) of all trees with dbh > 10cm. Ring-width series were visually cross-dated (Yamaguchi 1991). The starting year of growth releases were noted. As in the test of Assumption 2, a release was defined as an increase in radial growth of ≥ 50% that was sustained for at least 10 years, so that a comparison of consecutive 10-year periods showed that mean ring width had increased by a factor of at least 1.5 (Lorimer and Frelich 1989). Historic gaps were delineated from the release dates and tree growth histories were compared for trees stratified by species and canopy position (Daniels and Klinka 1996).

Fig. 6. Diameter distributions of subcanopy and canopy trees (dbh > 10 cm) in eight study stands. Tree species are western redcedar (black), western hemlock (hatched) and Pacific silver fir (grey). Sites S to V were on north-facing slopes (left column); sites W to Z faced south (right column). Trees are grouped in 15 cm diameter classes from 10 cm (after Daniels 1994).

For western redcedar, complete ring-width series were sampled for only seven of 21 trees in plots V and Z because of the low density of subcanopy trees, the large size of canopy trees,

and the high incidence of heartwood decay in trees of all sizes (Daniels and Klinka 1996). Thus, the ring-width series from the 55 western redcedar sampled in eight clearcuts in the

Seymour watershed (See “Test of Assumption 2”) supplemented the data and increased sample size. For these 55 trees, dbh ranged from 96 to 238 cm; thus, I assumed they had occupied the canopy prior to cutting.

Results and discussion

If you assume that many seedlings and saplings are required to replace a few canopy trees or that the diameter distribution must form a “reverse-J” shape or “balanced” distribution, then it is logical to classify western redcedar populations as declining and western hemlock and Pacific silver fir as increasing in many stands (Table 1 and Fig. 6). However, this interpretation implicitly assumes that rates of seedling and sapling establishment, survival, mortality, and recruitment to successive canopy strata are equivalent between species. Instead, differences in the life histories, including regeneration niche and mode of recruitment, may explain contrasting population structures of western redcedar, western hemlock, and Pacific silver fir (Turner and Franz 1985, Keenan 1993, Daniels 1994).

Seedlings and saplings western redcedar, western hemlock, and Pacific silver fir were significantly aggregated at fine spatial scales ($p < 0.001$ for all quadrats $\leq 256 \text{ m}^2$; Daniels 1994). Common rooting substrates among the three species indicate spatial overlap of their regeneration niches (Table 2; Daniels 1994). Decaying wood and mineral soil, substrates created by gap-phase disturbances, were important substrates for seedlings and saplings, respectively. More than 70% of seedlings and saplings of western hemlock and western redcedar were growing on decaying wood, although CWD accounted for only 39% of ground cover within plots, on average. Pacific silver fir also established on decaying wood but was most common on undisturbed forest floor. For all three species, the proportion of saplings growing on mineral soil was greater than the proportion of seedlings on mineral soil. Assuming similar ingress of seedlings over time, these results suggest seedlings rooted in mineral soil grow rapidly and/or have high rates of successful recruitment to the sapling stratum relative to seedlings growing on decaying wood and the forest floor. Given the overlap in substrate use by the three species, spatial partitioning of the regeneration niche does not appear to explain the differences in population structures (Daniels 1994). Additional research is needed to clarify the influence of microsite characteristics on seedling establishment of the three study species in these forests.

Opportunities for tree regeneration in old-growth forests may be partitioned temporally via different rates of recruitment between canopy strata (e.g., understorey to subcanopy to canopy strata). The trends in Table 3 suggest that the three study species may respond differently to canopy gaps (Daniels and Klinka 1996) or exhibit with different “modes of recruitment” (Canham 1989). Pacific silver fir and western hemlock appear to depend on gaps to recruit to the canopy. Although individual Pacific silver fir were up to 60 m tall, this species was rare in the canopy (Daniels 1994). Most Pacific silver fir trees were suppressed in the subcanopy with ages up to 360 years. Sixty trees had released one to four times but had not recruited from the subcanopy to the canopy (Daniels and Klinka 1996). Western hemlock trees were up to 423 years old and 55 m tall (Daniels 1994). Western hemlock populations included suppressed subcanopy trees and many canopy trees that had recruited in gaps. Nine suppressed trees remained in the subcanopy; another 32 trees had released but not recruited to the canopy. More than half of

Table 2. Distribution of regeneration of western redcedar, western hemlock, and Pacific silver fir on different substrates. The mean percent cover followed by standard deviation in parentheses is provided for each substrate type ($n = 8$ study sites)

Species Size class	Percentage of individuals by substrate type		
	Forest floor	Decaying wood	Mineral soil
	53 (12)	39 (10)	6 (4)
Western redcedar			
Seedlings ($n = 1840$)	12	79	9
Saplings ($n = 921$)	16	70	14
Western hemlock			
Seedlings ($n = 1483$)	8	90	2
Saplings ($n = 1303$)	12	81	7
Pacific silver fir			
Seedlings ($n = 490$)	61	38	1
Saplings ($n = 883$)	50	44	6

Table 3. Number of releases in the ring-width series of trees (dbh > 10 cm) stratified by species and canopy position

Species	Number of releases	Subcanopy	Canopy
Pacific silver fir ¹	0–1	53	2
	≥ 2	32	1
Western hemlock ¹	0–1	30	10
	≥ 2	11	13
Western redcedar ¹	0–1	1	5
	≥ 2	1	0
Western redcedar ²	0–1	n.a. ²	28
	≥ 2	n.a.	27

¹ Data from Daniels and Klinka (1996) included all trees with dbh ≥ 10 cm.

² Data from Daniels (1996) were from stumps with dbh of 96 to 238 cm and were assumed to be upper canopy trees before cutting. Smaller stumps were not sampled in this study.

trees in the canopy had released two to four times indicating recruitment facilitated by multiple gap events (Daniels and Klinka 1996).

Only two western redcedar were located in the subcanopy of plots V and X where canopy gaps were reconstructed (Daniels and Klinka 1996). One subcanopy tree was 166 years old and had released once; the other tree was 224 years old and had released twice. The age of the 60 canopy trees ranged from 199 to 959 years. Eight canopy trees had never released but had grown to diameters of 110 to 200 cm; 25 trees were initially suppressed and had released only once; 27 trees had released two to four times.

The radial growth pattern of western redcedar may indicate that it does not depend on gaps to recruit from the subcanopy to the canopy. Its mode of recruitment may be slow, consistent growth of subcanopy trees that rarely respond to gaps. Over their lifetime, such trees are likely influenced by gaps and release, although they are not dependent on gaps to recruit (Canham 1988, 1989; Schupp *et al.* 1989). Three observations support this interpretation. First, under low light conditions western redcedar maintains apical dominance and height increment but western hemlock and Pacific silver do not (Carter and Klinka 1992, Klinka *et al.* 1992). Second, the average delay between establishment and the first release for western redcedar was 111 years (s.d. = 50, $n = 50$), when trees average about 20 cm in diameter (s.d. 21 cm, $n = 50$). The consistent, sustained release of trees of relatively small diameter suggests a critical size threshold beyond which the trees successfully recruit to the canopy. The release and recruitment of western redcedar may depend

on crown exposure to light at critical heights in the canopy, rather than the chance occurrence of a canopy gap. Third, releases of western redcedar are infrequent relative to western hemlock and Pacific silver fir, especially given the long lifespan of western redcedar that affords more opportunity for multiple periods of suppression and release (Table 3).

Differences in mode of recruitment between western redcedar, western hemlock, and Pacific silver fir may explain the differences in their population structures. Western hemlock and Pacific silver fir appear to depend on canopy gaps, thus opportunities to recruit to the canopy are limited by the availability of canopy gaps. Abundant regeneration in the understorey provides a "seedling bank" able to respond rapidly and exploit resources available in a gap. This "gap-dependent" model predicts variable radial growth with periodic suppressions and releases of individual trees and relatively high rates of both recruitment and mortality between successive canopy strata for western hemlock and Pacific silver fir populations. In contrast, if western redcedar is "gap-independent," then it does not depend on gaps to recruit to the canopy and opportunities to recruit are not limited by the availability of gaps. This model predicts slow radial growth until trees reach a critical size that increases their exposure to light allowing them to recruit into the canopy during a single, sustained release. At the population level, the rate of mortality of saplings and understorey trees would be relatively low and it would not require a seedling bank.

I have undertaken two approaches to test the hypothesis that recruitment of western hemlock and Pacific silver fir depends on canopy gaps, while western redcedar recruitment is independent of gaps. The first approach combines population modelling with monitoring of permanent plots to examine rates of population change. Life-cycle models based on size- and age-class data estimated rates of ingress to the understorey, recruitment to the subcanopy and canopy tree strata, and mortality from all three strata (Daniels and Tait 1996). The modelling results concur with the inferences made from tree population structures. For example, low ingress of western redcedar is followed by negligible mortality in the subcanopy and high recruitment success to the canopy (Table 4). However, both the modelling results and population structure interpretations are restricted by the assumptions and limitations inherent to static demographic data (Veblen 1992). Thus, these estimated rates of population change provide the basis for interspecific comparisons to be tested with permanent plot data. Since 1992, I have monitored tree recruitment and mortality in seven research plots (sites T to Z in Fig. 1). Re-sampling of 1318 tagged trees in 1997 revealed more tree deaths and recruitment of western hemlock and Pacific silver fir relative to western redcedar, but rates of population change were slow (Daniels and Daniels 1997), as noted in similar long-term studies (Franklin and DeBell 1988, Spies *et al.* 1990, Edmonds *et al.* 1993). The permanent plots will be re-measured in 2002.

The second approach to test for differences in modes of recruitment of western redcedar, western hemlock, and Pacific silver fir is a replicated dendroecological analysis of old-growth stands. This study includes an intensive analysis of species-specific growth responses to canopy gaps, expanding on the research of Daniels and Klinka (1996).

Conclusions and Management Implications

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. Below are my conclusions drawn from the tests of four assumptions about western redcedar dynamics:

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

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 is more common than previously thought.

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

Assumption 4. Regeneration is insufficient to maintain canopy dominance. Preliminary evidence suggests 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 despite low density of seedlings and saplings in the understorey. 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.

Returning to the contemporary view of old growth, it is evident that gap dynamics prevail in western redcedar-dominated old-growth forests. Establishment of western redcedar seedlings on CWD and exposed mineral soil follows a gap-phase mode, although recruitment of trees from the subcanopy to the canopy appears continuous. Establishment and recruitment of western hemlock and Pacific silver fir are associated with canopy gaps. In this model of stand dynamics, fine-scale canopy gaps in old-growth forests are essential to sustain coexisting populations of western redcedar, western hemlock, and Pacific silver fir. This contemporary view distinctly contrasts with the traditional view of forest succession in which western redcedar is replaced by western hemlock and Pacific silver, under the dominant influence of regional climate and in the absence of disturbance.

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 (*sensu* Klinka *et al.* 1990), when managing western redcedar in coastal British Columbia.

Ecosystem management aims to conserve biodiversity and maintain ecosystem function while sustaining renewable resources (BCMof 1995, Christensen *et al.* 1996, Lertzman *et al.* 1997).

Table 4. Estimated annual rates of tree population change in old-growth stands dominated by western redcedar. Estimates were derived from species-specific life-cycle models developed using size and age data from the study area (after Daniels and Tait 1996)

Species	Annual rates of change					
	Ingress	Understorey mortality	Recruitment to subcanopy	Subcanopy mortality	Recruitment to canopy	Canopy mortality
Western redcedar	49	4.26×10^{-2}	2.03×10^{-4}	0	5.87×10^{-3}	4.09×10^{-3}
Western hemlock	255	3.59×10^{-2}	2.05×10^{-4}	5.36×10^{-3}	2.58×10^{-3}	9.04×10^{-3}
Pacific silver fir	84	2.04×10^{-2}	1.26×10^{-4}	9.78×10^{-3}	0.81×10^{-3}	9.57×10^{-3}

To achieve these goals, patterns of natural variation can be used to guide management activities (Lertzman *et al.* 1997, Landers *et al.* 1999). 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 (Bunnell *et al.* 1999, Drever 2000). 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 (Franklin *et al.* 1997, Dunsworth and Beese 2000, Beese *et al.* 2003). VR has been proposed as one method toward a sustainable approach for timber management of coastal old-growth forests (Lertzman *et al.* 1996, 1997; Scientific Panel 1995; Pojar *et al.* 1999; Drever 2000).

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.

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