

Multiple-pathway succession in coastal *Tsuga heterophylla*, *Thuja plicata*, and *Abies amabilis* forests on northeastern Vancouver Island, British Columbia

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Abstract: Sustainable forest practices are often designed to mimic natural disturbance and successional processes, yet succession is poorly understood in many ecosystems. On northeastern Vancouver Island, the “disturbance hypothesis” is a widely assumed succession model asserting that shade-tolerant western redcedar (*Thuja plicata* Donn ex D. Don) and the ericaceous shrub salal (*Gaultheria shallon* Pursh) invade and colonize highly productive western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) – Pacific silver fir (*Abies amabilis* Douglas ex J. Forbes) stands (HA) on zonal sites in the absence of stand-replacing wind disturbance. This leads to the development of low-productivity, low-density, uneven-aged, open-crowned redcedar–hemlock–salal stands (CH). In conflict with this model, old, apparently stable HA stands lacking redcedar can be found on such sites as well. We sought evidence for the predicted transition to CH stands by examining stand composition, crown closure, tree size class frequency distributions, salal cover, and redcedar establishment on young HA (~90 years old), old HA (>160 years), and CH (>160 years) stands. When adjacent to a redcedar stand, young HA stands had fewer redcedar seedlings but more redcedar adult trees than old HA stands. However, redcedar abundance did not differ between young and old HA stands at distances further than 10 m from adjacent redcedar stands. This could indicate that redcedar recruits into HA stands at stand establishment and that redcedar seedling establishment is low under the thick canopy of young HA stands. The chronosequence data also suggest that both old HA and CH stands are self-replacing stand types in these forests, contrary to the disturbance hypothesis. We develop a new, multipathway model for this ecosystem that is based on the chronosequence data and life-history traits of the focal tree species and suggest that disturbance plays a role opposite to the equilibrium model.

Key words: forest succession, multiple-pathway model, forest regeneration, stand-replacing disturbance, forest ecotones.

Résumé : Les pratiques forestières durables sont souvent conçues pour imiter les perturbations naturelles et les processus de succession bien que la succession de plusieurs écosystèmes soit mal comprise. Dans le nord-est de l'île de Vancouver, « l'hypothèse de la perturbation » est un modèle de succession largement hypothétique qui soutient qu'en l'absence de chablis majeur, le thuya géant (*Thuja plicata* Donn ex D. Don) tolérant à l'ombre et la gaulthérie shallon (*Gaultheria shallon* Pursh), une éricacée arbustive, envahissent et colonisent les peuplements hautement productifs de pruche de l'Ouest (*Tsuga heterophylla* (Raf.) Sarg.) et de sapin gracieux (*Abies amabilis* Douglas ex J. Forbes) (HA) établis sur des stations zonales. Ceci conduit au développement de peuplements ouverts, inéquiennes, peu productifs et à faible densité composés de thuya, de pruche et de gaulthérie (CH). Contrairement à ce modèle, de vieux peuplements HA sans thuya et apparemment stables peuvent aussi se développer sur de telles stations. Nous avons cherché des preuves de la transition prévue vers des peuplements CH en étudiant la composition des peuplements, la fermeture du couvert, la distribution du diamètre des arbres, le couvert de gaulthérie shallon et l'établissement du thuya géant dans des peuplements HA jeunes (environ 90 ans), HA vieux (plus de 160 ans) et CH (plus de 160 ans). Lorsqu'ils sont adjacents à un peuplement de thuya, les jeunes peuplements HA comportent moins de semis de thuya, mais plus de thuyas adultes que les vieux peuplements HA. Cependant, l'abondance du thuya était similaire dans les jeunes et les vieux peuplements HA à des distances plus grandes que 10 m du peuplement adjacent de thuya. Ceci pourrait indiquer que le thuya se régénère dans les peuplements HA lors de l'établissement du peuplement et que l'établissement de cette régénération est faible sous le couvert dense des jeunes peuplements HA. Les données de la chronoséquence indiquent aussi que les vieux peuplements HA et CH sont des types de peuplement qui s'autorégénèrent dans ces forêts, contrairement à l'hypothèse de la perturbation. Nous avons mis au point un nouveau modèle à voies multiples pour cet écosystème qui est fondé sur les données de chronoséquence et les caractéristiques du cycle biologique des espèces d'arbre visées. Nous croyons que la perturbation joue un rôle inverse à celui du modèle d'équilibre. [Traduit par la Rédaction]

Mots-clés : succession forestière, modèle à voies multiples, régénération forestière, perturbation majeure, écotones forestiers.

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Introduction

Modern community ecology relies on dynamic events (disturbances, fluctuations in seedling establishment, and mortality rates) that result in multiple pathways of forest succession (Holt 2006; Clark 2009). These successional pathways depend on disturbance type, intensity and frequency (Chen and Popadiouk 2002), the effects of the existing plant community on subsequent invasion and colonization (Connell and Slatyer 1977), and differences between the plants on a site at both a species level (Tilman 1993) and an individual level (Huston and Smith 1987). It is still controversial, however, whether these different pathways converge on a similar type of stable ecosystem state. For example, when studying successional processes in forest ecosystems containing long-lived trees (up to hundreds or even thousands of years of age), it is extremely difficult to distinguish between a stable community and an intermediate state that can last for centuries.

Successional mechanisms can have implications for forest management, which should be related to natural disturbance and successional processes if historical ranges of variation and associated ecosystem values are to be maintained (Perera et al. 2004). This requires an accurate understanding of both disturbance and succession (Keane et al. 2009). For example, on northern Vancouver Island, logging companies have often had difficulties regenerating stands after clearcutting old-growth western redcedar (*Thuja plicata* Donn ex D. Don) – western hemlock (*Tsuga heterophylla* (Raf.) Sarge) forests (CH), despite success in adjacent western hemlock–Pacific silver fir (*Abies amabilis* Douglas ex J. Forbes) sites (HA) (Prescott and Weetman 1994). Lewis (1982) was the first to explain this phenomenon as part of a natural succession in these forests and proposed the possibility of converting CH sites into HA sites by silvicultural treatments. Lewis' suggestion was followed by the Salal Cedar Hemlock Integrated Research Program (SCHIRP) managed by the British Columbia Ministry of Forests and Range for the following 10 years (Prescott and Weetman 1994). This program was based on the assumption that the phenomenon of different forest types (CH or HA) occupying similar sites could be related to successional processes. Indeed, these forest types are distributed in a mosaic across the landscape on zonal sites (mesic moisture and mesotrophic nutrient status), with sharp boundaries between them (Prescott and Weetman 1994).

Prescott and Weetman (1994) identified four theories that could explain the coexistence of self-replacing HA and CH forest types in the landscape: (1) the disturbance hypothesis predicts that HA stands will slowly evolve into CH stands in the absence of disturbance or management (based on the original Lewis model; Fig. 1); (2) the salal hypothesis posits that the darker HA understories prevent salal (*Gualtheria shallon* Pursh), an ericaceous shrub with strong allelopathic and competitive effects of on other species, from colonizing; however, in more open CH forests, salal dominates the understory and reduces tree growth; (3) the cedar hypothesis, which states that windthrow-origin HA stands are suitable for cedar but it does not become established because of the speed and density of hemlock and fir regeneration; however, on CH forests with abundant decay-resistant redcedar logs and litter, redcedar and salal can more readily obtain N than hemlock or fir; and (4) the site hypothesis in which differences between HA and CH are related mostly to site condition, with HA sites established in well-drained sites exposed to wind disturbances that prevent humification and gleziation (Banner et al. 2005).

Prescott and Weetman (1994) did not find evidence to support the cedar hypothesis. Since then, Prescott and Sajedi (2008) have discarded the salal hypothesis, concluding that the presence of salal was the effect rather than the cause of low nutrient availability on CH stands. Also, several lines of evidence support the site hypothesis indicating that CH sites might be slightly wetter and less aerated than HA sites. DeMontigny (1992) found indications on CH sites of humus formed in poorly drained soils, and a thresh-

old related to soil oxygen that could separate CH from HA sites has been identified (Sajedi et al. 2012; Prescott et al. 2013). Although the latter studies showed significant differences in mean soil characteristics (soil moisture and redox potential), there was a high level of overlap among samples in both stand types. Other studies have failed to find differences between CH and HA in parent material, soil chemistry, and topography (Keenan et al. 1993; Weber et al. 2003, 2005). This evidence could indicate that rather than sites being inherently different, successional processes cause sites to diverge over time into different forest types.

The mosaic of CH and HA stands on the landscape may also be influenced by historic differences. Western redcedar began establishing approximately 3000 years ago in a forest dominated by Sitka spruce (*Picea sitchensis* (Bong.) Carrière), western hemlock, and Pacific silver fir (Hebda 1995). The current landscape reflects this historical influence; the CH stand type currently occupies about 27% of the forested area of northern Vancouver Island, or 100 000 ha (Prescott and Sajedi 2008), but there is no certainty that this area would not change if successional processes were allowed to continue unaltered.

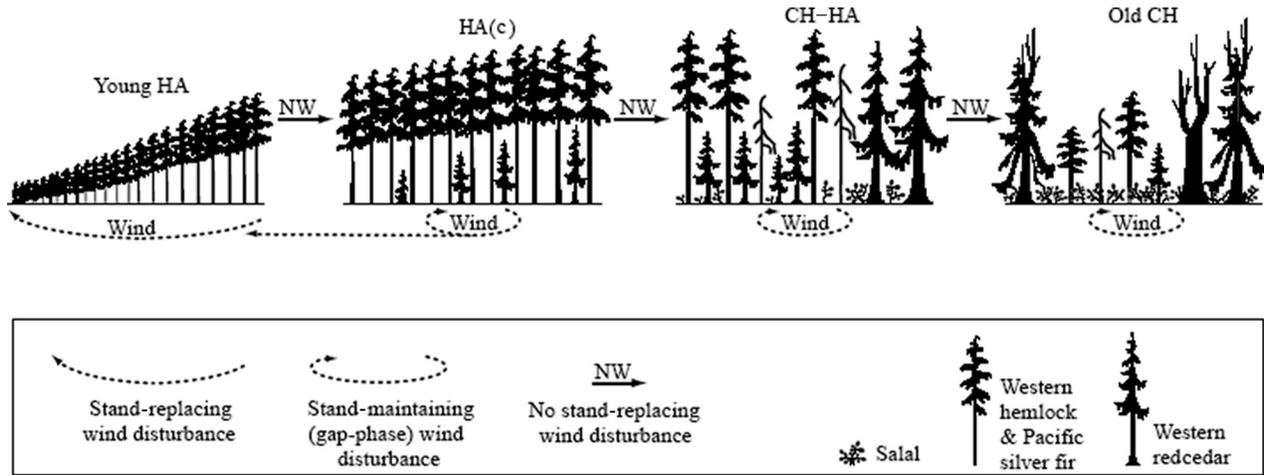
The composition and structure of CH stands are different from other forest types; they are usually uneven-aged, dominated by old western redcedar trees of up to a thousand years old or more, and support slow growth of nutrient-deficient western hemlock and Pacific silver fir of various ages (Prescott and Weetman 1994). The CH generally has low net commercial stemwood productivity, in the 0–4 m³·ha⁻¹·year⁻¹ range. The canopy is relatively open and vertically heterogeneous, permitting light penetration that supports a vigorous shrub layer dominated by salal (Prescott et al. 2013).

The HA forest type occupies approximately 50% of forests in the region (175 000 ha). It is typically densely stocked with a closed, vertically uniform canopy that permits little light penetration. It is dominated by tall western hemlock and Pacific silver fir with low stem taper and has only trace amounts of redcedar (Prescott and Weetman 1994). The HA stands are highly productive (15–20 m³·ha⁻¹·year⁻¹ stemwood) and are darker, housing fewer species than CH forests (Sajedi et al. 2012). In higher light situations such as near stand edges that permit lateral light penetration or where canopy gaps have formed, seedling regeneration is almost entirely of Pacific silver fir and western hemlock (Weber et al. 2003). Probability of stand-replacing windthrow increases with age in HA stands (Prescott and Weetman 1994), and most of the HA stands in the study area were initiated by catastrophic stand-replacing windstorms in 1908 (Prescott et al. 1993), although both older and younger HA stands can be found dispersed across the landscape.

Forest succession in CH and HA stands

The disturbance hypothesis posits that in the absence of stand-replacing wind disturbance, HA stands will transition to CH stands due to the invasion of HA stands by redcedar seedlings, which would become HA(c) stands (Prescott and Weetman 1994). According to this theory, relatively frequent stand-replacing windstorms (approximately every 100 to 200 years) are predicted to maintain HA stands by creating dense, even-aged, fast-growing hemlock and Pacific silver fir stands that shade out slower growing redcedar. The HA stands are susceptible to subsequent stand-replacing wind events due to their density, structure, and species composition. In contrast, CH stands appear to resist stand-replacing windthrow that would convert them back to HA stands (Prescott and Weetman 1994). This is because redcedar architecture combines loss of foliage under high winds with high stem taper, a broad root system, and lower susceptibility to stem breakage and windthrow than hemlock and Pacific silver fir (Mitchell et al. 2001; Harrington 2010). As a consequence, partial wind disturbances remove hemlock and fir from the stand more frequently than

Fig. 1. Linear model of forest succession on zonal sites on northern Vancouver Island ruled by the frequency and intensity of wind disturbance. Young HA is assumed to approximate the stem exclusion phase, HA(c) is the understory re-initiation stage with redcedar seedling recruitment, and HA-CH is the old growth phase of HA stand development, transitioning to CH. (Elaborated upon from Prescott and Weetman 1994.)



redcedar, and CH stands are maintained on the landscape as redcedar-dominated sites.

According to the disturbance hypothesis, old HA(c) stands should exist only as a transition state from a young HA stand to a CH stand (Fig. 1). Therefore, they should show evidence of redcedar recruitment in the understory that eventually leads to mature redcedar establishment. This transition state is predicted to occur as gaps develop in the HA canopy as it ages (understory reinitiation phase of stand dynamics; Oliver and Larson 1996), resulting in sufficient light levels for the establishment of salal and shade-tolerant redcedar, as well as hemlock and Pacific silver fir. Previous studies have reported the absence of seedling banks in the understory, especially of redcedar (Weber et al. 2005), although large seedling banks of hemlock and especially Pacific silver fir have been described at higher altitudes in the same region (Antos et al. 2005).

Despite the ability of the disturbance hypothesis to explain the coexistence of two distinct stand types on zonal sites, field observations and experiments have raised several potential inconsistencies, leading some to reject Lewis' original disturbance hypothesis (Prescott et al. 2013). For example, field studies have shown a lack of evidence in the study area of young or old HA stands currently being actively colonized by redcedar, probably as a consequence of low light, interaction with the HA stand substrate, and lack of suitable mycorrhizal fungi (Weber et al. 2003, 2005). Nonetheless, <2000–3000 ha is believed to be in some type of intermediate state between HA and CH (i.e., HA stands with some redcedar) at any time; this amounts to 1%–2% of the current extent of the HA stands (T. Lewis, unpublished data). Recent research on the HA–CH phenomenon has focused on differences in environmental characteristics (Sajedi et al. 2012), leading to a change in site classification and management strategies in the area (Prescott et al. 2013). On the other hand, when different plant communities are established on initially similar sites, differences in physicochemical site characteristics could evolve through time, especially if these communities last for centuries. For example, in northern sites of the same biogeoclimatic zone of British Columbia, Banner et al. (2005) have described how in the absence of stand-replacing disturbances, old-growth stands could eventually develop into bogs as soils became increasingly paludified. Therefore, the disturbance and site hypotheses are not necessarily mutually exclusive. Early stages of our investigation indicated that successional process may also be involved in the HA-CH phenomenon. Redcedar germinants (defined as young redcedar that have not yet developed the secondary, scalelike foliage typical of this species, and

generally younger than 1 year old) are common in windthrow-origin HA stands, with 18 germinants·m⁻² occurring at 15 m into HA stands from an adjacent CH stand (A. Weber, unpublished data). Antos et al. (2005) reported the capacity of western hemlock and Pacific silver fir to form seedling banks that can survive for a long time in the understory of mountain forests on Vancouver Island. This evidence suggest that all of these species may well be present in HA stands and able to invade when forest gaps open, as proposed by the disturbance hypothesis.

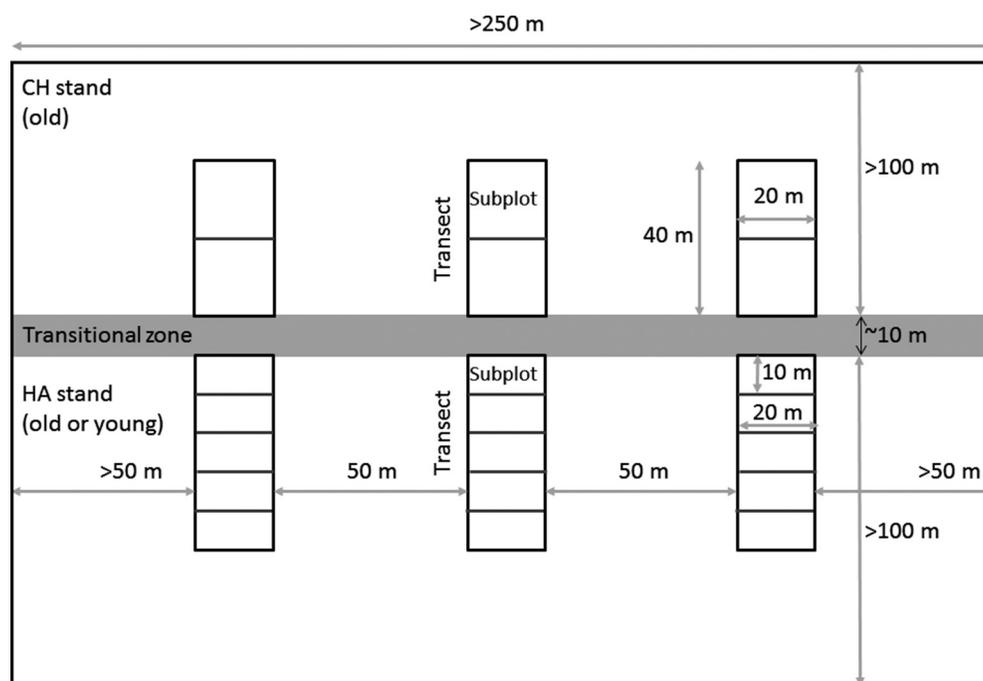
In this study, we aim to test the validity of the disturbance hypothesis by using a chronosequence approach. Our assumption is that current and historical patterns of succession in these forests have not changed significantly. If successional convergence towards CH-dominated forests as described in the disturbance hypothesis is occurring in this area, we would expect to see the following: (i) old HA stands should have less crown closure than young HA stands, (ii) old HA stands should have higher salal cover in the understory than young HA stands, and (iii) old HA stands should have a higher abundance of redcedar than the young HA stands. We test these predictions in old and young HA stands by first identifying stands of these types that are adjacent to CH stands and then sampling along transects from the edge of the CH into the HA stand. This approach ensures that ample cedar and salal seed will be present in our sample areas, so that any trends that are not consistent with the disturbance hypothesis would not be due to a lack of propagules. Moreover, if changes are occurring, we would expect the transects to show the “invasion front” of redcedar and salal into old HA stands.

Materials and methods

Study sites

All HA and CH stands on zonal sites recorded for the Port McNeil (50°35'25"N, 127°05'5"W) area were identified using Western Forest Products Inc. forest cover type maps for Tree Farm License 6. HA sites are classified as poor to medium in nutrient regime and fresh to moist in moisture regime, whereas CH sites are classified as nutritionally poor but with the same moisture regime as HA sites. Slope was minimal (<10%) on all sites except one old HA stand, and consequently aspect was not controlled. Elevation ranged from 300 to 600 m above sea level. All sites were within the coastal western hemlock, submontane very wet maritime biogeoclimatic zone (CWHvm1; Pojar et al. 1987). Meteorological data from the Port Hardy airport (approximately 15 km north of the study area) showed a mean annual precipitation of 1700 mm, with

Fig. 2. Transect establishment in pairs of young HA – old CH stands (five stands) and pairs of old HA – old CH stands (eight stands). Stands can have three to five transects, depending on the stand length parallel to the transition zone (250–350 m).



most of this occurring in the winter months (Keenan et al. 1993). Mean daily temperatures range from 2.4 °C in January to 13.8 °C in August. The average mass of forest floors in HA stands is 211 Mg·ha⁻¹ (Keenan et al. 1993). The CH forests are unevenly aged and contain cedars more than 500 years old and hemlocks up to 400 years old. The CH forest floor (i.e., the humus layer) has an average mass of 280 Mg·ha⁻¹ (Keenan et al. 1993). Soils are typically humo-ferric podzols with 0.25 m of mor humus (combined LFH layers) overlying surficial unconsolidated morainal and fluvial outwash material, with similar depths of humus in CH and HA stands (Sajedi et al. 2012).

Sampling transects

In the year 2000, five pairs of young (~90 years old) HA stands and adjacent CH stands were selected at random from the population of stands. HA stands were evenly aged, originating from a catastrophic windstorm in 1908 (Prescott et al. 1993). In addition, eight pairs of old (>160 years old) HA stands and adjacent CH stands were also randomly selected from sites neighbouring the young stands previously selected. The HA stands were required to have a minimum of 250 m of edge with the adjacent redcedar and salal-dominated CH stand and at least a 100 m wide strip of uniform HA stand running parallel and next to the HA-CH interface that was free of old (>1 m dbh (diameter at breast height, 1.3 m)) redcedar trees. Both forest types were separated by a sharp transitional zone of approximately 10 m (Prescott et al. 1993).

We used transects running from the CH into the HA to determine if differences between young and old HA stands were consistent with the disturbance hypothesis. We conducted sampling adjacent to CH stands to ensure that any differences between old and young HA stands were due to differences in site conditions and not seedrain. Placement of the transect perpendicular to the CH stand edge was to allow us to determine the influence of seedrain and potentially observe an invasion front of cedar into old HA stands if the disturbance hypothesis was indeed correct.

Three to five (depending on stand size) 20 m wide × 50 m long transects were established in the HA component of each pair of HA-CH stands oriented perpendicular to the HA-CH interface. Transects were established in both young HA-CH and old HA-CH

combinations. The first transect in each HA stand was placed at a random starting point within the second 50 m along the stand edge (leaving a 50 m buffer from adjacent stands that were not a part of the selected HA-CH pair). Additional transects were placed at 50 m intervals along the edge. The final transect was >50 m from the transition to a different stand. These transects were subdivided into 10 m intervals to create five 10 m × 20 m subplots per transect. Plots landing in nonmesic (nonzonal) microsites were excluded (Fig. 2). Each of the subplots was assessed for crown closure, number of redcedar trees and seedlings, and salal cover and height (Fig. 2). Within each transect, all trees greater than 1.3 m tall were also measured for dbh. To complement the HA transects, 40 m long × 20 m wide transects were established on the CH stands adjacent to the young HA transects and perpendicular to the young HA-CH edge. These transects were subdivided into two 20 m × 20 m subplots and were assessed for the same characteristics as the young and old HA plots to provide a baseline for vegetation characteristics in cedar-dominated stands. Because there was little apparent effect of distance from the edge on CH stands, we did not subdivide these transects as finely as the HA transects.

All redcedar with secondary, scale-leaf foliage (to exclude 1 year old germinants that have only needle-like leaves) and greater than 5 cm tall were included in our sampling, with those less than 1.3 m tall being recorded as seedlings. Redcedar of seed origin were included in the analysis as long as they had established roots. Redcedar of vegetative origin were also included, as this is a common reproductive strategy in closed-canopy stands (Minore 1990). Salal cover and crown closure were determined to the nearest 5% by taking visual estimates and comparing with computer-generated images. Overstory crown closure was estimated as the percentage of the total horizontal area at 1.3 m height in each plot that had leaves or branches directly above it to account for the cover cast by all trees (i.e., all individuals ≥1.3 m). This method estimates cover as the percentage of open space occluded and thus does not account for leaves that overlap each other in different strata of the forest canopy. Average height of salal, also estimated

visually, was determined as the average height of the uppermost branches of salal plants within a plot.

In five of the old HA stands, three plots were established at random to estimate nominal stand age by sampling the two largest hemlock and Pacific silver fir trees in each of these plots (six trees per stand). Each tree was aged by two increment cores at 1.3 m, and all ages given in this paper are from this height. Age values at this height are an underestimate of true tree ages. Based on more detailed aging of cedar trees (Table 1), true ages may well be 40 or more years greater than those stated. Nonetheless, these ages do give an accurate estimate of age beyond 1.3 m and thus provide a reliable estimate of age after any initial suppression period. The age distribution of randomly selected large trees is expected to be relatively wide in uneven-aged stands. The remaining three old HA stands had one or two co-dominant trees aged in each of three plots to ensure that these large trees were older than those reported for young HA stands. Ages in the latter three stands were used for stand age classification only. Ages in the young HA stands have been assessed through several field studies and show that trees in these stands are evenly aged, presumably due to stand-initiating wind storms in 1908 (Prescott and Weetman 1994). Trees in the CH stands were not aged, as the larger redcedar trees were too large to core. The forest cover map for the area classified all of these stands as older than 160 years, maybe up to 1000 years old, but consistent heart rot in large cedar makes the upper limits of these ages impossible to verify (Prescott et al. 1993).

Seedlings that were believed to be of seed origin (based on presence of primary leaves or root morphology) were sampled to establish seedling ages by counting rings at the root collar. This is a minimum estimate of age, as the number of stem growth rings at the base of the live crown of heavily shaded seedlings or saplings can be greater than at the root collar because of insufficient photosynthate to stimulate cell division at the root collar, especially if buried in the forest floor (Antos et al. 2005). Redcedar saplings in young and old HA stands were also aged by increment coring. Estimated ages were adjusted if the core missed the pith by less than an estimated 5 years. Where a core missed the pith by more than 5 years, the core was rejected and the tree was re-cored. Trees with stem decay were excluded from analysis, and those originating from branch layering that were still attached to the parent by a live branch were recorded as the age of the parent stem.

Stem size class distributions were determined for each stand type, with data pooled from all transects within each stand. Basal area was calculated for each species within each stand type.

Statistical tests

Student's *t* tests were performed on differences in basal area of redcedar, hemlock, and Pacific silver fir between young and old HA stands. Observations within stands were pooled for all tests. Due to skewed distributions, all data presented on redcedar seedlings use median values calculated as the median of stand averages (i.e., the central tendency of each stand type, using each stand as one observation). Overstory crown closure showed no trend with distance to edge in either stand type, so observations were pooled and a Student's *t* test for crown closure was carried out between the young and old HA at all distances.

The Mann–Whitney–Wilcoxon rank-sum test was used to compare the distributions of redcedar seedlings and trees in the young and old HA. Nonparametric statistics were used due to the small sample size and non-normal distribution of data (Stewart-Oaten 1995). An $\alpha = 0.1$ was used for all tests to reduce the probability of causing a type II error. Because redcedar seedlings in the young HA stands were very infrequent and showed no trend with distance from the transitional zone, we pooled these across all distances for statistical comparisons. As a result, seedling comparisons were performed by comparing the old HA at each distance with the pooled data from the young HA. Visual inspection

Table 1. Age (in years, estimated as the median of the sample) at breast height (trees) or root collar (seedlings) of western redcedar (*Thuja plicata*) in the western hemlock (*Tsuga heterophylla*)–Pacific silver fir (*Abies amabilis*) sites (HA; years).

Forest type	Crown class	Age			N
		Median \pm SD	Minimum	Maximum	
Old HA	Codominant	168.5 \pm 1.5	167	170	2
	Intermediate	123.0 \pm 0.0	—	—	1
	Saplings	26.2 \pm 8.5	19	42	5
	Seedlings	21.7 \pm 11.5	4	41	32
Young HA	Codominant	127.9 \pm 48.4	68	235	8
	Intermediate	70.7 \pm 9.9	59	99	10
	Saplings	52.0 \pm 10.7	34	77	14
	Seedlings	14.2 \pm 4.8	8	24	5

Note: Crown class types (sensu Oliver and Larson 1996): codominant is A2 layer, main canopy trees; intermediate is A3 layer, lower canopy trees >10 m tall; saplings are ≥ 1.3 m to <10 m tall; and seedlings are <1.3 m tall.

of redcedar seedling, sapling, and tree canopy data showed that the different canopy classes of trees followed the same pattern with distance from the HA–CH edge in both young and old HA stands. Therefore, due to the low frequency of redcedar trees in each canopy class, all canopy classes for redcedar taller than 1.3 m were pooled within each stand. Unlike the seedling results, redcedar density showed a similar trend with distance from the CH edge in both young and old HA stands. Tests were therefore run to detect differences between the young and old HA at each distance.

Nonparametric statistics were used due to the non-normal distribution of data (Quinn and Keough 2002). All statistical tests were done with the statistical package SAS (SAS Institute Inc., Cary, North Carolina).

Results

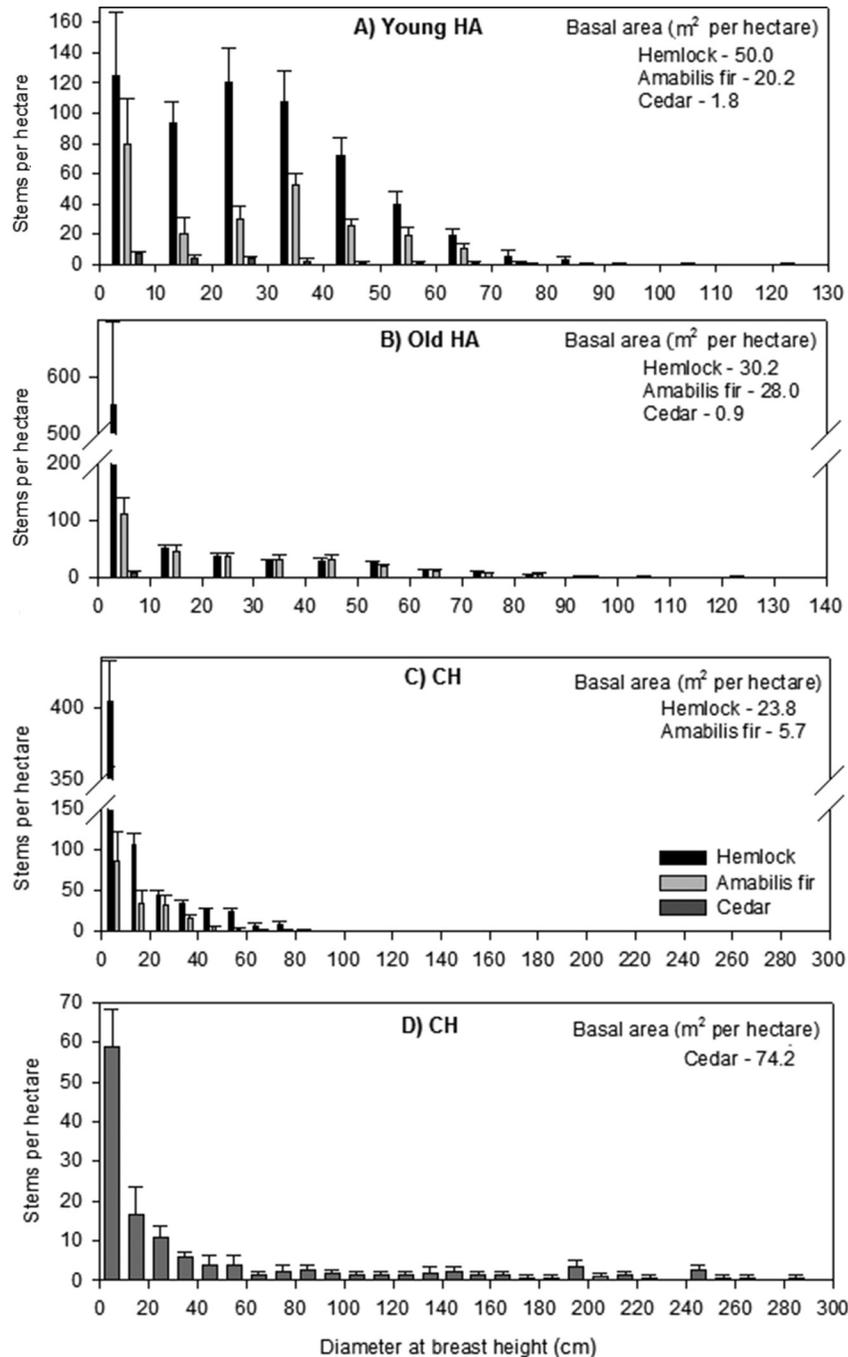
The western hemlock stem size distribution in the young, even-aged HA stands approached a normal distribution and had a fairly similar number of stems per size class up to 40 cm dbh, followed by a steady decline up to 70 cm dbh, and a few trees in larger size classes (Fig. 3A). The presence of a few large hemlocks (close to the maximum size observed in old HA) in young HA stands suggests that these were survivors from the stand that existed prior to the 1908 windthrow event. Pacific silver fir stem size class distribution had peaks in the 0–10 and 30–40 cm dbh classes and then declined in the same pattern as hemlock (Fig. 3A). These patterns likely reflect a single major period of tree growth from seed or seedlings following the stand replacing wind event of 1908, followed by more recent recruitment of additional, now suppressed, understory stems.

The old HA stands (Fig. 3B) had a different skewed stem size distribution than the young HA stands, with the highest frequency of stems in the 0–10 cm dbh class and a steady decrease in number of stems from 10 cm to 90 cm dbh—the classical distribution of an uneven-aged, self-replacing stand (Oliver and Larson 1996). Beyond the 90 cm dbh class, fir and hemlock density was fairly constant up to 140 cm dbh, the largest size of hemlock that occurred in our samples. Hemlock showed a higher recruitment than fir in the 0–10 cm class, but this was not reflected in numbers of trees at greater stem sizes.

Hemlock had a significantly greater basal area in the young HA stands than in the old HA stands (50 vs. 30.2 m²·ha⁻¹, $p < 0.0001$), but fir had a marginally significant difference in the opposite direction (20 vs. 28 m²·ha⁻¹, $p = 0.065$), suggesting that hemlock's relative importance declines as HA stands age. Redcedar basal area was higher in the young HA stands (1.8 m²·ha⁻¹) than in the old HA stands (0.9 m²·ha⁻¹), but the differences were not significant (Figs. 3A, 3B; $p = 0.2$).

Hemlock and Pacific silver fir showed high levels of recruitment in the 0–10 cm class in the CH stands (Fig. 3C), followed by a rapid

Fig. 3. Stem size distributions (cm dbh) of trees in CH and both young and old HA stands on northeastern Vancouver Island: (A) young HA; (B) old HA; (C) CH for western hemlock and amabilis fir; and (D) CH for western redcedar. Values represent means and standard errors of the means.



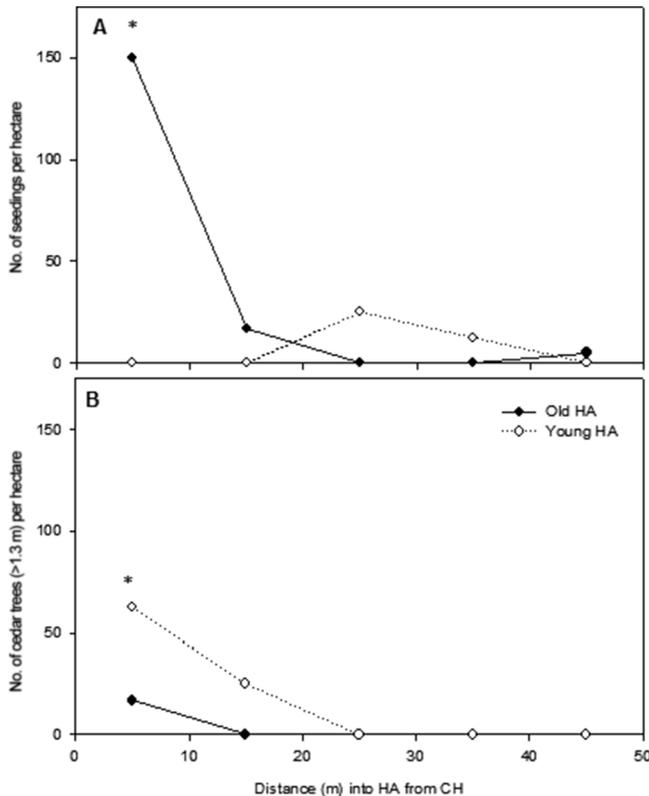
decline in abundance of both species as size class increases. No hemlock or fir trees with a dbh >90 cm occurred in the CH stands, unlike in the young and old HA stands. The stem size pattern of redcedar in the CH stands (Fig. 3D) was similar to that of fir and hemlock up to 50 cm dbh, but the number of stems in subsequent size classes was nearly constant up to very large sizes (approximately 3 m dbh; Fig. 3D).

Age estimates of large trees in five old HA stands were 207 ± 40 , 262 ± 57 , 300 ± 23 , 298 ± 101 , and 287 ± 63 years (mean \pm SD, $n = 8$ for first stand and 9 for all others). Analysis of diameter-to-age relationships showed no significant correlation between co-dominant and dominant tree diameters and ages. Estimates reflect mean ages of trees and not time since stand initiation because these

stands may have been self-replacing and the ages taken are not necessarily from the oldest trees on each stand. However, the estimates confirm that these stands are older than those designated as young HA stands.

Although redcedar seedling abundance in the old HA stands was significantly higher than in the young HA stands ($p < 0.013$) at 0–10 m from adjacent CH stands, there was no significant difference at greater distances (Fig. 4A). In contrast, abundance of redcedar >1.3 m tall was significantly greater in the young than in the old HA stands ($p < 0.05$) within 10 m of the CH stand (Fig. 4B). The distance of redcedar seedling recruitment into the old HA stands was extremely short (seedlings found only at <10 m, despite the

Fig. 4. (A) Number of redcedar seedlings per hectare and (B) number of redcedar >1.3 m per hectare with distance into HA stands from the HA-CH edge. Asterisk denotes a significant difference ($\alpha = 0.10$) between young and old HA at a given distance.



high mean age of adult trees) and greater abundance of redcedar >1.3 m tall in the young than in the old HA stands.

Redcedar ages in young and old HA stands show a large range at all stem sizes (Table 1). Co-dominant redcedar in the young HA stands were as old as 235 years (mean = 128 years) at 1.3 m, indicating that some redcedar from the prestorm stand survived the 1908 windstorm.

There appears to be little variation and no trend in salal cover and height in the young HA with distance from the adjacent salal-dominated CH stand, whereas both showed a decrease with distance into the old HA stands from an adjacent CH stand (Fig. 5). Salal cover in the young HA stands was marginally lower than in the old HA stands at all distances ($p < 0.07$). Salal height showed the same pattern, but differences were only significant at three of five distance classes. Mean tree crown closure was marginally higher ($p < 0.08$) in the young HA stands (94%) than in the old HA stands (85%) and did not appear to follow any clear trend with distance in either HA stand type.

Discussion

If redcedars were establishing in old HA sites as predicted by the disturbance hypothesis, we would expect to see a moving edge of redcedar in old HA sites. This moving edge, or invasion front, would include saplings and young trees closer to the CH edge, as the redcedar trees contribute fewer seeds at further distances. The patterns of redcedar establishment that we found were contrary to these predictions of the disturbance hypothesis. We observed higher redcedar abundance and basal area in the young HA stands than in the old HA stands and redcedar seedling recruitment into the old HA stands at only very limited distances from the CH edge. The differences in redcedar seedling and tree abundance suggest that current and historic recruitment are different in the old and

young HA ecosystems but that these differences are incompatible with the disturbance hypothesis.

The lack of redcedar establishment in old HA stands suggests that HA and CH stands will not converge in the absence of disturbance. A critical but difficult question then is whether they would converge as a result of disturbance. As indicated by redcedar over 1.3 m tall, the disturbance involved in creating a young HA ecosystem appears to be a major opportunity for recruitment. Previous research on the establishment of redcedar seedlings supports this hypothesis (Weber et al. 2003; Daniels 2003), suggesting that disturbance would be a necessary process for causing the convergence of these apparently different stand types.

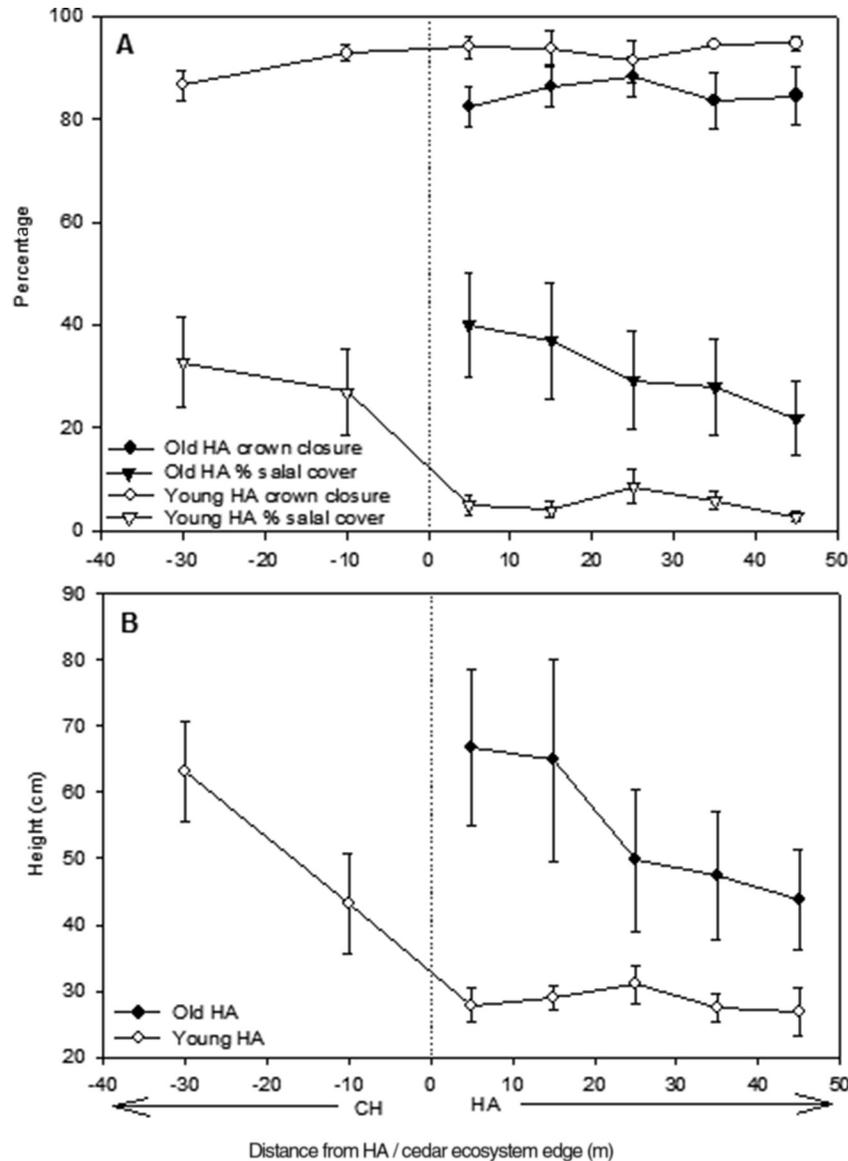
Both the CH and old HA stands show a large recruitment of individuals with small stems relative to the abundance of individuals with larger stems, a pattern that has been observed in and predicted for shade-tolerant trees in self-replacing stands (Whittaker 1970; Oliver and Larson 1996; Kimmins 2004). The size class distributions of old HA stands appears to be in conflict with the disturbance hypothesis, as we would expect a skewed distribution with the peak moved towards larger size classes. The single mode in tree sizes observed in the old HA stands (Fig. 3), along with the large variation in tree ages (Table 1), suggest that the larger trees in these stands are not the result of single, large-scale disturbances. The absence of a broad age range of redcedar in any of these old HA stands is inconsistent with the disturbance hypothesis and indicates that redcedar is unable to establish in these older stands.

There was no apparent trend in redcedar seedling abundance in either the young HA or the old HA stands at 10–50 m from an adjacent CH stand, suggesting that seedlings in the study area are limited by the availability of suitable microsites rather than by distance to seed source (Wright et al. 1998). Redcedar seedling recruitment was higher in the old HA stands within 10 m of the adjacent CH stand than at comparable locations in the young HA stands. This may be explained by a combination of closeness to seed source, greater light availability, and the species' ability to reproduce vegetatively close to adult trees (Minore 1990). Previous studies have shown that for large seedlings and saplings (>1.3 m tall), redcedar is more shade tolerant than hemlock (Carter and Klinka 1992; Kobe and Coates 1997; Khan et al. 2000). However, Weber et al. (2003) demonstrated that in young HA stands, redcedar was more shade intolerant, and its survival in the first two years after germination was lower than that for hemlock and fir. Moreover, redcedar germinants performed best in mineral soil and forest edge conditions, suggesting that establishment is most likely on disturbed soil with moderate to high light conditions (Weber et al. 2003). The generally low light levels in the HA stands, coupled with few sites with exposed mineral soil, may be sufficient to limit redcedar spread by those seeds that do disperse into the interior of this forest type.

The high redcedar seedling establishment in the first 10m of the old HA stands is not coupled with a detectable increase in number of adult redcedar trees, suggesting either that redcedar seedlings do not survive in significant numbers or that the process of redcedar invasion into the old HA is very slow. Black-tailed deer (*Odocoileus hemionus sitkensis* Merriam, 1898) could also be a factor removing redcedar seedlings (Stroh et al. 2008), but in that case, there should be no gradient in seedling survival from the edge of the HA-CH transitional zone, as deer are mostly indifferent to edges between forested stands (Kremsater and Bunnell 1992). As old HA stands appear to be self-replacing, the time frame required for succession to CH through gap invasion, as proposed by the disturbance hypothesis, cannot explain the abundance of CH ecosystems on the landscape today.

The higher numbers of redcedar saplings and trees in the young HA stands within 10m of the adjacent CH stand also contradicts the disturbance hypothesis and is surprising given that the opposite trend was found for redcedar seedlings. The ages of sapling

Fig. 5. (A) Percentage salal and tree crown closure with distance from an HA-CH edge. (B) Salal height with distance from an HA-CH edge.



and lower canopy redcedar in the young HA stands (median ages of 52 and 71 years, respectively) indicate that these trees established soon after the last major windthrow in 1908, the differences in age between the hemlock and redcedar being attributable to the difference in time for the two species to reach the height of measurement (1.3 m; the mean basal age of redcedar seedlings 1.3 m tall was 34 years). Redcedar has slow early growth, especially when shaded. Previous studies have indicated that redcedars are most likely to establish following large-scale disturbances (Daniels et al. 1995; Feller and Klinka 1998; Weber et al. 2003), which is consistent with the patterns observed from our sampling. Another possibility is that redcedar seedlings were present as suppressed individuals in the predisturbance stand understorey (Antos et al. 2005) and were released following windthrow (Weger et al. 1993), as proposed by Messier et al. (1999) for this ecosystem. Neither of these possibilities supports the disturbance hypothesis.

Despite the lack of evidence of cedar invading old HA stands, other stand attributes did suggest successional changes. Salal cover was marginally higher in old HA stands than in young HA stands at all distances, which may result from higher light availability (Messier 1992). Both salal height and cover showed a de-

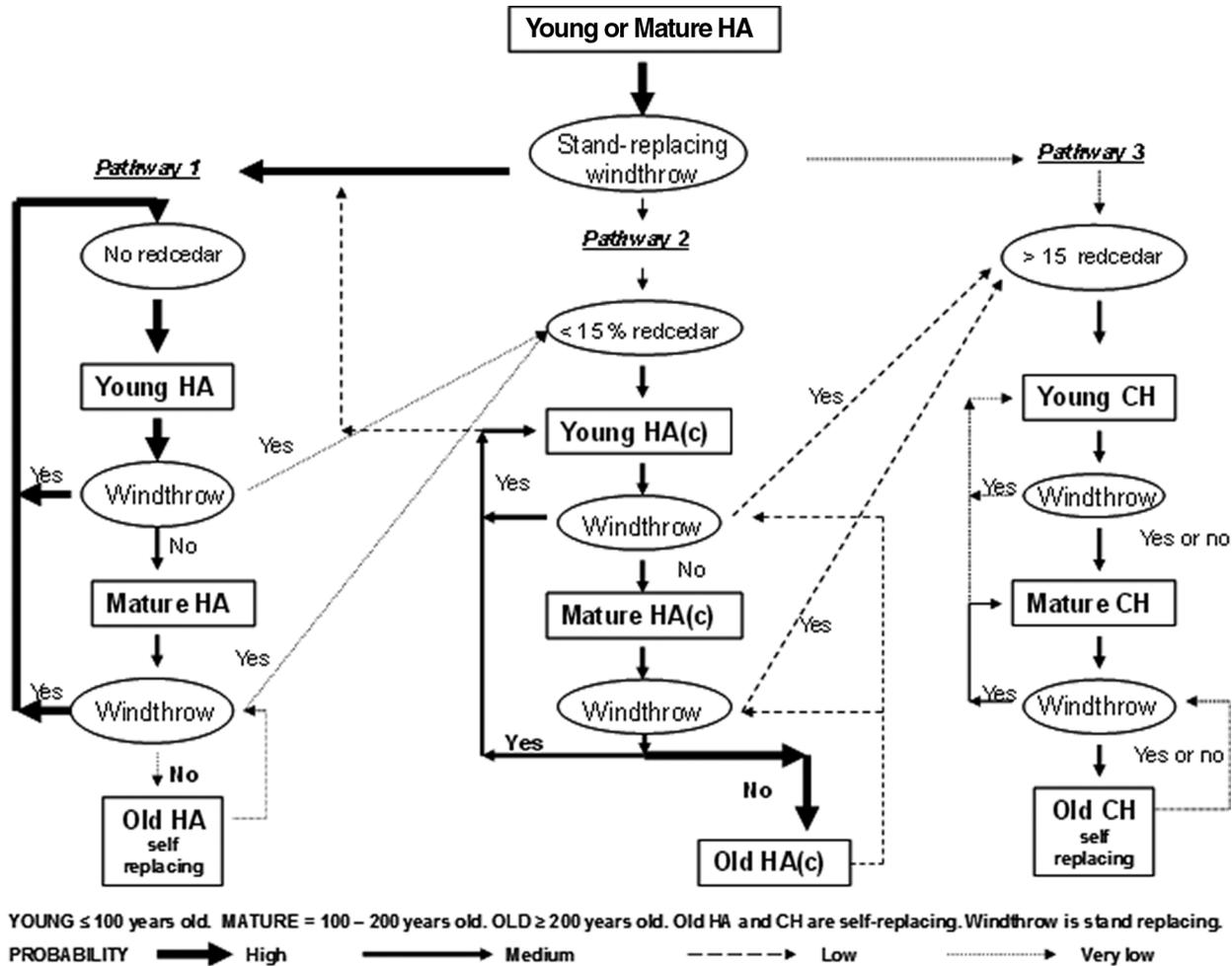
cline with distance from the CH stand edge. Nutrient availability is not affected by salal in a significant way (Prescott and Sajedi 2008), and therefore light is probably the factor limiting salal colonization of HA stands. The greater diversity of canopy heights in CH than HA stands may permit significant lateral light penetration into the HA stands from the HA-CH stand edge. This light, in combination with the lower canopy cover in the old HA stands, appears to be adequate for supporting a higher density of salal.

The distinct patterns of redcedar, salal, hemlock, and Pacific silver fir abundance in the young and old HA stands suggest that individual species are reacting to environmental conditions independently and that changes in the composition of plant communities are occurring on a species level, not on the level of entire plant communities (Lo et al. 2010).

Alternative successional hypotheses for northeastern Vancouver Island

There are two alternative hypotheses that explain the lack of concordance between our observations and the disturbance hypothesis. The first is that disturbance does not play a role in maintaining different stand types and instead other factors such as an

Fig. 6. Multiple-pathway hypothesis of succession on zonal sites on northeastern Vancouver Island. Commencing with stand-replacing wind disturbance of a young or mature HA stand, if there is no redcedar recruitment and (or) survival (pathway 1), the stand can follow a pathway back to young, mature, and (in the continued absence of disturbance) old HA. If redcedar recruits successfully but forms <15% of the basal area of the stand (pathway 2), young and then mature HA(c) may develop but greater advance regeneration and seed source increase the probability of developing towards CH with subsequent disturbance. If >15% of the basal area is redcedar (pathway 3), the stand may develop into young CH, and this may develop into mature and old CH. Windthrow may recycle CH within these categories, but once a site is a CH stand, it is unlikely to return to HA through natural disturbance.



underlying environmental threshold favor different species in each stand type. The most convincing argument for this hypothesis was made by Sajedi and colleagues, who showed significant differences in mean soil moisture and depth of aerated soil between CH and HA stand types (Sajedi et al. 2012). This mean difference was used to infer that CH and HA stand types have different environmental characteristics that favor distinct combinations of tree and understory species. However, despite mean differences between stand types, individual HA and CH stands showed considerable overlap. For example, the depth of aerated soil in the CH stands ranged from 6 to 80 cm, whereas the depth of aerated soil in the HA stands ranged from 31 to 73 cm, resulting in 77% of samples in the CH stands and 59% of samples in the HA stands showing the presence of anaerobic conditions. More generally, the standard deviation in the depth of aerated soils in both stand types was approximately half of the observed mean (mean CH, ~42 cm; mean HA, ~56 cm; SD ~20 cm for both), indicating that microsite heterogeneity in both stand types should allow establishment of species with a broad range of ecological requirements. Hence, even though environmental differences could influence species composition in some parts of some stands, such results suggest that environmental differences are not consistent

enough to be solely responsible for the clear patterns of stand differentiation that we observed.

The second hypothesis is that disturbance is indeed an important determinant of stand composition but that it plays a fundamentally different role than that proposed in the original disturbance hypothesis. We develop this hypothesis here by proposing a multiple-pathway model of succession in which several stable states could be reached (Fig. 6). This multiple-pathway, dynamic model integrates a nonequilibrium view of forests that is now widely accepted in the ecological literature (Campbell et al. 2009). Examples of multiple-pathway models such as the one introduced here are among the considerations prompting scientists to request an update of the BEC (Biogeoclimatic Ecosystem Classification) system (Haeussler 2011).

Our multiple-pathway model starts with a stand-replacing windthrow in a young or mature HA stand. Succession can then follow three different pathways, depending on the establishment of redcedar immediately following disturbance. Thus redcedar is predicted to be a keystone species in these ecosystems. Redcedar establishment can be influenced by factors such as soil moisture, gap size, light availability, and deer browsing. Pathways 1 and 3 are predicted to reach a stable state in the absence of disturbance,

which explains the abundance of both ecosystem types on the landscape. On the other hand, pathway 2 reaches an unstable community that could last for centuries but would eventually revert to one of the other two pathways, explaining the scarcity of this stand type at landscape level.

We propose a critical threshold level of redcedar abundance (arbitrarily marked as 15% basal area in Fig. 6, based on our field observations), which differentiates pathways 2 and 3 (HA(c) versus CH). Redcedar seedling recruitment appears to be limited unless a significant proportion of the surrounding forest is composed of mature redcedar to serve as a seed source, thus the critical threshold abundance in the model. Beyond this critical abundance, redcedar should be able to reproduce in the understory, initiating the transition to a CH stand. The adult redcedar in these transition stands would also be more resistant to windthrow and thus persist through wind events that thin the other species. The mechanism that makes the abundance of redcedar important is unclear, but the relative shade intolerance of redcedar germinants suggests that redcedar has a specific regeneration niche that limits its ability to establish in HA stands.

Redcedar seedling growth relative to that of hemlock and fir has not been tested in the intermediate light conditions that are believed to exist in the old HA stands, and until recently, there had been no investigation of redcedar regeneration in such stands (but see Weber et al. 2003, 2005). It also appears that the lack of arbuscular mycorrhizal symbionts in HA stands prevents the redcedar germinants from gaining sufficient nutrients to develop shade-tolerant secondary foliage, a limiting factor that would be eliminated once a critical threshold of adult cedar trees establishes (Weber et al. 2005). Redcedar competitiveness in wet soils and capacity to change site conditions could also be related to its capability of taking nitrate and calcium from the soil (D'Amore et al. 2009), but the effects of these changes has not been explored in this system.

In our model, disturbance (large-scale windthrow) may allow for changes in species composition, providing a higher probability of transition to a CH ecosystem. If such disturbances occur repeatedly over time, they would create a nonequilibrium distribution of stands and reduce the prevalence of the first pathway on the landscape. In other words, the frequency of large-scale disturbances is predicted to drive the relative abundance of each ecosystem type. However, unlike many successional models, infrequent disturbances can slow the loss of this first pathway from the landscape to such a degree that long-term climate change becomes an important determinant of ecosystem abundance. Since glaciation, northeastern Vancouver Island has had changes in climate and consequently in biological communities at an average interval of ~2800 years, with the current bioclimatic era beginning 3000 years before present (Hebda 1995). Thus, with an estimated windthrow return time of 250 years (Wong et al. 2003), there would be about 10 disturbance events in a single climatic era. Because redcedar only established at the beginning of the current era (Hebda 1995), this relatively low number of windthrow events would lead to a lower representation of the third pathway in Fig. 6, as CH stands would only be initiated following windthrow. This idea runs contrary to much of the successional literature, which tends to examine allogenic and autogenic succession within a given climate, not as they relate to changing climate. With long-lived species such as redcedar, hemlock, and fir that could reach 1000 years old (similar to the time scale of climatic changes) and changes in global climate, successional theories incorporating species composition and species features relative to climate change will become increasingly important (Lo et al. 2010). In such circumstances, concepts such as "climax" or "ecological stability" may need to be redefined.

Our multiple-pathway model is designed to predict successional trends by incorporating the life history characteristics of the main species involved and the stochasticity that is inherent with large-

scale disturbances. We hypothesize that the transition of HA to CH ecosystems is based on the creation of a redcedar regeneration niche in HA stands immediately following disturbance (Daniels et al. 1995; Feller and Klinka 1998; Weber et al. 2003). With appropriate conditions such as high redcedar seed production, favourable winds, and predisposition towards wetter conditions, significant amounts of redcedar will establish. This combination of events may be highly variable: redcedars only tend to produce large seed crops every four or more years (Gashwiler 1969), and a disturbance event (estimated to occur on average every 250 years) would need to coincide with a reasonably large seed crop to initiate large-scale redcedar establishment. Survival may also depend on other biotic factors such as herbivory by deer populations and the number of competing hemlock and fir seedlings establishing after disturbance, both of which may be variable (e.g., Antos et al. 2005). Nonetheless, the presence of some young HA stands on the landscape today with a small but significant component of redcedar in the canopy (B. Gilbert, personal observation) suggests that these transitions are ongoing. Although this variability makes the hypothesis difficult to test directly, it is amenable to tests for proposed mechanisms (i.e., regeneration rates and type of disturbance initiating CH or HA forests; threshold of redcedar abundance to switch between pathways 2 and 3; and the role of deer herbivory in directing the succession process towards each of the proposed pathways).

The reliance of our model on stochastic events (disturbance and relative seed abundance) suggests that history is a key determinant of tree species composition in young stands. Nonetheless, life history characteristics are important on a landscape level, as resistance of redcedar to windthrow appears to withstand disturbance events that negatively impact other species, allowing them to reach on average longer life spans than hemlock or Pacific silver fir (although these species too occasionally reach >900 years of age; Parish and Antos 2004). Likewise, the high shade tolerance of fir appears to cause a long-term shift from hemlock to Pacific silver fir dominance in HA stands not disturbed by wind. The establishment of salal appears to be based solely on light availability, which increased in all stands as they age (Messier 1992).

Conclusions

We have shown that the original disturbance hypothesis cannot explain the trends in species establishment currently seen on the landscape in northern Vancouver Island. According to this hypothesis, CH stands should only develop in the absence of disturbance. However, our data suggest that a more complex succession model could be compatible with site differences by showing that the transition from HA to CH is not currently occurring in the absence of stand-replacing disturbance. The multiple pathways hypothesis of succession is consistent with our findings and suggests that landscape-level differences in stand types may decrease with disturbance instead of being maintained by disturbance. These different predictions for the effects of disturbance highlight the general lack of understanding of the processes that lead to current species distributions at these fine spatial scales. Much of conservation and forestry planning is based on hypotheses about these processes, and our work underscores the need to test these hypotheses directly.

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