Long-term recovery of forest structure and composition after harvesting in the coastal temperate rainforests of northern British Columbia

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ARTICLE INFO

ABSTRACT

We examined young harvested (41–100) and naturally disturbed mature (101–250), and old (>250) temperate rainforests on the central and north coast of British Columbia to quantify the recovery rates of tree size, density, and species composition of young harvested stands towards old-growth condition. Significant variations in recovery rates were noted due to differences in site productivity. Nonmetric multidimensional scaling (NMS) ordinations, Multi-response Permutation Procedure (MRPP) summary statistics, and Sorensen's similarity coefficients (SC) all indicate moderate levels of similarity between young and old stands. Rich sites show greater similarity between young and old forests (SC = 55%) than do medium sites (SC = 41%), indicating more rapid recovery. Differences in tree species composition, especially for western redcedar, were apparent among young and older forests on all sites. We believe that proactive management is required to ensure that western redcedar, an ecologically, culturally, and economically valuable tree species, is maintained as a significant component in the managed second-growth forests of central and north coast British Columbia. Our results indicate that second-growth forests, while not as structurally developed as old-growth, are developing some ecologically important structural characteristics at relatively young ages (80–100 years) and as such, contribute towards ecological integrity and biodiversity of the coastal temperate rainforest landscape.

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1. Introduction

Old-growth forests have long been recognized as biologically diverse ecosystems, typically supporting a wide variety of habitats for plant and animal species (Marcot, 1997) and it is the structural and compositional characteristics that provide the foundation for the unique functional attributes of these forests (Franklin and Spies, 1991; Spies, 2004; Bunnell and Dunsworth, 2009). Although there are many different definitions of old-growth around the world, on the west coast of North America, these forests are often described as being centuries old, relatively undisturbed by humans, and containing large numbers of massive trees, dead and down tree boles, and numerous openings supporting a variety of understory plants and tree saplings (Hunter and White, 1997; Spies, 2004). For the purposes of this paper, we have classified coastal forests as old-growth if the main canopy trees are >250 years of age. These forests are considered by many to be critically important to the sustained functioning of numerous ecological processes (Hunter, 1990; Bunnell et al., 1999).

Around the turn of the last century, these old forests were extensive along the west coast of North America, from southern California through British Columbia (BC) and up to Alaska. As industrial activity expanded in the early 1900s, these forests were considered to be almost limitless and were targeted for harvesting to supply ever increasing demands for building materials and other wood and paper products. As industrial forest harvesting increased and became more efficient, larger areas of old-growth forests were impacted more rapidly and operations moved northward to more remote areas along the central and north coast of BC.

With the resulting gradual but steady decline of old-growth timber, public interest in protecting and preserving what remained began to increase (e.g. Hayter, 2003). During the latter part of the 20th century, the general public perception about forests evolved to recognize that, in addition to economic benefits, forests also provide a wide range of ecological and social services. Since that time, many scientific studies have been undertaken in order to better understand the myriad of attributes and functions of old-growth forests (Puettmann et al., 2008). While there have been extensive studies of the coastal old-growth Douglas-fir (*Pseudotsuga menziesii*) forests of the U.S. Pacific Northwest over the last few decades (e.g., Stewart, 1986; Franklin and Spies, 1991; Acker et al., 1998; Van Pelt and Nadkarni, 2004; Harrington and O'Callaghan, 2012)

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and southwestern BC (e.g., Arsenault and Bradfield, 1995; Wells, 1996; Gerzon et al., 2011), the forests of central and northern coastal BC have received far less attention (Banner and LePage, 2008).

Since the late 1990s there has been a focus on protected area establishment and old-growth representation as fundamental aspects of the ecosystem-based management initiative within the temperate rainforests of coastal BC (Price et al., 2009). While these are important conservation initiatives currently underway, it is also critical that we understand and quantify the contribution that the younger regenerating natural and managed forests make towards overall ecological integrity and biodiversity. This is particularly relevant where old-growth representation targets cannot be met, due to inventory deficits or other social or economic pressures, and there is greater reliance on maturing second-growth to help meet conservation targets (Holt and Sutherland, 2003; Coast Information Team, 2004). The second-growth forests now occupying a significant proportion of the coastal landscape will certainly develop old-growth structural characteristics and species composition given sufficient time (over centuries); however, the degree of recovery possible within management rotations of 80–100 years remains in question.

The recovery of a disturbed forest can be analyzed using a variety of ecosystem attributes including, but not limited to: terrestrial vegetation communities, bryophyte and lichen assemblages, forest growth and productivity, soil properties (including faunal communities), and tree structure and species composition. Our previous paper (Banner and LePage, 2008) presented results on the recovery of forest vegetation communities following logging disturbances over the last 100 years. This study is the first to analyze the structural development and tree species composition in second-growth forests, originating from timber harvesting, on the central and north coast of BC. To accomplish this, we compare second-growth forest tree size, species composition, and density data to analogous data from mature (101–250 years old) and old-growth forests (>250 years old). The intent of this study is to quantify the degree of forest canopy structural (size and density) and compositional recovery towards old-growth condition within second-growth temperate rainforest ecosystems that have developed after logging disturbance. While ecologists emphatically agree that coastal temperate rainforests that have developed over many centuries cannot fully "recover" from harvesting over a typical management rotation, our intent is to more accurately describe the contribution of recovering second growth structure and composition to the ecological integrity and biodiversity of our managed coastal forest landscape.

2. Methods

2.1. Study area

The geographic scope of this study encompasses the coastal temperate rainforests of central and north coastal BC (51°–55°N). Using the biogeoclimatic ecosystem classification system (Meidinger and Pojar, 1991), this study focuses on the forests of the Coastal Western Hemlock zone, Very Wet Hypermaritime subzone, Central variant (CWHvh2) as described by Banner et al. (1993). This variant includes all coastal islands and a mainland fringe along the central and north coast of BC between northern Vancouver Island and Southeast Alaska (Fig. 1). Specifically, the study examines the medium and rich productivity stands (500–1350 m^3 ha^{-1}) where timber harvesting has been concentrated since the early 1900s. These stands occur mainly on moderate to steep, freely drained colluvial slopes and old-growth forests are typically mixtures of western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*), Sitka spruce (*Picea sitchensis*), and amabilis fir (*Abies amabilis*). Depending on the site series (a reflection of moisture and nutrient status and productivity), stand age, and disturbance

history, minor amounts of yellow cedar (*Chamaecyparis nootkatensis*) and red alder (*Alnus rubra*) can also be present. The climate of the outer central and north coast of BC is oceanic, characterized by mild temperatures and high to very high annual precipitation (2100–3186 mm). As a result, stand-replacing wild-fires are very rare so natural disturbances are typically smaller in scale and dominated by landslides and windthrow events. Further details on the climate, vegetation, and soils of the study area are provided in Banner and LePage (2008) and Banner et al. (1993).

2.2. Field data collection

Data from "young forests" (41–100 years) were collected between Prince Rupert and Bella Bella (Fig. 1) from stands resulting from forest harvesting over the past century (24 plots). The stands were typically less than 20 ha in size and contained less than 25 stems/ha of dominant residual trees (trees remaining after harvest). At each potential sample location, four of the largest diameter, non-residual, dominant trees were cored at breast height (1.3 m; DBH) and the rings counted in the field using a 20X magnifying lens. Years to breast height corrections for total tree age were made using stem analysis data from similar forests (Banner et al., 2005) and the oldest total age was used as the approximate stand age (time since stand establishment). Field counts of tree age were verified in the lab using a high-powered dissecting microscope.

Prior to final plot establishment, each location was assessed to ensure the sites series was uniform throughout the plot area and there were no recent (post logging) natural or human-caused openings or disturbances (i.e. windthrow patches, landslides, roads, or recent logging) within fifty meters, that might impact stand development. At each suitable sample location, two independent variable radius plots were established 15–20 m apart. Using standard British Columbia variable plot sampling procedures (British Columbia Ministry of Forests and Range, 2006), a basal area factor (BAF) was selected to ensure that a minimum of seven and no more than fifteen trees ≥12.5 cm DBH were included (average of ten trees per plot). Total height was measured to the nearest 0.1 m using a Vertex Laser Hypsometer and DBH was measured to the nearest 0.1 cm for each tree in the plot.

In order to compare the forest structure of second-growth stands with older forests, we utilized mensuration data collected from the same geographic area during the British Columbia Biogeoclimatic Ecosystem Classification Program (2012). These data were separated into two age groups: "mature forests"; 101–250 years old (34 plots) and "old forests"; >250 years old (29 plots). Stands in these age categories originated from natural disturbances such as landslides, windthrow and possibly fire. For stands less than 250 years old, stand age was considered equal to the age of the oldest dominant (non-residual) tree. Rotten tree cores typically prevented an accurate determination of total tree age in old-growth stands and therefore all stands with tree ring counts >250 in the solid portion of the core were assigned an age of 250 years. To account for the potential effect of site productivity on structural development, we further separated the stands into 2 groups: submesic, nutrient medium (CWHvh2/04 site series); and submesic – subhygric, nutrient rich (CWHvh2/05, /06, and /07 site series). This classification of site series is based primarily on soil moisture and nutrient status as reflected by distinct vegetation communities (Banner et al., 1993; Kranabetter et al., 2003). For the purposes of this paper, these forest site series will be referred to as "medium" and "rich" forests, respectively.

2.3. Data analysis

We used non-metric multidimensional scaling (NMS) ordination to examine the tree species mensuration data for compositional and
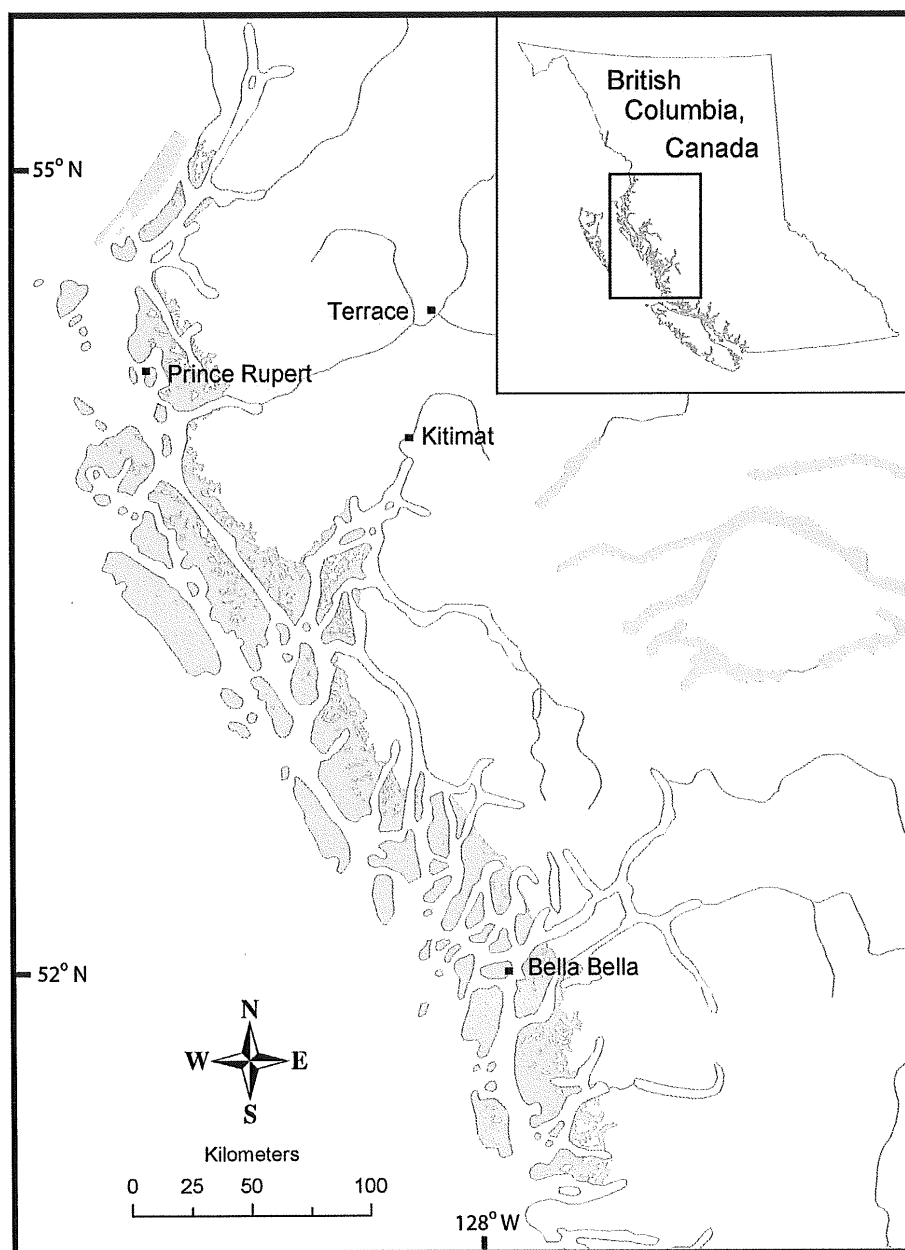
Fig. 1. Map of study area; Coastal Western Hemlock zone, Very Wet Hypermaritime subzone, Central variant (CWHvh2 = shaded area below 600 m in elevation), in British Columbia.

structural patterns in relation to time since stand establishment. NMS is currently considered the most generally effective ordination method for ecological community data because: (1) it avoids the assumption of linear relationships among the variables, (2) its use of ranked distances tends to linearize the relationship between distances measured in species space and distances in environmental space, and (3) it allows the use of any distance measure or relativization (Minchin, 1987; McCune and Grace, 2002). Ordinations were performed using tree species/diameter category combination as variables in order to compare the differences in structure of the forest canopies between old-growth, mature, and younger second-growth stands. We used four diameter categories: ⩾12.5–50 cm, >50 cm, >50–75 cm, and >75 cm. (e.g., a western hemlock tree of 20 cm DBH is treated as a different "species/diameter category" than a western hemlock tree of 55 cm DBH). Dead trees (snags) were also included in the ordination analyses as two size categories (⩾12.5–50 cm, and >50 cm). Due to the relatively low number of snags and inconsistencies in accurate species identification, snags were not separated by species. A primary matrix was created for the NMS ordination using basal area per hectare (BAPH) data for the species/diameter class combinations occurring in the 87 sample plots. The corresponding secondary matrix consisted of stand age (considered equivalent to years since stand establishment), age class ("young" – 41–100 years, "mature" – 101–250 years, and "old" – 250+ years), site series (medium and rich), as well as the basal area data contained in the primary matrix. Ordinations were performed on the medium and rich sample stands separately because our initial exploratory statistical comparisons of site series revealed significant differences in some stand attributes.

We used the ordination program PC-ORD (McCune and Mefford, 1999; McCune and Grace, 2002) to perform the NMS analyses using the Sorensen (Bray–Curtis) distance measure and a random starting configuration. Fifty runs were performed with both real and randomized data to provide the basis for the Monte Carlo test of significance at each dimensionality. Ordination results are presented in two-dimensional graphical format showing plot scores

along the axes that represent the greatest proportion of variation (having the highest R^2 values). Ordination axes were rotated to maximize the correlation of stand age with ordination scores (maximizing Pearson's r value for stand age) along the horizontal ordination axis. Joint plots (McCune and Grace, 2002) were used to illustrate which stand attributes are most important in driving the grouping or separation of sample stands in the ordinations. Multi-response Permutation Procedures (MRPPs; Miekle, 1984) in PC-ORD were used to quantitatively examine the separation between age classes based on tree species composition and structure. The test statistic (T) describes the separation between groups, with smaller or more negative values indicating greater separation. The agreement statistic (A) describes within-group homogeneity compared to random expectation; values close to zero indicate the degree of heterogeneity expected by chance, values close to one indicate highly homogeneous groups while values less than zero indicate highly heterogeneous groups. A p value provides the statistical significance of the separation between groups. Sorensen's similarity coefficients (Bray and Curtis, 1957; Faith et al., 1987) were also used to describe the similarity among the three age classes in terms of mean basal area for tree species/diameter category combinations and snag diameter classes.

We also examined the stand structure data using analysis of variance procedures to look for differences among the age classes within a site type based on mean basal area and mean stems per hectare (SPH) data. We used the PROC GLM Procedure in SAS to accommodate the unbalanced number of plots in each category (SAS Institute Inc., 2011). The results are presented as pairwise comparisons of the least squared means (LSMeans). Our comparison of young, mature, and old forest structure included analyses using all trees $\geqslant 12.5$ cm DBH as well as separate analyses of trees greater than 50 cm DBH. We also looked for structural patterns or trends by plotting the basal area and density data against stand age and comparing the results to the mean values and 95% confidence intervals for the old-growth (>250 years) plots (e.g. Gerzon et al., 2011). The species composition of natural forests commonly changes through time following a variety of successional patterns (Kimmins, 1997) so to further look for differences among age classes, we also compared the tree species composition of these northern coastal forests and looked for pronounced differences or similarities within a site type across age classes. To simplify the visual presentation of the results, very minor species such as red alder, shore pine, and yellow-cedar are not displayed.

3. Results

3.1. NMS ordinations

The NMS ordination of basal area data for medium forest plots is shown in Fig. 2 and Table 1 lists the R^2 values for the three axes. Axes 1 and 2, having the largest R^2 values, were chosen for the 2-dimensional ordination display. The Pearson's r value for age along this axis is 0.613 (Table 1), indicating a moderate correlation between age and axis score. This relationship is apparent in Fig. 2, where the youngest age class plots are concentrated on the left hand side of the ordination with some overlap with mostly mature (but also some old-growth) age class plots. There is considerable overlap of the mature and old age classes on the right hand side of the ordination diagram. Also evident is the significant spread of all age classes along the vertical axis (and in the 3rd dimension, not illustrated) on the ordination, reflecting considerable variation in tree species composition and/or structure within all age classes.

The MRPP analysis for medium forest plots (Table 2) helps to quantify the degree of separation among age classes as well as degree of variation within each age class. The MRPP agreement

statistic (A) is slightly greater than zero, suggesting a generally moderate degree of heterogeneity among the plots in each age class. Average distance values for each age class indicate that the youngest forests are more homogenous, as a group, than are the mature and old-growth forests. The low (negative) overall T value and low associated p value indicate considerable separation among age classes. The pair wise comparisons confirm our expectation that the old-growth and young forests show the greatest distinction, mature and young forests are less, yet still significantly distinct, while the mature and old forests show much greater similarity, based on tree canopy composition and structure (Table 2). The joint plot overlays in Fig. 2 illustrate what specific stand attributes are driving the ordinations and thus the distinction among age classes. The attributes defining all of the different size categories for western redcedar (Cw all, Cw >50 and Cw >75) are the most important in driving the higher scores on axis 2 for the older forest types. Western hemlock and, to a lesser extent, Sitka spruce attributes, across the small to large diameter classes (Hw 12.5–50, Hw >50, Ss all, and Ss 50–75) are more important in distinguishing the younger forests on the ordination (Fig. 2).

The ordination of rich forest plots (Fig. 3) contrasts with that of medium forest plots by having a greater overlap of young plots with the mature and old. The Pearson's r of 0.205 for axis 1 indicates a much weaker relationship between stand age and horizontal axis scores and thus greater similarity among age classes. MRPP statistics also illustrate the greater overlap in age class scores (Table 2). T values are higher (less negative) and only significant (defined as $\alpha = 0.05$) for the old vs young comparison. Again, the young forest plots show the greatest within group similarity of 49%. Overall, the ordinations suggest that for the rich, more productive forests, there is less distinction (compared with the medium forest types) between young, mature, and old age classes, in terms of the composition of tree species/diameter category combinations. The joint plot vectors (Fig. 3) show that Sitka spruce (even in larger diameter classes) is most important in driving the separation of the younger age class, while western hemlock is more important in distinguishing the mature and old forests. Western redcedar is less important in distinguishing the old forests from the young for the rich forest type, compared with the medium forests.

The percent similarity among the young, mature, and old-growth forests is expressed in Table 3, using Sorensen's similarity coefficients. For the medium forest type, based on the basal area of tree species/diameter category combinations and snag diameter classes, the young and mature forests show 41% and 76% similarity, respectively, to the old forests. For the rich forest type, the young and mature forests show 55% and 70% similarity, respectively, to the old forests. Percent similarity between the young and mature forests differs dramatically between the medium and rich forest types; 48% similarity for the medium forests and 77% similarity for the rich forests (Table 3).

3.2. Basal area and stand density comparisons

The analysis of variance (Anova) of basal area per hectare for all trees $\geqslant 12.5$ cm DBH showed no significant difference (defined as $\alpha = 0.05$) among any of the age classes for either medium or rich site types (Table 4). On medium sites, there was slightly more basal area in the young forests than either the mature or old forests. This pattern, however, was reversed on rich sites where the oldest forests had more basal area. The Anova of stems per hectare for the same size range of trees did show a highly significant difference between the young and mature age classes, as well as between the young and old age classes on medium sites (Table 4) with the younger age class having considerably more trees. There was no significant difference between the density found in mature
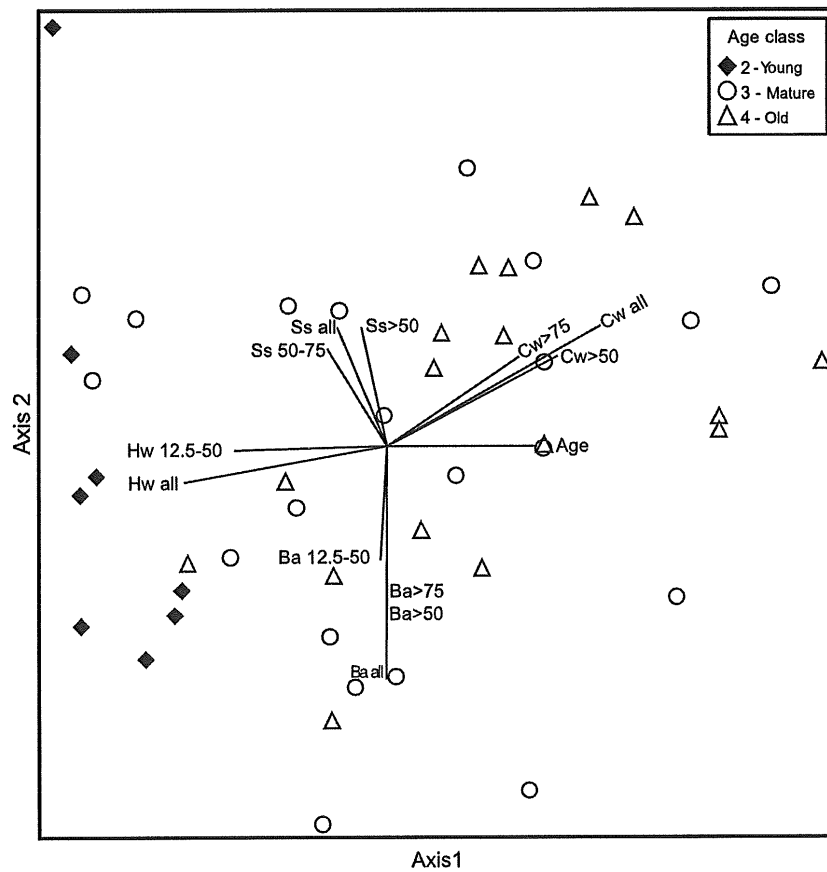
Fig. 2. NMS ordination of basal area per hectare data for medium forest plots. Joint plot vector overlays illustrate the correlation between stand attributes and plot ordination axis scores. Stand attribute vectors are labelled using a two letter species code (Ba = amabilis fir, Cw = western redcedar, Hw = western hemlock, Ss = Sitka spruce), followed by the diameter category (see Section 2.3, Data analysis). Only those attributes having a Pearson's r value above 0.250 are shown.

Table 1
Coefficients of determination (R^2) for the correlations between NMS ordination distances and distances in the original n-dimensional space for the medium and rich forests. Minimum stress and Monte Carlo test p values as well as Pearson's r values, for the correlation of age with rotated horizontal axis scores, are also presented for each ordination run.

Forest type	Axes unrotated	Axes rotated	Minimum stress (Monte Carlo test p value for 3 dimensional solution)	Pearson's r for correlation of age with horizontal axis
Medium forests	R^2 Increment	R^2 Increment		
Axis 1	0.316	0.399		0.613
Axis 2	0.366	0.283		
Axis 3	0.171	0.171		
Cumulative R^2	0.853	0.853	15.5 (0.0196)	
Rich forests				
Axis 1	0.274	0.427		0.205
Axis 2	0.383	0.230		
Axis 3	0.213	0.213		
Cumulative R^2	0.869	0.869	13.6 (0.0196)	

and old age classes on medium sites. On rich sites there was no significant difference among any of the age classes, though the old stands had 182–250 less stems per hectare on average than the young and mature stands (Table 4).

Anovas on basal area data for trees >50 cm DBH showed considerably different results. On medium site types, there was a highly significant difference between young and mature forests, and young and old forests, with the younger stands having markedly less basal area in larger stems (Table 5). There was no significant difference in the average basal area of large stems in medium mature and old stands although the older stands do contain more on

average. On rich sites, where the trees are growing more rapidly, there was no significant difference between young and mature stands but there was between the young and old and the mature and old stands (Table 5). The Anova for density showed the same general pattern with the number of large stems on medium sites being significantly lower in young stands than in either of the older age classes. On rich second-growth sites (young stands) where tree growth is more rapid, there was no significant difference in the number of large trees among all three age classes (Table 5). On average, there were, however, more large trees in the young rich second-growth stands than in the mature age stands.

Table 2
Multi-response Permutation Procedure (MRPP) test results for the separation of age classes based on tree species composition and structure.

Age class	Medium forests		Rich forests	
	Average within-group distance[a]	Within-group similarity[b] (%)	Average within-group distance[a]	Within-group similarity[b] (%)
Young	0.46	54	0.51	49
Mature	0.64	36	0.61	39
Old	0.54	46	0.63	37

MRPP summary statistics for overall comparison of age classes				
T		−7.90		−4.83
A		0.09		0.06
p		0.0000		0.0003

MRPP Summary statistics for pairwise comparison of age classes					
	T	A	p	T	A	p
Old vs young	−16.9	0.16	0.0000	−7.38	0.09	0.0000
Old vs mature	−1.75	0.01	0.0909	−1.12	0.02	0.1303
Mature vs young	−8.38	0.09	0.0000	−1.57	0.08	0.0761

[a] Sorensen's distance was used as the measure of within-group distance.
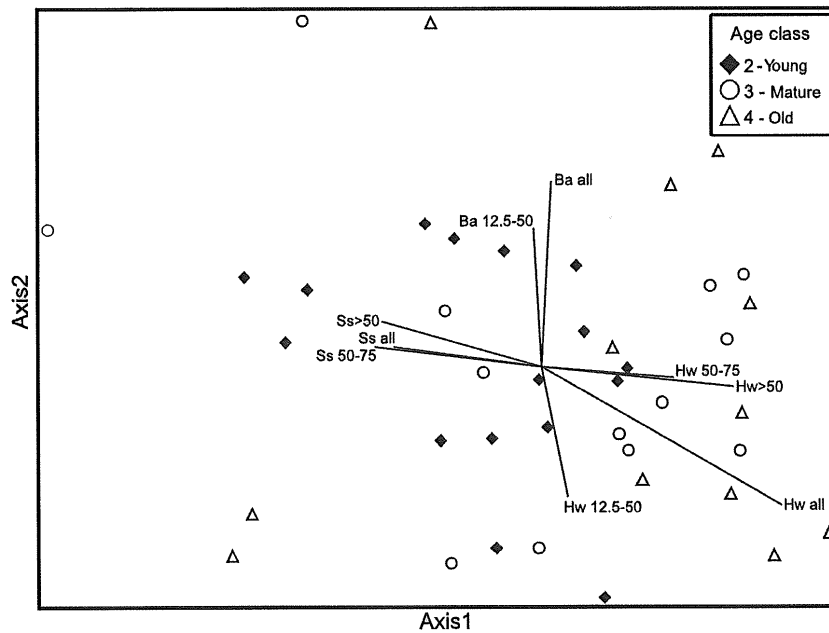[b] % Similarity = (1 − distance) × 100.

Fig. 3. NMS ordination of basal area data for rich forest plots. Joint plot vector overlays illustrate the correlation between stand attributes and plot ordination axis scores. Stand attribute vectors are labelled using a two letter species code (Ba = amabilis fir, Cw = western redcedar, Hw = western hemlock, Ss = Sitka spruce), followed by the diameter category (see Section 2.3, Data analysis). Only those attributes having a Pearson's r value above 0.250 are shown.

Comparing the basal area of the 3 age classes and two site types revealed considerable variability in stand composition and structure in these northern temperate coastal forests, regardless of age. When looking at the basal area of trees >50 cm DBH on medium sites, all of the sampled young stands fall below the average value for old-growth stands and well outside the 95% confidence interval (CI – Fig. 4a), while almost half of the mature stands fall within the old-growth 95% confidence interval. On rich sites, the young stands have a higher average basal area for trees >50 cm and some stands do fall within the 95% CI indicating better growth and more rapid structural recovery (Fig. 4b). It should be noted, however, that a significant number of the rich mature stands sampled also fall below the mean (and the lower 95% confidence interval) for the old-growth stands. Despite the significant variation in basal area within an age class and the resulting low R^2 values for the curves, there is a discernible increasing trend in the BAPH development of larger trees in the rich forests and a more prominent trend for the medium forests.

The variability of these forests is also seen in the number of stems per hectare of trees >50 cm DBH. The mean number of large trees in the old-growth stands is 109 per hectare on medium sites, and like the basal area results, all of the young age class stands

Table 3
Sorensen's percent similarity matrix for young (41–100), mature (101–250), and old (>250) forests based on basal area per hectare data for the medium and rich forest types.

	Young	Mature	Old
Medium forest type			
Young	100	48	41
Mature	48	100	76
Old	41	76	100
Rich forest type			
Young	100	77	55
Mature	77	100	70
Old	55	70	100

Table 4
Least squares means (LSMean) and pairwise comparisons (p-values) among age classes for basal area per hectare (BAPH) and stems per hectare (SPH) for all trees ⩾ 12.5 cm DBH. Values in italics indicate a significant difference (α = 0.05) between the two age class LSMeans.

Site type	Age class	LSMean BAPH	vs. Mature	vs. Old	LSMean SPH	vs. Mature	vs. Old
Medium	Young	82.3	0.491	0.532	1339	*0.0011*	*0.0003*
Medium	Mature	75.8	–	0.955	621	–	0.4812
Medium	Old	76.2	–	–	506	–	–
Rich	Young	68.0	0.964	0.415	636	0.6583	0.2507
Rich	Mature	68.3	–	0.461	704	–	0.1347
Rich	Old	74.5	–	–	454	–	–

Table 5
Least squares means (LSMean) and pairwise comparisons (p-values) among age classes for basal area per hectare (BAPH) and stems per hectare (SPH) for all trees > 50 cm DBH. Values in italics indicate a significant difference (α = 0.05) between the two age class LSMeans.

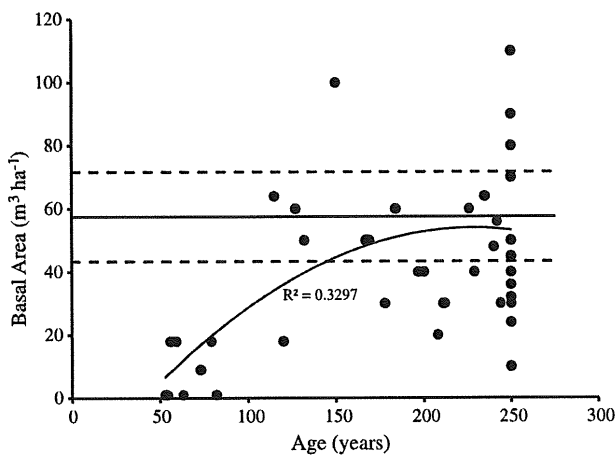| Site type	Age class	LSMean BAPH	vs. Mature	vs. Old	LSMean SPH	vs. Mature	vs. Old
Medium	Young	15.8	*0.013*	*0.002*	57	*0.0166*	*0.0283*
Medium	Mature	47.1	–	0.161	113	–	0.7605
Medium	Old	57.5	–	–	109	–	–
Rich	Young	34.9	0.782	*0.005*	100	0.3145	0.1909
Rich	Mature	33.0	–	*0.003*	80	–	*0.031*
Rich	Old	55.5	–	–	128	–	–

Fig. 4a. Average basal area per hectare of all live trees >50 cm DBH on medium site types. Solid line = mean for all old-growth plots, dashed lines = upper and lower 95% confidence intervals.
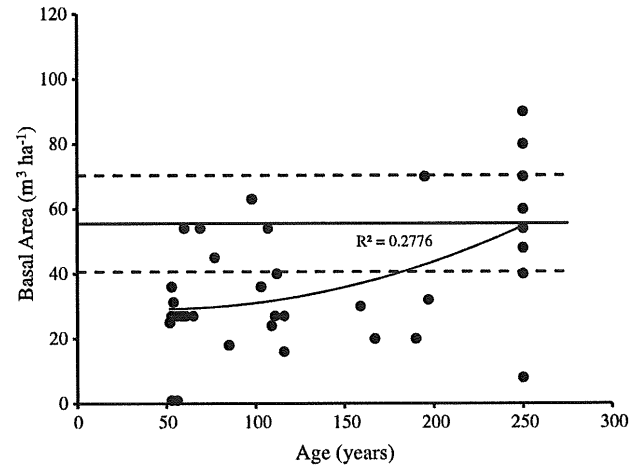

Fig. 4b. Average basal area per hectare of all live trees >50 cm DBH on rich site types. Solid line = mean for all old-growth plots, dashed lines = upper and lower 95% confidence intervals.

have significantly fewer large trees (Fig. 5a). The number of large trees in the mature stands covers a wide range from a low of 44 to a high of 232; a wider range than seen in the old-growth stands. On rich sites there are higher numbers of large stems in the young stands and with the significant variation in old-growth large stem density (15–263) almost 70% of the younger age class sites fall within the 95% CI limits of the old-growth average (Fig. 5b). As was noted for the basal area data, there is an increase in the number of large stems in older stands with the trend being stronger for medium site types than for rich ones (indicating faster growth and structural recovery on the rich sites).

3.3. Tree species composition

When examining all stems ⩾12.5 cm DBH, it is clear that both site types of the mature and old forests, while dominated by western hemlock, contain moderate amounts of western redcedar and amabilis fir and minor amounts of Sitka spruce (Fig. 6a). The younger stands, however, are heavily dominated by hemlock in both site types; 88% of the total in medium forests and 79% in rich forests, resulting in a significant decline in the amount of the other

species. Redcedar shows the largest drop in prominence; from an average of 19% and 27% of the species composition in old-growth and mature forests, respectively, to just 0.2% in young stands on medium site types. This pattern repeats itself in the rich forest types where redcedar composition drops from16% and 22% of the stand in old-growth and matures forests, respectively, to just 1% in the young stands. On both medium and rich sites, the prominence of amabilis fir remained relatively constant over time. Sitka spruce numbers also remained relatively constant on the medium sites but showed a significant increase in younger forests on rich sites, where it now occurs as an average of 17% of the trees.

When we examine the stand species composition of large trees (>50 cm DBH), we again find the mature and old stands of both site types dominated by western hemlock but there are no large hemlock in the young forests on medium sites and only a small component (22%) on the rich sites (Fig. 6b). The prominence of large redcedar has also dropped significantly on medium sites; from 38% to 28% in old and mature forests, respectively, to just 10% of the large trees in young forests. Another dramatic change over time is the dominance of large spruce in young stands on both the
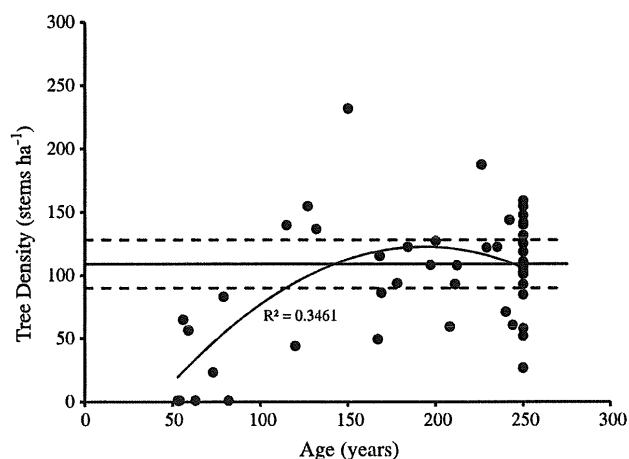
Fig. 5a. Average stems per hectare of all live trees >50 cm DBH on medium site types. Solid line = mean for all old-growth plots, dashed lines = upper and lower 95% confidence intervals.
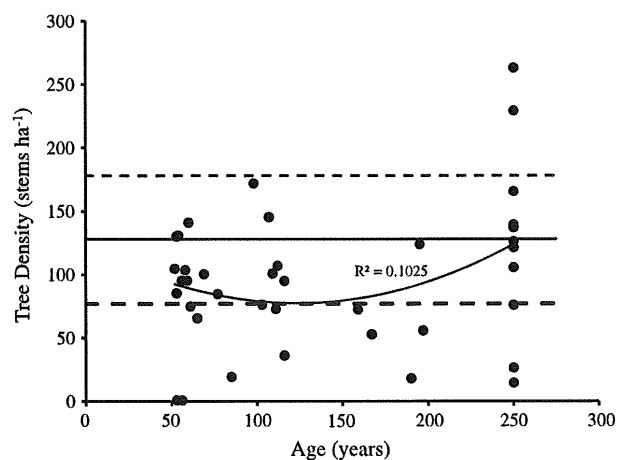

Fig. 5b. Average stems per hectare of all live trees >50 cm DBH on rich site types. Solid line = mean for all old-growth plots, dashed lines = upper and lower 95% confidence intervals.

medium and rich sites – accounting for 69% and 56% of the >50 cm DBH stems per hectare, respectively. There are less large redcedar in the young stands of the rich forest types than in the older ones; however, there is generally less cedar in the natural older forests on these rich site types compared with the medium sites.

4. Discussion

4.1. Old-growth structural recovery

Recovery of structural elements in regenerating coastal temperate rainforests provides the foundation for ecosystem recovery toward the old-growth condition (Spies, 2004). Other ecosystem components critical to ecological integrity and biodiversity, such as understory vegetation development, wildlife habitat features, epiphytic bryophyte and lichen communities, and canopy and coarse woody debris invertebrate communities, are all closely tied to stand structure and composition (Bunnell and Dunsworth, 2009). Our results, using natural old-growth stands as benchmarks, indicate that there is potential for significant structural recovery in harvested second-growth stands within established management rotation ages (80–100 years old). The time required to approach

full structural recovery, however, is likely at least double current rotation ages.

Our analyses of basal area and density data for tree species/diameter categories, indicates mean structural similarities in the range of 40–55% between old-growth temperate rainforests and 80–100 year old harvested and naturally regenerated coastal stands. Stands were highly variable in their rates of structural development; many had specific structural attributes (e.g. basal area and density of trees >50 cm DBH) that reached old-growth thresholds (95% CI limits of the old-growth average) in 50–100 years while other mature stands, 150–200+ years old, were still below old-growth thresholds. Though the study approach used by Gerzon et al. (2011) on the south coast of BC is not directly comparable to our study, they also found considerable variability in the development rates of many structural attributes. We emphasize that while the recovery of forest structure is fundamental to full old-growth recovery, other important ecosystem attributes like epiphytic bryophyte and lichen communities, that first require this structure to establish, will take considerably longer to fully recover to pre-disturbance diversity and biomass levels (Lesica et al., 1991; Price and Hochachka, 2001).

4.2. Western redcedar in regenerating stands

Our results indicate that the differences in tree species composition between the unmanaged harvested and naturally disturbed and regenerated stands are important in driving the separation of young and old forests. Older forests, while dominated by western hemlock, still contain a diversity of species. It is the presence of western redcedar in the mature and old forests in all size classes, however, that distinguishes them from the younger stands where this species is almost absent. While redcedar is typically more abundant on medium sites in the older natural stands, very few redcedar were found in either the medium or rich young second-growth stands resulting from harvest. The near elimination of western redcedar in harvested, naturally-regenerated second-growth stands on our north and central coast (92–97% reduction) is of particular concern. Following a small-scale natural disturbance (e.g. landslide or windthrow) in this area, a typical successional pathway for these forests is the rapid invasion by pioneer species such as red alder, western hemlock, and Sitka spruce. The sites continue to develop in structure and species composition with the seeding-in of slower growing, shade tolerant species like western redcedar, yellow-cedar, and amabilis fir. Over a very long time, redcedar grows up through the canopy to form a significant component of the old-growth species composition (although still hemlock dominated). In the rare cases where hypermaritime forests are disturbed by fire, the authors have observed that western redcedar can be a dominant pioneer species in these naturally regenerated forests, as seedbeds are favorable and competition from western hemlock is greatly reduced (Burns and Honkala, 1990).

The current industrial model for British Columbia's central and northern coastal second-growth forests will see them scheduled for harvest at 80–100 years of age. This is far too short a time period for redcedar to develop along natural successional pathways and current post-harvest management strategies on the mid- and north coast are leading to a de-emphasis of western redcedar to the detriment of biodiversity (Forest Practices Board, 2009). Although considerable effort is being made to re-establish redcedar through planting, the trees are typically overwhelmed by natural western hemlock ingress within a few years of establishment (Klinka and Brisco, 2009). Seedling protection from browsing by black-tailed deer (Odocoileus hemionus) (Pojar, 2002) can be an effective treatment but it is very costly and requires ongoing efforts to ensure survival. As a result, redcedar in new managed stands are often relegated to the understory within the first two
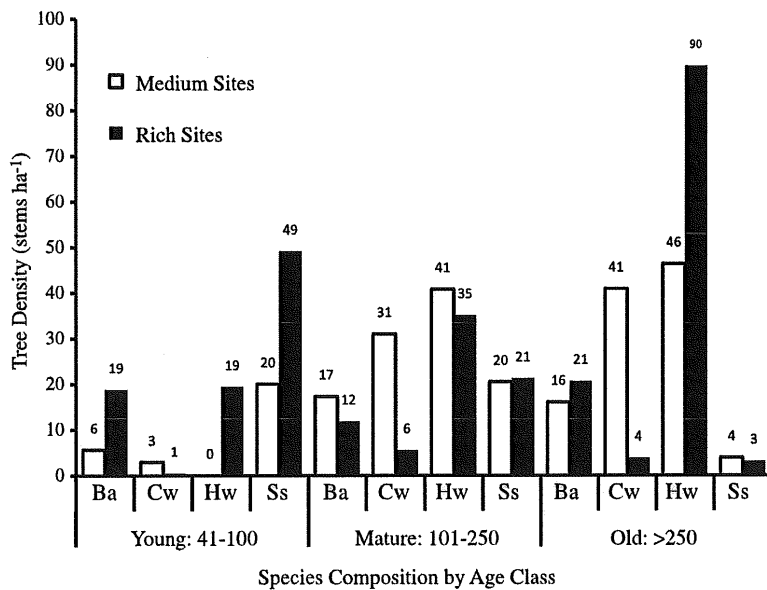
Fig. 6b. Tree density by species and age class for all trees >50 cm DBH on medium and rich sites.
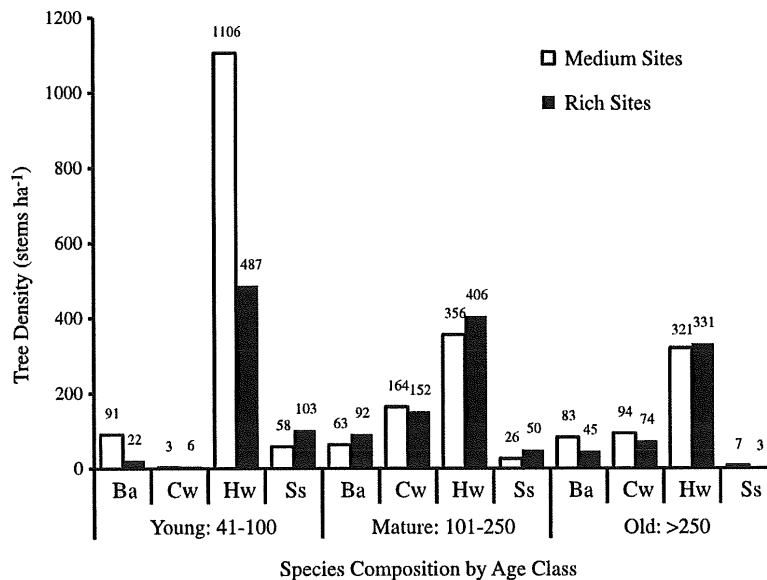

Fig. 6a. Tree density by species and age class for all trees ⩾12.5 cm DBH on medium and rich sites.

decades (British Columbia Ministry of Forests, Lands & Natural Resource Operations: unpublished data). Our results indicate that if western redcedar is to remain an important part of these northern temperate rainforests, then proactive planting and seedling protection, followed by ongoing stand tending programs (e.g. thinning and fertilization) will be required to ensure its continued representation in our managed landscape. Although not a common practice, western redcedar has been shown to respond very positively to stand tending treatments (e.g. Devine and Harrington, 2009). Given that a large proportion of the global coastal western redcedar habitat resides in British Columbia, the absence of a prominent redcedar component in our second-growth stands has significant ecological, cultural, and economic implications for our coastal temperate rainforests (Klinka and Brisco, 2009).

4.3. Effect of site quality on recovery rates

When forest stands are stratified by site type it is clear that there is greater similarity between age classes for rich forest types,

suggesting faster recovery of stand composition and structure, compared with the medium productivity forests. This emphasizes the importance of acknowledging the range in site characteristics and productivity within our coastal forests and the danger in generalizing about how these forests respond to disturbance. In an earlier study of understory and overstory vegetation recovery in these coastal forests, we also found faster recovery rates on the richer sites with similarities in plant species composition and cover between young and old-growth forests slightly higher (53% on medium sites and 58% on rich sites) than in this study (Banner and LePage, 2008). Wells (1996) also found that site quality was positively correlated with rates of stand structural development in the coastal western hemlock forests of southwestern B.C. In contrast, Gerzon et al. (2011) found no differences in structural attributes among different site types on the southwest coast of B.C. In this case, it is likely that small sample sizes combined with high variability in sample plots masked the differences due to site productivity. Because average forest productivity is generally lower on the central and north coast, compared with the southern mainland

coast and Vancouver Island, differences in recovery due to site productivity might also be better expressed further north.

The young harvested forests we studied are significantly dominated by western hemlock with lesser amounts of Sitka spruce and amabilis fir. On both medium and rich site types, the smaller diameter classes of hemlock characterize young stands but on rich sites, larger-sized Sitka spruce and amabilis fir are more common. A greater abundance of larger diameter classes (>50 cm DBH) is generally considered a characteristic feature distinguishing old-growth forests (Franklin and Spies, 1991). In our study, this holds true for the medium sites where the total density of trees >50 cm is significantly higher in the old forests than in the younger ones. On the rich sites, however, there was no significant difference in the number of trees >50 cm DBH between the young harvested and natural old-growth sites, while the natural mature forests have significantly fewer of these larger stems than the old-growth forests. It is the presence of these larger stems in relatively young forests that results in the rich sites recovering old-growth characteristics more rapidly than the medium ones (55% vs. 41% similarity). In addition to providing vertical forest structure, over time these larger trees can provide critical habitat for other old-growth features such as lichen development (e.g. Price and Hochachka, 2001) and nesting platforms for a variety of bird species (e.g. Hamer and Nelson, 1995).

4.4. Logging practices of the early to mid 1900s

One explanation for the abundance of larger trees in these rich second-growth stands is the significant levels of ground disturbance and exposed mineral soil created by the older A-frame logging methods which led to the seeding-in of Sitka spruce. The subsequent rapid growth of the spruce on the rich sites led to more trees passing the 50 cm DBH cut-off at a younger age than on sites with lower productivity. In addition, the logging practices of the mid-1900s typically targeted specific species and tree sizes and thus some residual stems, too small to harvest or of undesirable (at the time) species, remained after harvest (most were simply cut down and left but some remained standing). Release of these residual trees resulted in a greater percentage of larger trees in these second-growth forests than would have resulted from clear-cutting followed by planting or natural regeneration. Although our sampled stands typically had less than 25 stems per hectare of large (and thus obvious) residuals, an unknown percentage of main canopy trees in these second-growth stands could have resulted from release of residual trees that were quite small at the time of harvest. One might argue that the second-growth stands we studied are not representative of those resulting from the industrial clearcuts of the latter 1900s; however, our findings provide good evidence that the partial retention harvesting practices currently being implemented on coastal BC (e.g., Bunnell and Dunsworth, 2009; Pojar, 1999; Price et al., 2009), have considerable potential to increase recovery rates of stand structure in managed second-growth.

4.5. Snags and coarse woody debris

Except for the inclusion of snags in the NMS ordinations, we did not do a detailed statistical comparison of this structural component between the young, mature, and old stands. This is a difficult component to analyze effectively because of the large degree of variability of snags in these coastal forests (Arsenault and Bradfield, 1995). Snag density in second-growth stands is highly dependent on levels of retention of live and dead trees and many studies remove the residual snags from the analysis because the focus is on rates of new snag recruitment in second-growth stands (Gerzon et al., 2011). Characterization of the living structure in these stands, however, indicates that there is considerable potential for large snag recruitment in second-growth stands, particularly on rich sites, provided harvest rotations are long enough or active snag creation (trees are killed and left standing) is part of the management regime (e.g. Cole, 1995). Coarse woody debris (CWD) is another structural attribute of old-growth stands important to a variety of organisms (Bunnell and Dunsworth, 2009) as well as to soil and humus development. Again, recruitment of new CWD will be dependent on future harvesting and management practices and rotation length. Although there has been a move away from broadcast burning in recent years, shorter rotations leading to smaller tree sizes, combined with higher utilization standards, will likely lead to a dramatic reduction in CWD volumes through successive rotations (Wells and Trofymow, 1997; Wells, 1996; Stone et al., 1998).

5. Conclusion

The results of this and other recent ecosystem recovery studies (Banner and LePage, 2008; Gerzon et al., 2011) should provide some guidance to forest planners and managers responsible for implementing the ecosystem-based management program within the coastal temperate rainforests of BC (Price et al., 2009). While conservation of old-growth, through protected areas and old-growth representation, is an important component of that program, considerable data are accumulating to better quantify the rates and degree of recovery in second-growth forests and substantiate their potential contribution to ecosystem integrity and biodiversity. This is particularly important in watersheds where historical harvesting rates have been so high that old-growth representation targets cannot be met. In these situations, recovering second-growth will have to contribute to the representation targets (Holt and Sutherland, 2003). Knowledge of potential recovery rates related to site productivity will help to prioritize second-growth stands for potential inclusion in long term forests reserves. In addition, it is important to recognize that harvesting practices on the coast of BC have changed dramatically over the last 100 years. The retention of existing stand structure (i.e. partial cutting) has the potential to increase the overall rate of recovery by providing a diversity of tree species and a wider range of sizes than would be found in a typical clearcut.

In this study, we examined the development of post-harvest forest composition and structure occurring over the past century and compared this with much older forests that were established prior to significant (human-induced) climate change. Given the current predictions for global warming and the uncertainties about how precipitation regimes will change and interact with temperature on the coast (Zhang et al., 2007), we must apply our results of historical ecosystem recovery with some caution. Under the future climatic regimes, the old-growth benchmark or "recovery target" will be different from what we are now using for comparison. Forest growth rates may increase with increasing temperatures on the coast, which may bode well for structural recovery rates, but tree species and other forest organisms will also be affected by this change in many different and unpredictable ways – some positive, some negative. For example, some climate change impact models predict a decrease in climatically suitable habitat for many commercial tree species in southern BC but an increase in northern BC by 2085 e.g. Hamann and Wang, 2006). This example of potential climate change impacts on tree species highlights the need to continue monitoring second-growth forest succession and actively manage for structural development and species composition that is not driven solely by timber objectives. Partial cutting or retention harvesting, maximizing diversity in tree species regeneration prescriptions (including a significant increase in the western redcedar

component), and implementing more active stand management activities in maturing second-growth stands, will be essential to ensure a significant degree of tree species and structural recovery in younger managed stands toward an "old-growth-like" condition.

Acknowledgements

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