

Long-term recovery of vegetation communities after harvesting in the coastal temperate rainforests of northern British Columbia

Allen Banner and Philip LePage

Abstract: We sampled second-growth forests ranging in age from 28 to 98 years and compared them with old-growth forests to quantify rates of terrestrial vegetation recovery following harvesting on the northcentral coast of British Columbia. Species richness approximately doubles, while Simpson's index of diversity increases from 0.81 to 0.91 from young to old forests. Nonmetric multidimensional scaling ordinations showed differentiation, with some overlap, of old-growth and second-growth forests and a fairly strong correlation of stand age with plot scores, driven by plant species presence and cover. Vegetation succession following logging disturbance is driven primarily by predisturbance species composition; most species found in the young forests are present in old forests and the higher species richness typical of old growth is largely due to the establishment of additional cryptogam and herb species of low cover and constancy. Significantly higher cover of shrub, herb, and bryophyte species differentiates old forests from second-growth forests. Forests 41–100 years old average 63%–73% similarity (depending on site type) to old-growth forests based on species presence–absence and 53%–58% similarity based on species cover. The scarcity of western redcedar (*Thuja plicata* Donn ex D. Don) in second-growth stands is of particular concern because of the high ecological, cultural, and economic importance of this tree species.

Résumé : Nous avons échantillonné des forêts de seconde venue dont l'âge variait de 28 à 98 ans et nous les avons comparées à de vieilles forêts pour quantifier le taux de récupération de la végétation terrestre après coupe dans le centre-nord de la région côtière de la Colombie-Britannique. La richesse en espèces des vieilles forêts est environ le double de celle des jeunes forêts tandis que l'indice de diversité de Simpson augmente de 0,81 à 0,91. Les ordinations par étalonnage non métrique multidimensionnel ont montré que les vieilles forêts se différenciaient, avec un certain recouvrement, des forêts de seconde venue et qu'il y avait une corrélation relativement étroite entre l'âge des peuplements et les résultats des placettes, due à la présence et à la couverture des espèces végétales. La succession de la végétation qui suit la perturbation causée par la coupe est fonction principalement de la composition en espèces avant la perturbation; la plupart des espèces retrouvées dans les jeunes forêts sont présentes dans les vieilles forêts et la plus grande richesse en espèces, typique des vieilles forêts, est due en grande partie à l'établissement de nouvelles espèces de cryptogames et de plantes herbacées dont la présence et la couverture sont faibles. Les vieilles forêts se distinguent des forêts de seconde venue par un couvert significativement plus important d'arbustes, de plantes herbacées et de bryophytes. Les forêts âgées de 41 à 100 ans ont un degré de similarité avec les vieilles forêts qui est en moyenne de 63 à 73 % (dépendamment de la station) sur la base de la présence ou de l'absence des espèces et de 53 à 58 % sur la base de la couverture des espèces. La rareté du thuya géant (*Thuja plicata* Donn ex D. Don) dans les peuplements de seconde venue est particulièrement préoccupante étant donné la grande importance écologique, culturelle et économique de cette essence.

[Traduit par la Rédaction]

Introduction

The temperate rainforests of central and north coastal British Columbia are an important ecological, cultural, and economic resource for the province. While there has been extensive sampling of old-growth forest ecosystems (>250 years old and without any human-caused disturbances) throughout this area over the past 35 years during the development of the biogeoclimatic ecosystem classification program (Pojar et al. 1987; Banner et al. 1993), studies of ecosystem recovery following disturbance in this forested

landscape are virtually nonexistent. Relevant studies from Vancouver Island and Southeast Alaska have begun to examine issues related to ecosystem recovery but their applicability to the north and central coast of British Columbia is uncertain (Alaback 1982; Ryan et al. 1998).

On coastal British Columbia, provincial ecosystem-based management planning teams have developed recommendations for applying a variety of forest management and harvesting practices (Coast Information Team 2004) without adequate data on how these forests have responded to, and recovered from, past disturbances. Disturbance is a driving force in successional development and one that must be recognized and understood to make sustainable ecosystem management possible (Bormann et al. 1995; Jöngiste et al. 2007). During the development of a strategic resource management plan for the north and central coast of British Columbia (North Coast LRMP Planning Table 2005), the provincial planning teams modelled the predicted future

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ratios of second-growth versus old-growth forests and compared this with the extent of old growth expected to result from natural disturbance regimes. The results of this modelling were used as a basis for an “environmental risk assessment” (Holt and Sutherland 2003). Field data on the rates of ecosystem recovery would enable this modelling to better portray the contribution that second-growth stands make to the ecological integrity, resilience, and stability of our managed coastal forest landscape.

Forests are long-lived, complex, and dynamic ecosystems and they are typically subject to a wide variety of both natural and anthropogenic disturbances at several spatial and temporal scales. Although large-scale, stand-replacing disturbances such as fire are infrequent on the mid- and north coast of British Columbia, smaller-scale disturbances such as windthrow, landslides, and flooding are important factors for maintaining forest productivity (Bormann et al. 1995, Lertzman et al. 1996). The concepts of ecosystem resilience and stability have been studied and discussed in the ecological literature for a long time (Holling 1973; Gunderson 2000). In very general terms, resilience can be described as the ability of an ecosystem to absorb external influences and remain intact, while stability can be described as the ecosystem’s ability to recover and return to a steady or equilibrium state after a disturbance (Holling 1973). While these concepts have been described in a theoretical sense with worldwide examples to illustrate different degrees of resilience and stability, there has been relatively little work examining how long it actually takes specific forest ecosystems to recover to predisturbance (mature or old-growth) conditions.

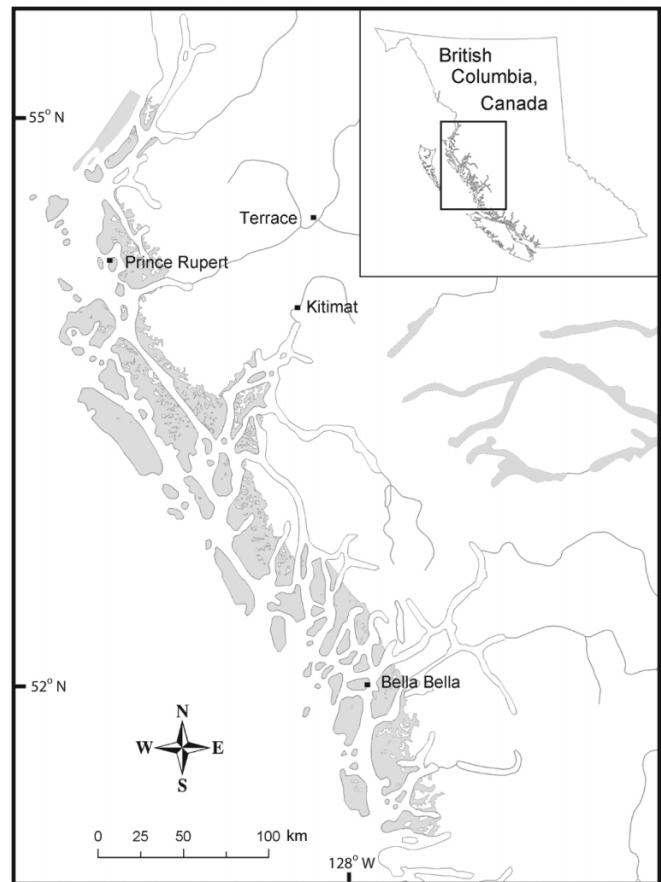
The overall goal of our study is to quantify the degree of recovery of second-growth temperate rainforest ecosystems by comparing data on a variety of ecosystem attributes with analogous data from old-growth forests. Our study of ecosystem recovery rates is being accomplished through an examination of existing second-growth forest stands that have developed after logging disturbance. The intent is to characterize the ecological condition and level of ecosystem recovery toward “old-growth” stand conditions. This paper specifically examines forest vegetation recovery following logging disturbances over the last 100 years. While we recognize that the development of vegetation communities is not the only criterion used to characterize an old-growth forest, we chose to report on the recovery of the vegetation community first because it represents a major biological component of these forests and directly influences, or is influenced by, many of the other ecological attributes of the forest ecosystem that we are studying (stand structure, forest growth and productivity, epiphytic bryophyte and lichen composition, and soil properties including faunal communities) and that will be reported on in other papers.

Materials and methods

Study area

The general geographic scope of this study encompasses the coastal temperate rainforests of central and north coastal British Columbia (51–55°N). The 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 subzone includes all coastal

Fig. 1. Map of the study area, Coastal Western Hemlock zone, very wet hypermaritime subzone, central variant (CWHvh2 = shaded area below 600 m in elevation), in British Columbia.



islands and a mainland fringe along the central and north coast of British Columbia between northern Vancouver Island and Southeast Alaska (Fig. 1). The climate of the outer north and central coast is oceanic, characterized by mild temperatures (mean annual temperature 6.7–8.5 °C), high rainfall (mean annual precipitation 2104–3186 mm), and low evapotranspiration. The winters are extremely wet and relatively mild (mean temperature of the coldest month –0.2–2.9 °C), although subzero temperatures may occur for short periods when cold Arctic air covers the area (Banner et al. 2005).

The vegetation of the study area is a complex of upland coniferous forests in areas of steep to moderate slopes, with bog forests, bog woodlands, and blanket bogs dominating the areas of gentle relief (Banner et al. 1988, 1993, 2005). Landslides, wind, and alluvial flooding are the typical natural disturbance agents of the outer coast, with gap phase dynamics being the dominant regeneration process in these forests. As a result, most forests are old growth with an uneven age structure (Lertzman et al. 1996) dominated by the shade-tolerant conifers western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and western redcedar (*Thuja plicata* Donn ex D. Don) that, depending on site conditions, form intimate mixtures with yellow-cedar or cypress (*Chamaecyparis nootkatensis* (D. Don) Spach), shore pine (*Pinus contorta* Dougl. ex Loud. var. *contorta*), Sitka spruce (*Picea sitchensis* (Bong.) Carr.), amabilis fir (*Abies amabilis*

Table 1. Description of vegetation layers used for field sampling.

Vegetation layer	Layer description
A1	Dominant trees: dominant (tallest) trees of the main canopy, usually a minor portion of the stand composition
A2	Codominant trees: the main layer of tree cover composed of trees whose crowns form the upper layer of foliage; typically the major portion of the stand composition
A3	Subcanopy trees: trees >10 m high that do not reach the main canopy
B1	Tall shrub layer: woody plants 2–10 m tall including shrubs and advance tree regeneration
B2	Low shrub layer: woody plants <2 m high and advance tree regeneration, except low (<15 cm) woody or trailing plants
C	Herb layer: herbaceous – graminoid species, regardless of height, and some low woody plants <15 cm tall
D	Bryophyte and lichen layer: terrestrial mosses, liverworts, lichens, and tree seedlings

Table 2. Coefficients of determination (R^2) for the correlations between NMDS ordination distances and distances in the original n -dimensional space for the rich and medium forest types (R^2 values are presented for separate ordinations run using raw percent cover data and presence–absence data).

Forest type	R^2 increment			
	% cover data	% cover data axes rotated	Presence–absence data	Presence–absence data axes rotated
Rich forests				
Axis 1	0.186	0.186	0.031	0.031
Axis 2	0.382	0.351	0.040	0.182
Axis 3	0.222	0.253	0.188	0.045
Cumulative R^2	0.790	0.790	0.259	0.259
Medium forests				
Axis 1	0.155	0.155	0.265	0.482
Axis 2	0.489	0.558	0.357	0.140
Axis 3	0.214	0.145	0.168	0.168
Cumulative R^2	0.858	0.858	0.790	0.790

(Dougl. ex Loud.) Dougl. ex Forbes), and mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.) (nomenclature for scientific and common names of vascular and nonvascular plants follows Meidinger et al. 2004).

This study focuses on the more productive stands (approximately 500–1000 m³/ha) where timber harvesting has been concentrated since the early 1900s. These stands are typically mixtures of western hemlock, western redcedar, Sitka spruce, and amabilis fir occurring on moderate to steep slopes, with understories characterized either by a variety of ferns (*Gymnocarpium dryopteris* (L.) Newman, *Athyrium felix-femina* (L.) Roth, and *Polystichum munitum* (Kaulf.) K.B. Presl) or by mosses (*Rhytidiadelphus loreus* (Hedw.) Warnst. and *Hylocomium splendens* (Hedw.) Schimp) with very little herbaceous development, depending on the moisture and nutrient status (Banner et al. 1993). Podzols developed in colluvial parent material with surface organic layers <25 cm thick and a history of soil mixing characterize the soils on these forest sites.

Field data collection

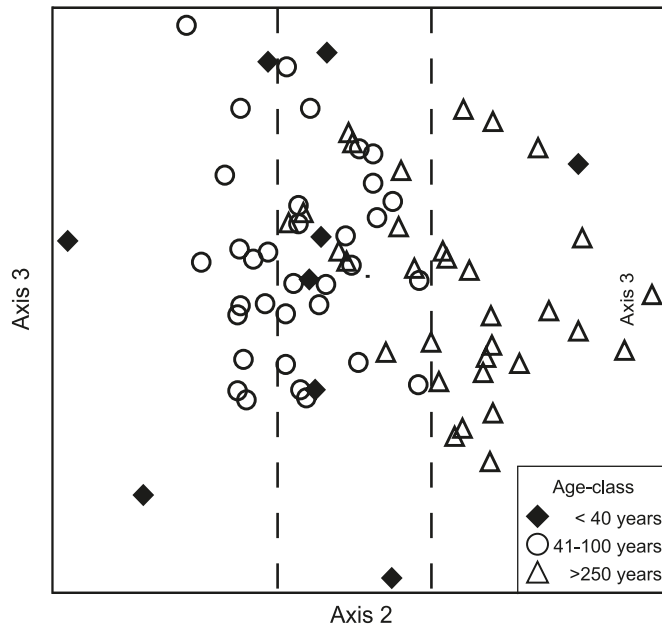
To quantify levels of recovery in second-growth stands, we utilized data from two different sources. Old-growth data (61 plots) were collected from sites located within the CWHvh2 variant primarily between Prince Rupert and Bella Bella (Fig. 1) during the British Columbia Forest Service ecosystem classification program (Banner et al. 1993). Sec-

ond-growth data (88 plots) from the same geographic area were collected from stands resulting from forest harvesting over the past century. Second-growth stands resulting from harvesting ranged in age from 28 to 98 years. Stands were typically <20 ha in size and only those containing <25 stems/ha of dominant and co-dominant residual trees were selected for sampling to minimize the variation in overstory retention and its potential impact on understory development. Industrial logging activities on the north and central coast of British Columbia have only occurred over the past century and, as a result, harvested stands older than 100 years are essentially nonexistent.

To account for the potential effect of site productivity on vegetation recovery, we stratified our sampling by the two dominant forest site types within the portions of the study area where harvesting operations have occurred: submesic, nutrient rich (CWHvh2/05 and CWHvh2/06 site series) and submesic, nutrient medium (CWHvh2/04 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 “rich forests” and “medium forests”, respectively.

All vegetation data were collected using the same methods. At each potential sample stand, several of the largest, nonveteran dominant trees were cored to determine approxi-

Fig. 2. NMDS ordination analysis of terrestrial vegetation plots representing three age-classes in the rich forest type. Vertical broken lines indicate areas of overlap in ordination scores between old-growth and younger forests.



mate stand age (time since stand establishment). Prior to the establishment of a plot, each location was assessed to ensure that the sites series was uniform throughout the plot area and that there were no recent natural or human-caused openings or disturbances (i.e., windthrow patches, landslides, roads, or recent logging) within 50 m that might impact vegetation development. At each suitable sample location, a 20 m × 20 m vegetation assessment plot was established. For each plot, we recorded the species and percent cover of all terrestrial vegetation in each of seven vertical layers (Table 1), including bryophytes and lichens growing on humus and well-decomposed rotting wood. Species cover values for each layer were determined by ocular estimation to the nearest 1%. Scattered individuals occupying <1% were assigned values of either 0.5% or 0.1%.

Data analysis

We used nonmetric multidimensional scaling (NMDS) ordination to examine the vegetation data for compositional and structural patterns in relation to time since stand establishment. NMDS is currently considered the most generally effective ordination method for ecological community data because (i) it avoids the assumption of linear relationships among the variables, (ii) its use of ranked distances tends to linearize the relationship between distances measured in species space and distances in environmental space, and (iii) it allows the use of any distance measure or relativization (Minchin 1987; McCune and Grace 2002). To compare the differences in structure of the vegetation between old-growth and second-growth stands, we performed ordinations using species–layer combinations. With this method, the vertical differentiation of species is recognized (e.g., a dominant western hemlock tree (A1 layer) is treated as a differ-

ent “species” than western hemlock in the low shrub layer (B2)).

The primary matrix for the NMDS ordinations consisted of percent cover data for the species–layer combinations found in each of the 149 sample plots. The secondary matrix consisted of stand age (considered equivalent to years since stand establishment), age-class (<40, 41–100, and 250+ years), and total cover for the tree, shrub, herb, and bryophyte–lichen layers. For stands <250 years old, stand age was considered equal to the counted age of the oldest dominant 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 were assigned an age of 250 years.

Ordinations were performed using both plant species cover data and species presence–absence data. Separate ordinations were performed for both the rich and medium forest types to minimize the variation owing to differences in moisture and nutrient regime and thus vegetation communities among the plots. This allowed us to focus our analysis on the effect of stand age on vegetation community development. We used the ordination program PC-ORD (McCune and Mefford 1999; McCune and Grace 2002) to perform the analyses using the Sorensen (Bray–Curtis) distance measure and a random starting configuration. NMDS arranges the plots in a configuration that minimizes the disparity (stress) between the interplot distances and those in the original n -dimensional space. The stability of each solution was assessed using plots of stress versus iteration number with a final stability criterion of 0.00001. Fifty runs were performed with both real and randomized data to provide the basis for the Monte Carlo test of significance at each dimensionality. The proportion of variation represented by each axis, based on the R^2 between distance in the ordination space and distance in the original space, is also reported. Ordination results are presented in a two-dimensional graphical format showing plot scores along the axes that represent the greatest proportion of variation. A comparison of plant species diversity among age-classes is presented using species richness and Simpson’s index of diversity (McCune and Mefford 1999). A comparison of mean percent cover of terrestrial vegetation, by layer and forest type, between young and old forests was also performed. Duncan’s multiple-range test was used to compare means in both cases. Maximum likelihood was used to estimate the regression parameters for changes in species richness over time using the NLMIXED procedure in SAS (SAS Institute Inc. 2004). The similarity in presence–absence and cover of plant species among age-classes was calculated using the Sorensen similarity (Bray–Curtis) coefficient (Bray and Curtis 1957; Faith et al. 1987). We also used the multiresponse permutation procedures (MRPP) (Mielke 1984) in PC-ORD (McCune and Mefford 1999) to quantitatively examine the separation between age-classes based on their plant species composition and cover. 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 with random expectation; values close to zero indicate the degree of heterogeneity expected by chance, values close to 1 indi-

Table 3. MRPP test results for the separation of age-classes based on plant species composition and cover.

Age-class (years)	Rich forests		Medium forests	
	Average within-group distance	Within-group similarity (%)	Average within-group distance	Within-group similarity (%)
<40	0.69	31	0.56	44
41–100	0.57	43	0.49	51
>250	0.59	41	0.50	50
MRPP summary statistics	$T = -17.84, p = 0.0001, A = 0.07$		$T = -25.63, p = 0.0001, A = 0.13$	

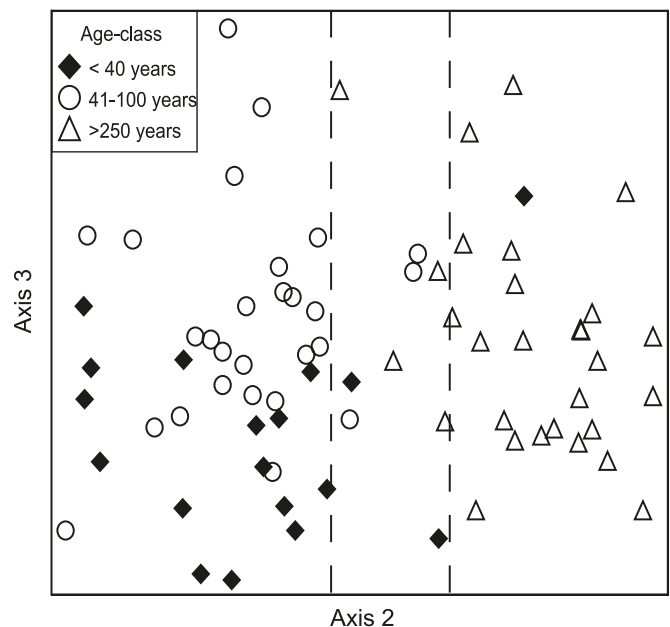
Note: Sorensen's distance was used as the measure of within-group distance. % similarity = $(1 - \text{distance}) \times 100$.

cate highly homogeneous groups, and values less than zero indicate highly heterogeneous groups. Based on all possible partitions of the data set, a p value provides the statistical significance of the separation between groups.

Results

The results of the NMDS ordination of the rich forest plots, using species cover data, recommended a three-dimensional solution. The proportion of variation accounted for by axes 1, 2, and 3 is reflected in their R^2 values of 0.186, 0.382, and 0.222, respectively, for a cumulative R^2 of 0.790 (Table 2). A two-dimensional plot using axes 2 (horizontal) and 3 (vertical) is shown in Fig. 2. To better quantify the relationship between forest age and ordination scores, Pearson correlation coefficients (r) (McCune and Mefford 1999) were calculated from an overlay of stand age (from the secondary matrix) on plot ordination scores. The ordination axes were then rotated to maximize the correlation (Pearson r value) of stand age with plot scores along the horizontal axis (Fig. 2). Rotation of these axes results in no change to the cumulative R^2 (Table 2). A Pearson r value of 0.677 for age along the horizontal axis indicates a fairly strong correlation between age and axis score. There is separation of most of the plots in the oldest age-class from the younger plots but there is also a central zone of overlap in plot scores (the area between the broken lines in Fig. 2) indicating some similarity in plant species composition and cover. The MRPP analysis yielded a very low (negative) T value and a low p value, confirming the separation among age-classes, based on plant species composition and cover (Table 3). Pairwise comparisons were also performed and these confirmed that each of the three age-classes is distinct. The MRPP agreement statistic (A) greater than zero indicates a moderate degree of heterogeneity among the plots in each age-class. This is confirmed by average within-group (age-class) plot similarities ranging from 31% in the <40-year-old rich forest group to 51% in the 41- to 100-year-old medium forest group (Table 3).

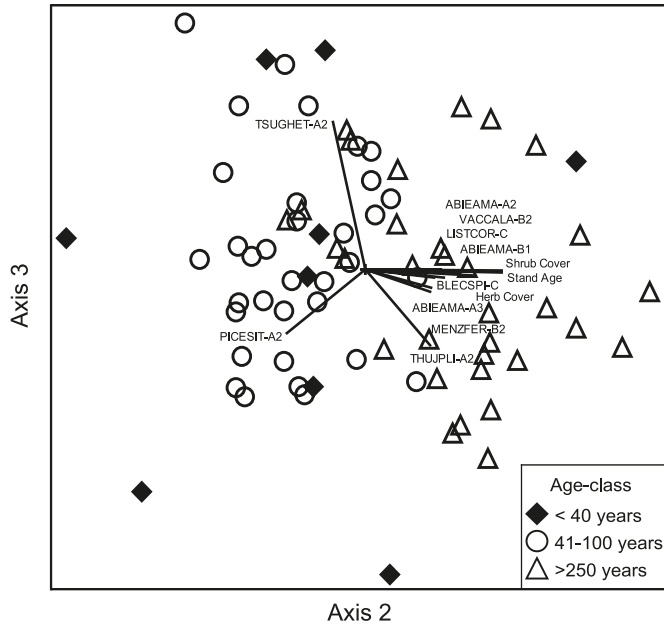
The results of the NMDS ordination of the medium forest plots, using species cover data, also recommended a three-dimensional solution with a cumulative R^2 of 0.858 (Table 2). The two axes accounting for the largest proportion of variation are plotted in Fig. 3. As with the ordination of rich forest plots, these axes were rotated to maximize the correlation of stand age with plot scores along the horizontal axis. A Pearson r value of 0.836 for age along the horizontal axis indicates a stronger correlation between age and axis

Fig. 3. NMDS ordination analysis of terrestrial vegetation plots representing three age-classes in the medium forest type. Vertical broken lines indicate areas of overlap in ordination scores between old-growth and younger forests.

score than exists for the rich forests. This is reflected in the reduced overlap of plots along axis 2 between the old-growth and younger forest plots (Fig. 3). The same ordinations for both forest types were also performed using species presence-absence data. While the overall distribution of plots along the two main axes was very similar to that resulting from the species cover ordinations, there was a decrease in the R^2 values for all axes (Table 2). This decrease in the amount of variation accounted for by the ordination axes was particularly dramatic for the rich forest type (cumulative R^2 reduced from 0.790 to 0.259). As with the rich forest types, the MRPP analysis confirmed the separation among the age-classes based on species composition and cover (low T and p values and an A value close to zero; Table 3). A larger negative T value, compared with the rich forests (-25.6 versus -17.8), substantiates the greater separation of younger vegetation communities from the old-growth communities for the medium forest type.

To further examine how stand attributes and the occurrence and relative abundance of specific plant species were correlated with the ordination axes, Pearson r values were calculated from overlays of the primary and secondary

Fig. 4. Joint plot overlay of Pearson r vectors for selected species–layer combinations and other stand attributes on NMDS plot ordination scores for the rich forest type. Vectors are labelled using the first four letters of the genus and the first three letters of the species followed by the vegetation layer (see Table 1) in which they occur. For clarity, species and stand attribute vector labels have been separated vertically.



matrix. We used joint plots (McCune and Grace 2002) to display the species and stand attributes having the highest correlation with each of the ordination axes (Figs. 4 and 5). The length and direction of the vector lines indicate the strength of the relationship (higher Pearson r value) with each of the ordination axes. For both rich and medium forests, most of the important species and stand attribute vectors align with the horizontal axis in the direction of older forests (i.e., to the right of the centroid), indicating strong relationships with stand age. Examples include total shrub and herb cover and cover of *Thuja plicata*, *Menziezia ferruginea* Sm., *Blechnum spicant* (L.) Roth, and *Listera cordata* (L.) R. Br. (Figs. 4 and 5). Cover of *Tsuga heterophylla* and *Picea sitchensis* in the main canopy show a stronger relationship with younger forests (i.e., the vectors align to the left of the centroid).

Summary vegetation tables for the rich and medium forest types (Tables 4 and 5) provide detailed comparisons of plant species constancy and cover values among age-classes. In these tables, common species–layer combinations (constancy values \geq III) showing higher constancy and cover in old-growth forests relative to younger forests (resulting in higher Pearson r values along the NMDS horizontal axis) are bolded. Of the 76 commonly occurring species–layer combinations in rich forests, there are 20 that have their highest constancy and cover values in older forests together with relatively high Pearson r values on the horizontal NMDS axis. It is these species that are largely responsible for the differentiation between old growth and second growth in the NMDS ordinations. For medium forest types, there are 24 out of 65 commonly occurring species–layer combinations that are more strongly associated with old growth.

Fig. 5. Joint plot overlay of Pearson r vectors for selected species–layer combinations and other stand attributes on NMDS plot ordination scores for the medium forest type. Vectors are labelled using the first four letters of the genus and the first three letters of the species followed by the vegetation layer (see Table 1) in which they occur. For clarity, species and stand attribute vector labels have been separated vertically.

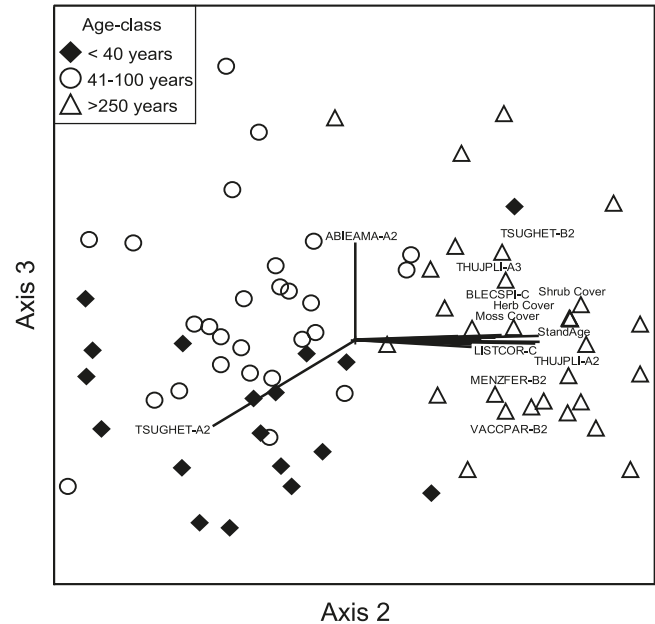


Table 6 presents two measures of plant species diversity by age-class for rich and medium forest types. Average species richness approximately doubles from very young forests (<40 years) to old forests (>250 years), from 20 to 38 species per plot and from 17 to 37 species per plot for rich and medium forest types, respectively. This increase in species richness with stand age is illustrated in Fig. 6a by a regression line ($R^2 = 0.60$) through the plot data for the rich forest type. A similar relationship between species richness and age was also found for the medium forest type (Fig. 6b) ($R^2 = 0.70$). Simpson's index of diversity, which combines richness and cover, shows a small but statistically significant increase from 0.81 to 0.91 from young to old stages of both forest types (Table 6).

A comparison of mean percent cover by vegetation layer between the maturing second-growth (41–100 years) and old-growth (>250 years) forests is presented for both rich and medium forests in Table 7. For both forest types, there is a statistically significant increase in shrub, herb, and moss cover as the forests age. As these forests mature, dramatic changes in cover occur in the low shrub layer, which increases from 7% to 46% and from 4% to 50% for the rich and medium forest types, respectively. The herb layer in the medium forest type also showed large increases in cover in older stands, with values increasing from 2% to 31% (Table 7).

Overall Sorensen similarities among age-classes within forest type based on the summary tables of plant species cover by layer values (Tables 4 and 5) are presented in Table 8. For the rich forests, similarity to old growth increases as stands age, with young forests (<40 years) showing 53%

Table 4. Summary terrestrial vegetation table with Pearson r values for NMDS ordination axes, constancy class (CC), and percent cover (PC) by species–layer combinations for three age-classes of the rich forest type.

Vegetation layer	Species	Axis 2 r	Axis 3 r	CC–PC <40 years ($n = 9$)	CC–PC 41–100 years ($n = 34$)	CC–PC >250 years ($n = 32$)
A1	<i>Picea sitchensis</i>	-0.433	0.035	III–5	III–8	II–2
A1	<i>Abies amabilis</i>	-0.089	0.256		II–3	I+
A1	<i>Thuja plicata</i>	0.37	-0.01		I+	II–2
A1	<i>Tsuga heterophylla</i>	-0.146	0.265	I+	II–2	II–3
A2	<i>Tsuga heterophylla</i>	-0.332	0.702	IV–23	V–29	V–27
A2	<i>Abies amabilis</i>	0.508	0.029	IV–8	III–7	IV–13
A2	<i>Thuja plicata</i>	0.472	-0.504	II–5	I–2	IV–13
A2	<i>Alnus rubra</i>	-0.242	0.349	II–2	III–5	I+
A2	<i>Picea sitchensis</i>	-0.519	-0.462	III–16	III–10	II–2
A3	<i>Tsuga heterophylla</i>	0.094	0.259	III–9	V–13	V–15
A3	<i>Abies amabilis</i>	0.471	-0.274	II–1	II–1	IV–7
A3	<i>Thuja plicata</i>	0.23	-0.397		II–2	III–4
A3	<i>Picea sitchensis</i>	-0.221	-0.065		II–2	I+
B1	<i>Tsuga heterophylla</i>	0.295	0.022	V–12	IV–3	IV–12
B1	<i>Thuja plicata</i>	0.199	-0.256	IV–1	II+	I–1
B1	<i>Abies amabilis</i>	0.562	-0.105	II+	I+	III–3
B1	<i>Alnus rubra</i>	0.081	0.243	II+		
B1	<i>Menziesia ferruginea</i>	0.181	-0.062	II+	I+	II–3
B1	<i>Oplopanax horridus</i>	-0.024	0.152	II+	I+	I+
B1	<i>Picea sitchensis</i>	-0.274	-0.192	II–1	I+	I+
B1	<i>Rubus spectabilis</i>	-0.024	0.213	II–2	I+	I+
B1	<i>Vaccinium parvifolium</i>	0.067	0.108	II–1	I+	II–2
B2	<i>Menziesia ferruginea</i>	0.474	-0.248	II–1	III+	V–6
B2	<i>Rubus spectabilis</i>	-0.034	0.077	V+	III–1	III+
B2	<i>Tsuga heterophylla</i>	0.442	-0.069	II–1	III–2	V–15
B2	<i>Vaccinium alaskaense</i>	0.555	-0.055	I+	II–1	V–8
B2	<i>Vaccinium parvifolium</i>	0.313	0.011	IV–2	III+	V–4
B2	<i>Abies amabilis</i>	0.408	-0.183		I+	IV–5
B2	<i>Oplopanax horridus</i>	0.362	0.156	III+	I+	IV–2
B2	<i>Vaccinium ovalifolium</i>	0.337	0.03	I+	I+	III–2
B2	<i>Gaultheria shallon</i>	0.168	0.002			II–2
B2	<i>Picea sitchensis</i>	0.247	-0.225		I+	II+
B2	<i>Sambucus racemosa</i>	-0.189	0.022	II+	II+	I+
B2	<i>Thuja plicata</i>	0.288	0.015	I+		II–2
C	<i>Blechnum spicant</i>	0.485	-0.165	V+	V–2	V–9
C	<i>Dryopteris expansa</i>	-0.186	0.158	V–1	V–4	IV–1
C	<i>Athyrium filix-femina</i>	0.069	0.017	II+	III–1	IV+
C	<i>Cornus canadensis</i>	0.439	-0.125	I+	I+	IV–5
C	<i>Gymnocarpium dryopteris</i>	0.323	-0.158	II+	II–1	IV–5
C	<i>Listera cordata</i>	0.52	-0.169			IV+
C	<i>Maianthemum dilatatum</i>	0.082	-0.14	I+	III+	III–3
C	<i>Streptopus amplexifolius</i>	0.369	-0.055		II+	IV+
C	<i>Streptopus lanceolatus</i>	0.385	-0.006		I+	III+
C	<i>Tiarella trifoliata</i>	0.265	-0.054	I+	III+	IV–2
C	<i>Listera caurina</i>	0.167	-0.039		I+	III+
C	<i>Phegopteris connectilis</i>	0.134	-0.052	II+	III–2	III–2
C	<i>Polystichum munitum</i>	0.05	0.211	II+	III–2	III–3
C	<i>Rubus pedatus</i>	0.461	-0.08		I+	III–5
C	<i>Clintonia uniflora</i>	0.206	-0.068			II–1
C	<i>Coptis asplenifolia</i>	0.448	-0.129		I+	II–2
C	<i>Huperzia haleakalae</i>	0.264	0.042		I+	II+
C	<i>Luzula parviflora</i>	-0.05	0.238		II+	I+
C	<i>Lysichiton americanus</i>	0.37	-0.134	I+	II+	II+
C	<i>Moneses uniflora</i>	0.15	-0.138		I+	II+
C	<i>Polygonum minimum</i>	0.006	-0.106	II+	II–2	
D	<i>Hookeria lucens</i>	0.082	-0.218		II+	III+

Table 4 (concluded).

Vegetation layer	Species	Axis 2 <i>r</i>	Axis 3 <i>r</i>	CC-PC <40 years (<i>n</i> = 9)	CC-PC 41–100 years (<i>n</i> = 34)	CC-PC >250 years (<i>n</i> = 32)
D	<i>Hylocomium splendens</i>	0.183	-0.207	V-9	IV-6	V-15
D	<i>Plagiothecium undulatum</i>	0.066	0.002	II+	II+	V-2
D	<i>Rhizomnium glabrescens</i>	0.405	0.148	IV-5	V-4	V-7
D	<i>Rhytidiadelphus loreus</i>	-0.1	-0.24	V-17	V-32	V-34
D	<i>Scapania bolanderi</i>	0.203	0.003		II+	III-2
D	<i>Eurhynchium oregonum</i>	-0.205	-0.151	III-2	IV-7	III-2
D	<i>Polytrichastrum alpinum</i>	-0.158	0.021	II+	IV-3	IV-1
D	<i>Sphagnum girgensohnii</i>	0.288	-0.067	II-1	II-1	IV-5
D	<i>Abies amabilis</i>	0.138	-0.036		II+	III+
D	<i>Pellia neesiana</i>	0.43	-0.127	II+	III+	III-3
D	<i>Plagiomnium insigne</i>	-0.162	-0.129	III-2	I+	
D	<i>Tsuga heterophylla</i>	0.174	0.175	II+	II+	III-1
D	<i>Atrichum selwynii</i>	0.091	-0.061			II+
D	<i>Conocephalum conicum</i>	-0.133	0.053		II+	I+
D	<i>Dicranum fuscescens</i>	0.318	-0.073	I+	I+	II+
D	<i>Lophozia</i> sp.	0.074	0.043	II-1	I+	I+
D	<i>Peltigera aphthosa</i>	0.264	-0.111			II+
D	<i>Plagiochila asplenioides</i>	-0.119	0.024		I+	II+
D	<i>Plagiochila porelloides</i>	-0.068	0.035	II+	I+	
D	<i>Thuja plicata</i>	0.185	-0.114	I+	I+	II+

Note: Bolded species-layer combinations are those showing higher constancy and cover in old-growth forests relative to younger forests. CC (percentage of total plots within each age-class containing species): I = 1–20, II = 21–40, III = 41 = 60, IV = 61–80, and V = 81–100. Percent cover values are plot means. Values <1% are indicated by a “+”. To reduce the size of the table, plant species authorities and species-layer combinations with a maximum constancy and cover value across all age-classes of I+ are not included. Species nomenclature follows Meidinger et al. (2004).

similarity and maturing forests (41–100 years) showing 58% similarity (Table 8). Medium forests show similar relationships, with 51% and 53% similarity for young and maturing forests, respectively (Table 8). A comparison of age-classes based on plant species presence-absence by layer values resulted in higher similarity between young and old forests. For the rich forest type, young and maturing forests showed 55% and 73% similarity to old-growth forests, respectively (Table 8). For the medium forests, these similarity values were 59% and 63% (Table 8).

Discussion

A chronosequence approach to the examination of vegetation community development in northern temperate rain forests is an effective way of assessing ecosystem recovery because of the extremely long time frames required to monitor complete successional development (Alaback 1982; Clark et al. 2003). Although there are limitations to this approach owing to the variability in disturbance history and site conditions (Pickett 1989; Aravena et al. 2002), we have addressed most of these limitations by focusing our study on terrestrial vegetation community recovery following timber harvesting, restricting our sampling to one biogeoclimatic variant (CWHvh2) with a relatively uniform macroclimate, and stratifying our samples by site type (similar moisture and nutrient regime and characteristic vegetation community). Current commercial rotation lengths for medium to rich forests on the central and north coast of British Columbia are projected to range from 80 to 120 years (British Columbia Ministry of Forests 1999), and thus, a significant management concern is the degree to which forests of this age have recovered toward old-growth conditions and con-

tribute to ecosystem integrity and resilience (North Coast LRMP Planning Table 2005). Our study is able to address this issue because we have an extensive old-growth (>250 years) and postlogging second-growth (<100 years) data set.

The NMDS ordinations and MRPP analyses that we performed, based on the percent cover data of species-layer combinations, are helpful in illustrating the successional relationships among forest age-classes. While there is a clear separation of old-growth and young second-growth plots, emphasized by the good correlation between “stand age” (time since stand establishment) and axis score and supporting MRPP statistics, there are also areas of overlap (Figs. 2 and 3). These areas of overlap suggest that while old and young forests have distinct vegetation composition, cover, and structure, they share many of the same species. The rich forest plots show greater similarity between the young and old age-classes than do the medium forest plots, suggesting that moisture and nutrient regime (and thus inherent productivity) are impacting rates of recovery of terrestrial vegetation communities and their resilience to disturbance. This highlights the importance of recognizing and accounting for differences in forest site factors when assessing ecosystem resilience and recovery.

The bulk of the species listed in Tables 4 and 5 show relatively low Pearson *r* values on all ordination axes, indicating no clear affinity with either young or old forests. There are, however, several species-layer combinations that do show greater constancy and cover in the old forests (bolded in Tables 4 and 5). These species have higher Pearson *r* values on the horizontal ordination axes and are responsible for the clear separation of age-classes on the ordinations (Figs. 4 and 5). A significant species in this regard is west-

Table 5. Summary terrestrial vegetation table with Pearson r values for NMDS ordination axes, constancy class (CC), and percent cover (PC) by species–layer combinations for three age-classes of the medium forest type.

Vegetation layer	Species	Axis 2 r	Axis 3 r	CC–PC <40 years ($n = 18$)	CC–PC 41–100 years ($n = 27$)	CC–PC >250 years ($n = 32$)
A1	<i>Abies amabilis</i>	-0.146	0.46		III–3	I+
A1	<i>Picea sitchensis</i>	-0.169	0.028	III–3	III–5	II–2
A1	<i>Tsuga heterophylla</i>	-0.255	-0.244	III–4	II–3	I+
A1	<i>Thuja plicata</i>	0.296	0.107			II–2
A2	<i>Abies amabilis</i>	0.001	0.593	II–4	V–12	IV–10
A2	<i>Thuja plicata</i>	0.791	-0.118	I–4	I–1	V–27
A2	<i>Tsuga heterophylla</i>	-0.703	-0.558	V–42	V–32	V–15
A2	<i>Picea sitchensis</i>	-0.212	0.348	IV–7	III–8	II–5
A2	<i>Alnus rubra</i>	-0.22	-0.098	II–2	I+	I+
A3	<i>Thuja plicata</i>	0.595	0.109	I+	II–2	V–6
A3	<i>Tsuga heterophylla</i>	-0.106	0.346	IV–9	V–16	V–13
A3	<i>Abies amabilis</i>	0.231	0.376	I–1	II–3	III–6
A3	<i>Picea sitchensis</i>	0.001	0.157	II+	I+	I+
B1	<i>Tsuga heterophylla</i>	0.401	-0.007	IV–9	IV–4	V–14
B1	<i>Abies amabilis</i>	0.431	0.238	I+	I+	IV–4
B1	<i>Menziesia ferruginea</i>	0.232	-0.214	III–2	I+	III–3
B1	<i>Thuja plicata</i>	0.383	0.076	III–2	II+	III–2
B1	<i>Rubus spectabilis</i>	-0.077	-0.144	II–2	I+	I+
B1	<i>Vaccinium alaskaense</i>	0.086	-0.203	I–1	I+	II+
B1	<i>Vaccinium parvifolium</i>	0.212	-0.252	II–1	I+	II–1
B2	<i>Menziesia ferruginea</i>	0.635	-0.128	II–1	II+	V–8
B2	<i>Tsuga heterophylla</i>	0.713	0.132	II–1	II–2	V–12
B2	<i>Vaccinium alaskaense</i>	0.395	-0.044	II+	II–1	IV–4
B2	<i>Vaccinium parvifolium</i>	0.635	-0.156	IV–1	III+	V–7
B2	<i>Abies amabilis</i>	0.45	0.252	I+	I+	IV–4
B2	<i>Gaultheria shallon</i>	0.474	-0.182		I+	IV–9
B2	<i>Thuja plicata</i>	0.414	-0.048	I+	I+	IV–2
B2	<i>Rubus spectabilis</i>	0.153	0.177	III+	I+	II–1
B2	<i>Oplopanax horridus</i>	0.173	0.262			II+
B2	<i>Picea sitchensis</i>	0.232	-0.176			II+
B2	<i>Vaccinium ovalifolium</i>	0.336	-0.054	I+		II+
C	<i>Blechnum spicant</i>	0.626	0.064	V–2	IV+	V–14
C	<i>Dryopteris expansa</i>	0.026	0.17	IV+	III+	III+
C	<i>Listera cordata</i>	0.66	-0.021		I+	IV+
C	<i>Streptopus amplexifolius</i>	0.428	-0.048		I+	IV+
C	<i>Tiarella trifoliata</i>	0.358	0.071	I+	I+	IV–2
C	<i>Cornus canadensis</i>	0.527	0.031	I+		III–3
C	<i>Listera caurina</i>	0.358	-0.115			III+
C	<i>Lysichiton americanus</i>	0.338	0.003		I+	III+
C	<i>Maianthemum dilatatum</i>	0.275	-0.023	I+	II+	III–2
C	<i>Rubus pedatus</i>	0.478	0.177			III–2
C	<i>Coptis aspleniifolia</i>	0.256	0.012	I+		II+
C	<i>Gymnocarpium dryopteris</i>	0.122	-0.017	I+	I+	II–1
C	<i>Moneses uniflora</i>	0.203	0.05			II+
C	<i>Phegopteris connectilis</i>	0.115	0.186	I+	II+	II+
C	<i>Polystichum munitum</i>	0.237	0.111	I+	II+	II–1
D	<i>Hylocomium splendens</i>	0.473	-0.225	V–11	V–8	V–19
D	<i>Plagiothecium undulatum</i>	-0.142	-0.017	II–1	II–2	V–2
D	<i>Rhizomnium glabrescens</i>	0.133	-0.022	IV–5	IV–2	V–5
D	<i>Rhytidadelphus loreus</i>	0.402	-0.181	V–24	V–35	V–40
D	<i>Sphagnum girgensohnii</i>	0.431	-0.07	II–1	III–1	V–5
D	<i>Tsuga heterophylla</i>	0.218	-0.039	I+	III+	IV+
D	<i>Abies amabilis</i>	0.24	0.039		I+	III+
D	<i>Eurhynchium oreganum</i>	-0.138	0.476	I–2	III–6	III–2
D	<i>Hookeria lucens</i>	0.33	-0.016		II+	III+
D	<i>Polytrichastrum alpinum</i>	-0.182	0.05	II+	III+	III+

Table 5 (concluded).

Vegetation layer	Species	Axis 2 <i>r</i>	Axis 3 <i>r</i>	CC-PC <40 years (<i>n</i> = 18)	CC-PC 41–100 years (<i>n</i> = 27)	CC-PC >250 years (<i>n</i> = 32)
D	<i>Scapania bolanderi</i>	0.311	0.133	I+	II+	III–2
D	<i>Thuja plicata</i>	0.319	–0.059			III+
D	<i>Dicranum fuscescens</i>	0.367	0.12	I+	I+	II–1
D	<i>Diplophyllum albicans</i>	0.313	0.114			II+
D	<i>Pellia neesiana</i>	0.268	0.199	I+	I+	II–2
D	<i>Picea sitchensis</i>	0.245	0.066		I+	II+
D	<i>Plagiochila asplenioides</i>	0.392	0.009			II+
D	<i>Plagiochila porelloides</i>	–0.209	–0.02	II+	II+	I+
D	<i>Plagiommium insigne</i>	–0.098	0.056	I–2	I+	

Note: Bolded species–layer combinations are those showing higher constancy and cover in old-growth forests relative to younger forests. CC (percentage of total plots within each age-class containing species): I = 1–20, II = 21–40, III = 41 = 60, IV = 61–80, and V = 81–100. PC values are plot means. Values <1% are indicated by a “+”. To reduce the size of the table, plant species authorities and species–layer combinations with a maximum constancy and cover value across all age-classes of I+ are not included. Species nomenclature follows Meidinger et al. (2004).

Table 6. Species richness and Simpson’s index of diversity values by age-class for rich and medium forest types.

Forest type	Age-class (years)	No. of plots	Species richness ± SD ^a	Simpson’s index of diversity ± SD ^b
Rich	≤40	9	20.0±5.7a	0.81±0.080a
Rich	41–100	34	24.9±5.1b	0.86±0.05b
Rich	>250	32	38.2±7.8c	0.91±0.04c
Medium	≤40	18	17.1±2.7a	0.81±0.08a
Medium	41–100	27	18.9±5.2a	0.83±0.04a
Medium	>250	29	37.0±7.7b	0.91±0.03b

Note: Within a forest type, values followed by a common letter are not significantly different ($\alpha = 0.05$) as determined by Duncan’s multiple-range tests.

^aAverage number of species in a sample plot.

^bLikelihood that two randomly chosen individuals in a sample plot will be different.

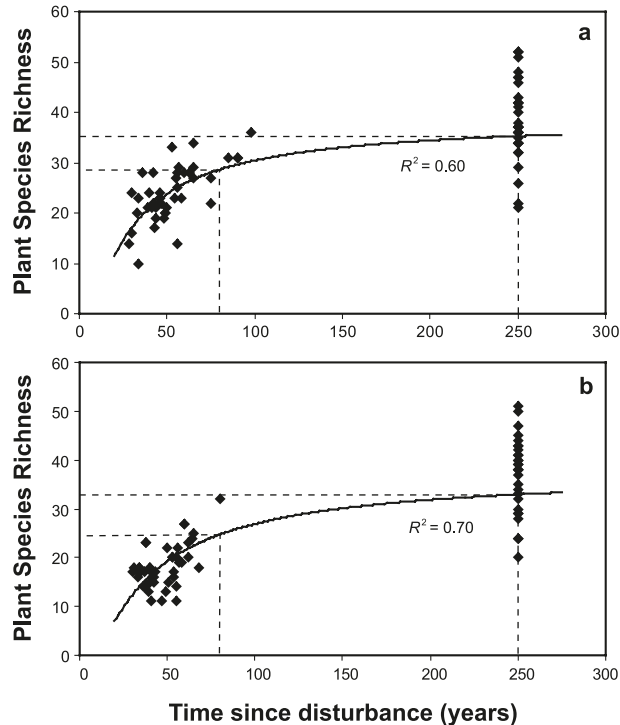
ern redcedar, which codominates old-growth forests with western hemlock but occurs only sporadically (constancy class of I or II) in naturally regenerated second-growth forests (Tables 4 and 5). The lack of western redcedar in these second-growth forests has significant management implications because of the high ecological, cultural, and economic importance of this tree species, unique to western North America (Burns and Honkala 1990; Turner 2004). Our results indicate that without active management for the establishment (planting) and maintenance of western redcedar following harvesting, this important tree species will form a very minor component of our coastal second-growth forests.

Our study examined terrestrial plant species diversity using two indices: species richness, which represents the total number of species per plot, and Simpson’s index of diversity, which combines richness with cover. This index represents the likelihood that two randomly chosen individuals in a plot will be different, and thus, species of very low cover contribute less to diversity. For both rich and medium forest types, average species richness in old-growth forests was approximately double that in second-growth forests between 41 and 100 years old, while Simpson’s index of diversity increased by only 12%. This indicates that while there are significantly more species present in the oldest forests, many of these species have very low cover values. All age-classes within both forest types show high Simpson’s index of diversity values, indicating that none are dominated by just a few species. Many of the same species dominate the

vegetation communities across all age-classes, although there are differences in species composition between the rich and medium forests (see Tables 4 and 5). As was found for the forests of Southeast Alaska, Washington, and Oregon, successional pathways in these coastal British Columbia forests appear to be driven largely by the predisturbance (old-growth) species composition (Alaback 1982; Halpern and Spies 1995). Virtually all of the species found in the young forests are present in old forests, and over time, additional species reestablish and contribute to the higher species richness typical of old growth. In British Columbia’s central and north coast rain forests, this trend of increasing species richness over time is clearly evident (Fig. 6) and is similar to what Halpern and Spies (1995) found in the Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) – western hemlock forests of Washington and Oregon. Our data indicate a high degree of variability in richness through all age-classes, but the regression model predicts that 80-year-old forests will have approximately 75% of the species richness found in old-growth forests that are at least 250 years old (Fig. 6). It is important to recognize that achieving any significant increase in terrestrial species richness beyond that reached in the first century will certainly be a very slow process.

In their study of succession in subboreal forests, Clark et al. (2003) reported a decrease in species richness in the oldest forests but acknowledged that this may have resulted from them excluding the diversity of bryophytes and lichens.

Fig. 6. Actual (diamonds) and predicted (solid line) species richness versus time since disturbance for (a) rich forest and (b) medium forest types. Broken lines indicate predicted species richness at 80 and 250 years.



In our study, these terrestrial nonvascular cryptogams are typically of low cover and constancy but obviously contribute to total species richness in old forests. Similar findings for subboreal forests were reported by Botting and Fredeen (2006). A chronosequence study of temperate rain forests on southern Vancouver Island (Trofymow et al. 1997; Ryan et al. 1998) also reported a decline in total species richness from young to old forests. In marked contrast with the remote and undeveloped forest landscape on the central and north coast, the forests harvested on southern Vancouver Island experience significant invasion of pioneer species present in the surrounding landscape but not found in old-growth forests. These are subsequently eliminated as tree canopies close, resulting in the reported decrease in species richness over time. The extent of human development in this area has contributed to the greater role of invasive species in successional development following forest disturbance, a factor that has yet to play an important role on the north and central coast.

While many of the same species occur across all age-classes, there are significant increases in the total cover of understory layers as forests mature (Table 7). The closed forest canopies of dense second-growth stands limit light penetration to the forest floor (Spies 1991; Greenberg et al. 1997), which results in reduced understory development. In contrast, the old-growth stands of coastal British Columbia have forest canopies that are more structurally heterogeneous with many gaps (Lertzman et al. 1996). This structure allows more light to penetrate (Canham 1989; Canham et al. 1990), which promotes more vigorous growth of the shrub and herb layers (Spies and Franklin 1989; Van Pelt

and Franklin 2000). By controlling density and manipulating overstories to open up second-growth forest canopies, there is an opportunity to hasten the recovery of understories toward old-growth conditions in younger coastal temperate rain forests (Coates and Burton 1997; DeBell et al. 1997). Many of the understory species that we found occurring across all age-classes are important wildlife forage species (Parker et al. 1999). The lower cover of these species in second-growth forests likely has implications for the development of wildlife habitat and other ecological functions such as nutrient cycling.

In evaluating the overall similarity between second-growth and old-growth forests, based on a comparison of the summary vegetation data for each age-class, it is important to note the variation that exists among the individual plots within each age-class group (Table 3). Average within-group plot similarity ranges from 31% to 51%, and thus, the overall similarities between the young and old forest communities of 53% to 58% are sufficiently high to indicate that these communities share many of the same vegetation characteristics. Using the presence-absence values to assess similarity, forests between 41 and 100 years old show a considerably higher similarity to old-growth forests compared with similarity based on percent cover data (Table 8). The NMDS ordinations based on species presence-absence showed lower R^2 values, also indicating a higher similarity between young and old forests compared with the ordinations based on percent cover. This reinforces the fact that an important distinction between coastal second-growth and old-growth vegetation communities is the abundance of plant biomass rather than simply the species that they contain (Alaback 1982; Halpern and Spies 1995).

From a vegetation composition standpoint, the recovery of these forest ecosystems following harvesting suggests a considerable degree of ecosystem resilience, largely because plant succession in these coastal forests tends to be driven by predisturbance species composition. The similarity in species composition between old and young forests clearly indicates that, despite the logging-imposed disturbance to these forests, the ecosystems have not shifted to an alternate ecological state or stability domain. Full development of overstories and understories toward a relatively stable, multilayered forest ecosystem, however, is a slow process with important species such as western redcedar needing long time periods to regain their former prominence. As previously noted, there are opportunities to impact rates of recovery (both positively and negatively) through harvesting, regeneration, and stand-tending activities.

While aspects of these results are encouraging from a forest management perspective, it is important to recognize that because of the exceedingly long life span of these forests, combined with the difficulty in determining the actual time since a stand initiating disturbance in old forests, we are uncertain about the time required to achieve full recovery. This final stage of recovery will, however, require considerably more time than current forest harvest rotation lengths allow. This emphasizes the importance of retaining areas of old-growth forests as well as accounting for the significant levels of recovery achievable in second-growth stands when developing a management strategy aimed at maintaining ecosystem resilience and integrity.

Table 7. Comparison of mean percent cover of terrestrial vegetation by layer and forest type between young (41–100 years) and old (>250 years) forests.

Vegetation layer	Mean cover \pm SE (%)			
	Rich forests		Medium forests	
	41–100 years	>250 years	41–100 years	>250 years
A1	12.9 \pm 2.6a	8.3 \pm 1.8a	11.1 \pm 1.8a	5.7 \pm 1.8b
A2	52.9 \pm 2.8a	55.7 \pm 3.6a	54.4 \pm 3.7a	57.5 \pm 2.6a
A3	17.6 \pm 1.8a	27.4 \pm 2.6b	22.4 \pm 2.8a	25.6 \pm 2.7a
B1	5.2 \pm 0.9a	21.1 \pm 4.0b	5.2 \pm 1.0a	26.0 \pm 3.7b
B2	6.6 \pm 1.5a	45.9 \pm 3.8b	3.7 \pm 1.7a	50.0 \pm 3.8b
C	17.0 \pm 2.7a	45.1 \pm 6.5b	2.3 \pm 0.9a	30.5 \pm 3.7b
D	58.6 \pm 4.8a	75.4 \pm 5.1b	56.9 \pm 4.4a	82.8 \pm 3.9b

Note: See Table 1 for a complete description of vegetation layers. Within a forest type and vegetation layer, values followed by a common letter are not significantly different ($\alpha = 0.05$) as determined by Duncan's multiple-range tests.

Table 8. Sorensen's percent similarity matrix based on vegetation percent cover data and presence–absence data from summary terrestrial vegetation tables (Tables 3 and 4) for the rich forest type and medium forest type.

	<40 years	41–100 years	>250 years
Rich forest type			
% cover data			
<40 years	100		
41–100 years	68	100	
>250 years	53	58	100
Presence–absence data			
<40 years	100		
41–100 years	68	100	
>250 years	55	73	100
Medium forest type			
% cover data			
<40 years	100		
41–100 years	72	100	
>250 years	51	53	100
Presence–absence data			
<40 years	100		
41–100 years	74	100	
>250 years	59	63	100

We recognize that extrapolating our findings on rates of vegetation recovery from historical logging practices during the first half of the 1900s to the larger industrial clearcuts of the 1970s and 1980s has limitations. Our results, however, are quite applicable to the current forest harvesting approaches being promoted as part of the ecosystem-based management initiative on coastal British Columbia (Coast Information Team 2004; North Coast LRMP Planning Table 2005). This initiative promotes variable levels of partial cutting together with relatively small openings that will result in harvested stands similar to the ones that we have studied. Over the next several decades, climate change will undoubtedly have an impact on the forest environment and has the potential to alter future rates of ecosystem recovery. Model predictions of the rates and degree of climate change are highly variable and our understanding of how these changes will impact on ecosystem recovery is limited. Our study provides some baseline information that can be used to monitor

and compare the impacts of climate change into the future. We also recognize that while vegetation communities are a critical component of forests, providing and contributing to a broad range of ecosystem services (Kimmins 1987), vegetation recovery must be considered in combination with many other elements of the forest environment. In addition to vegetation development, our ecosystem recovery project is currently focusing on other ecosystem attributes including tree growth and productivity, stand structure, coarse woody debris, epiphytic communities, and soil faunal communities. Some of these attributes, such as stand structure and epiphytic communities, are expected to require considerably longer time periods for recovery compared with terrestrial vegetation communities.

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