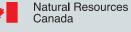
Stand structure and species composition in chronosequences of forests on southern Vancouver Island

Bruce A. Blackwell, Heather A. Hedberg, and J.A. (Tony) Trofymow

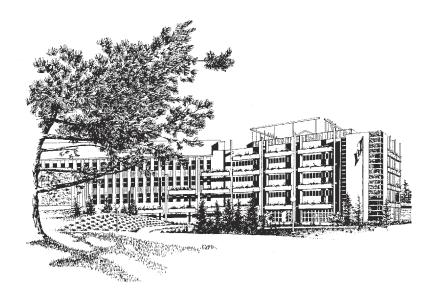
Pacific Forestry Centre • Victoria, British Columbia Information Report • BC-X-395



Ressources naturelles Canada

Canadian Forest Service Canada

Service canadien des forêts



The Pacific Forestry Centre, Victoria, British Columbia

The Pacific Forestry Centre of the Canadian Forest Service undertakes research as part of a national network system responding to the needs of various forest resource managers. The results of this research are distributed in the form of scientific and technical reports and other publications.

Additional information on Natural Resources Canada, the Canadian Forest Service, and Pacific Forestry Centre research and publications is also available on the World Wide Web at: **www.pfc.cfs.nrcan.gc.ca**. To download or order additional copies of this publication, see our online bookstore at: **bookstore.cfs.nrcan.gc.ca**.

Stand structure and species composition in chronosequences of forests on southern Vancouver Island

Bruce A. Blackwell and Heather A. Hedberg B.A. Blackwell and Associates Ltd. North Vancouver, British Columbia

and

J.A. (Tony) Trofymow Canadian Forest Service Victoria, British Columbia

Natural Resources Canada Canadian Forest Service Pacific Forestry Centre Information Report BC-X-395

2002

Canadian Forest Service Pacific Forestry Centre 506 West Burnside Road Victoria, British Columbia V8Z 1M5 Phone (250) 363-0600 http://www.pfc.cfs.nrcan.gc.ca

© Her Majesty the Queen in Right of Canada, 2002

ISSN 0830-0453 ISBN 0-662-32832-9

Printed in Canada

Microfiches of this publication may be purchased from:

MicroMedia Inc. 240 Catherine Street, Suite 305 Ottawa, ON K2P 2G8

National Library of Canada cataloguing in publication data

Blackwell, Bruce Alan, 1959-

Stand structure and species composition in chronosequences of forests on southern Vancouver Island

(Information report ; BC-X-395) Includes bibliographical references. ISBN 0-662-32832-9 Cat. no. Fo46-17/395E

Old-growth forests – British Columbia – Vancouver Island.
 Forest site quality – British Columbia – Vancouver Island.
 Hedberg, Heather A.
 Trofymow, J.A. (John Antonio)
 Pacific Forestry Centre.

IV. Series: Information report (Pacific Forestry Centre); BC-X-395.

SD387.O43B52 2002 333.75 097112 C2002-980234-2

Contents

Abstract and Résumé vi
Acknowledgments vii
Summary viii
Introduction 1
Methods
Site descriptions and plot layout
Field sampling 4
Data summary
Statistical analysis
Results and discussion
Stand density – total number of live trees per hectare
Stem diameters and stand density distributions7
Stem heights and stand density distributions
Crown depths and stand density distributions
Stem biomass and its distribution by size class 14
Snag density and its distribution by size class
Snag mass and its distribution by size class
Stem basal area and its distribution by diameter class 20
Species composition by stand density and basal area
Conclusions
Literature cited
Appendix I – Function parameters and r ² for stand density by diameter, height, or crown depth and for basal area by diameter (dbh)

or crown depth and for basal area by diameter (dbh)	37
Appendix II – Stems per hectare of species within diameter (dbh) class, for each plot	38
Appendix III – Stems per hectare of species within height class, for each plot.	42
Appendix IV – Stems per hectare of species within crown depth class, for each plot	46
Appendix V – Stem biomass per hectare of species within size class, for each plot	49
Appendix VI – Snags per hectare of species within size class, for each plot	52
Appendix VII – Snag mass per hectare of species within size class, for each plot	56
Appendix VIII – Stem basal area per hectare of species within size class, for each plot	59

Tables

1.	Names, numbers, ages and tree characteristics of the Canadian Forest Service Coastal Forest Chronosequences plots studied	28
2.	Regression equations used to estimate stem biomass	29
3.	Summary of F statistics and probability values for the effect of subzone and age class on number of live stems per hectare, stem biomass, snags per hectare, snag mass, stem basal area and percent species composition by basal area and stand density	30
4.	Numbers of live stems per hectare, stem biomass, snags per hectare, snag mass, and stem basal area in each plot	31
5.	Mean stems per hectare of tree species within and across age class for the CWHvm and CWHxm subzones.	32
6.	Mean stem biomass per hectare of tree species within and across age class for the CWHvm and CWHxm subzones.	32
7.	Mean number of snags per hectare of tree species within and across age class for the CWHvm and CWHxm subzones.	33
8.	Mean snag mass per hectare of tree species within and across age class for the CWHvm and CWHxm subzones	33
9.	Mean stem basal area per hectare of tree species within and across age class for the CWHvm and CWHxm subzones.	. 34
10.	Mean stand-density-based percent tree species composition within and across age class for the CWHvm and CWHxm subzones.	34
11.	Mean basal-area-based percent tree species composition within and across age class for the CWHvm and CWHxm subzones.	35
12.	Comparison of structural attributes from Washington/Oregon, California, and British Columbia with old-growth attributes of chronosequence plots in the CWHxm and CWHvm.	36

Figures

1	Locations of the ten Coastal Forest Chronosequences on southern Vancouver Island
2	Example of triangular survey plot layout showing mensurational subplot and woody debris transects
3	Mean number of stems per hectare of species within diameter (DBH) class by age class within biogeoclimatic subzone
4	Weibull function parameters for stand density and diameter (DBH) by age class within subzone. 9
5	Mean number of stems per hectare of species within height class by age class and biogeoclimatic subzone
6	Weibull function parameters for stand density and height by age class within subzone 11
7	Mean number of stems per hectare of species within crown depth class by age class and biogeoclimatic subzone
8	Weibull function parameters for stand density and crown depth by age class within subzone. 14
9	Mean stem biomass per hectare of species within size class by age class and biogeoclimatic subzone. 15
10	Mean number of snags per hectare of species within size class by age class and biogeoclimatic subzone. 17
11	Mean snag mass per hectare of species within size class by age class and biogeoclimatic subzone. 19
12	Weibull function parameters for basal area and diameter (DBH) by age class within subzone. 20
13	Mean stem basal area per of species within diameter (DBH) class by age class within biogeoclimatic subzone. 21

Abstract

Overstory stand structure was measured in 32 plots in a Canadian Forest Service study on the effects of converting coastal old-growth forest into managed forest. Stand density, tree height, tree diameter at breast height (DBH), crown depth, stem biomass and basal area (BA) of living stems, and density and mass of snags were measured in a chronosequence of three post-harvest stands (R - regeneration (3-8 years); I - immature (25-45 years); M - mature (65-86) years), and O - an old-growth control (> 200 years) at each of eight study sites on Vancouver Island. Four sites were within the very dry CWHxm and four in the very wet CWHvm biogeoclimatic subzones. Results of this study demonstrate that variability and complexity of overstory structure and composition in coastal forests increases with stand age, and that stands on the west side of the island (CWHvm) were more variable and structurally diverse than those on the east side (CWHxm).

Overstory structure attributes collected for Vancouver Island forests in the CWHxm and CWHvm compare favorably to those of others in the Pacific Northwest. However, old-growth plots do not match US Pacific Northwest definitions of old-growth Douglas-fir as well, likely due to regional differences in climate or because chronosequences were on medium to poor sites. Overstory attribute summaries from this study provide some direction for defining old-growth characteristics. However, the variability of many of these attributes is such that more data are required to rationalize a rigorous definition that will withstand scientific and operational scrutiny.

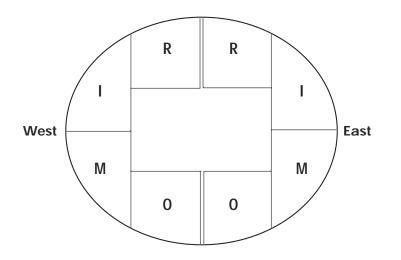
Résumé

Aux fins d une étude du Service canadien des forêts sur les effets de la conversion d une forêt ancienne côtière en une forêt aménagée, des données sur la structure de l **é**age dominant ont été obtenues dans trente-deux placettes. La densité de peuplement, la hauteur des arbres, leur diamètre à hauteur de poitrine (dhp), la longueur de houppier, la biomasse et la surface terrière des tiges vivantes ainsi que la densité et la masse des chicots ont été déterminés dans des chronoséquences de trois peuplements après-coupe (R - régénération [3-8 ans]; I - jeune [25-45 ans]; M - mûr [65-86 ans]) et O - ancien [> 200 ans] à chacun des huit sites d **é**ude dans l **l**e de Vancouver. Quatre sites se trouvent dans la sous-zone biogéoclimatique CWHxm, très sèche, et les quatre autres dans la sous-zone CWHvm, très humide. Les résultats indiquent que la variabilité et la complexité de la structure et de la composition de l **é**age dominant augmentent en fonction de l **ĝ**e des peuplements dans les forêts côtières et que les peuplements du côté ouest de l **l**e (CWHvm) sont plus variés et plus structurellement diversifiés que ceux du côté est (CWHxm).

Les attributs structurels de l *é*age dominant des forêts étudiées se comparent avantageusement à ceux des forêts d autres zones situées dans le Pacific Northwest. Les placettes de forêt ancienne, toutefois, ne répondent pas parfaitement à la définition de la forêt ancienne de douglas utilisée dans cette région des États-Unis, probablement en raison du climat différent ou de la qualité (moyenne à faible) des sites dans les chronoséquences. Globalement, les attributs de l *é*age dominant révélés par cette étude fournissent des renseignements utiles pour la définition des caractéristiques des forêts anciennes. Néanmoins, la variabilité d un grand nombre de ces attributs est telle qu il faudra plus de données pour établir une définition rigoureuse, soutenable scientifiquement et opérationnellement.

Acknowledgments

We gratefully acknowledge the following support. This work was funded (in part) by the Federal Panel on Energy Research and Development (PERD) through the ENFOR (Energy from the FORest) program of Canadian Forest Service projects P-404 and P-453. Additional support for the project was provided by Forest Renewal British Columbia, Award No. HQ96247. Funding for mensurational measurements at Greater Victoria South, Greater Victoria North and Koksilah was provided by the Canadian Forest Service Advanced Forest Technologies program. Richard Leach, Sue Seguire and Fiona Steele assisted with calculations and data summary. Gord Frazer assisted with preparation of Tables and Figures. R. Whitehead and F. He provided helpful review comments on an earlier version of the manuscript.



Cover

Representative post-harvest chronosequence (R - Regeneration, I - Imature, M - Mature) and O - Old-growth control stands from east (Koksilah site) and west (Klanawa site) Vancouver Island.

Center map - see figure 1 on page 3.

Summary

Overstory stand structure was measured in 32 plots in a Canadian Forest Service study on the effects of converting coastal Old-growth forest into managed forest. Stand density, tree height, tree diameter at breast height (DBH), crown depth, stem biomass and basal area of living stems, and density and mass of snags were measured in a chronosequence of three post-harvest stands at each of eight study sites — regeneration (3-8 years), immature (25-45 years), mature (65-86) years; and, an old-growth control (>200 years).

Four sites were on the southeastern side of Vancouver Island within the Very Dry CWHxm biogeoclimatic subzone. The remaining four sites were situated on the southwestern side of Vancouver Island in the very wet CWHvm biogeoclimatic subzone. Results of this study suggest that variability and complexity of overstory structure and composition in coastal forests increases with stand age, and that stands on the west side of the island (CWHvm) were more variable and structurally diverse than those on the east side (CWHxm).

With few exceptions, when trees in the stand were measured by diameter, crown depth, and height class, the largest number of stems were always in the smallest size class. Stand density differed significantly (p < 0.05) among age classes and followed the order *immature* > *mature* > *regeneration* > *old growth*. On average the total number of stems per hectare in the CWHxm significantly (p < 0.05) exceeded that of the CWHvm.

In plots of older trees (mature and old growth), the mean percentage of stems of DBH less than 20 cm was 64% in the CWHvm and 80% in the CWHxm. The mean number of stems per hectare with DBH over 80 cm was greater in the CWHvm (68 stems) than the CWHxm (50 stems). Only mature and old growth plots had stems over 80 cm in DBH. Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) dominated in regeneration, immature, and mature plots in the CWHxm in terms of both stems per hectare and stem biomass. Western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) dominated all age classes in the CWHvm. Stem biomass increased with stand age and was greater in the CWHvm than the CWHxm for all age classes. In the CWHvm, western redcedar (*Thuja plicata* Donn ex D. Don) stem biomass was dramatically greater in old-growth plots (325 Mg/ha) than in mature plots (0.3 Mg/ha).

There were more snags in the CWHvm than the CWHxm. In the CWHvm the number of snags per hectare decreased with stand age. Most snags in the CWHvm were western hemlock (78 %) or western redcedar (13%). In the CWHxm most snags were Douglas-fir and were most abundant in mature stands and least abundant in old growth. Snags in immature and mature stands were a function of early mortality that led to natural thinning. Less than 3% of snags exceeded 60 cm DBH in either subzone. Snag mass in the CWHvm subzone (20 Mg/ha) was double that measured in the CWHxm (9 Mg/ha).

Total live basal area increased with stand age. In each subzone, basal area of western hemlock followed the order *regeneration* < *immature* < *mature* < *old growth*. The average basal area for the CWHvm subzone (63 m²/ha) was greater than that in the CWHxm (50 m²/ha). As expected, the greatest basal area was recorded for old-growth plots for both the CWHvm and CWHxm subzones.

Overstory structure attributes collected for Vancouver Island forests in the CWHxm and CWHvm compare favourably to those of others in the Pacific Northwest. However, comparisons with sites in geographical locations outside British Columbia are not ideal. The lower fit of Coastal Forest Chronosequence old-growth plots to US Pacific Northwest definitions of old-growth Douglas-fir may be due to regional differences in climate or because most coastal forest chronosequences were on medium to poor sites.

Robust definitions of old growth in British Columbia are hindered by a lack of research describing structural, compositional, and functional characteristics of old growth (Hamilton, E.; Nicholson, A. 1991. Defining British Columbia s old-growth forests: discussion paper. B.C. Ministry of Forests, Research Branch, Victoria, BC. Draft paper). This study provides some data on which to base definitions and our

results support the suggestion by Wells *et al.* (1998) that definitions of old growth need to be based on fundamental ecological and physical characteristics to be useful for forest management and conservation. Overstory attribute summaries from this study provide some direction for defining old growth characteristics. However, the variability of many of these attributes is such that more data is required to rationalize a rigorous definition that will withstand scientific and operational scrutiny.

Introduction

Coastal forests of northwestern North America exhibit high structural complexity, including wide ranges in tree heights and diameters, canopy gap size and depth, and dead wood abundance (Franklin *et al.* 1981; Spies and Franklin 1988). These characteristics largely result from the longevity and size of the dominant conifers combined with slow decomposition rates and a variety of natural disturbances (Arsenault and Bradfield 1995). The numbers and sizes of live and dead trees and life history traits of tree species in old-growth forests can be used to infer regeneration patterns and to provide useful information to help manage second-growth forests (Goebel and Hix 1996).

Forest structure changes with succession. After a major disturbance, one that destroys the previous stand, forests go through a characteristic series of developmental stages leading, in the absence of further disturbances, to an old-growth stage (e.g., Oliver 1982; Oliver and Larson 1990; Wells *et al.* 1998). In early phases of succession the predominant and most obvious changes in stand structure are the increase in individual tree size, and, with canopy closure by the overstory dominants, the suppression of the understory plants and death of smaller trees. In the understory reinitiation phase, mature stands are transformed into old growth through the death of individual overstory dominants (Oliver 1982; Oliver and Larson 1990). This patchy mortality gives rise to gaps in the forest canopy, allowing increased light availability for growth of understory shrubs and trees. Dead canopy trees remain as snags and logs. Over time a stand with a wide range of tree sizes and ages develops; understory trees grow into successive gaps and the remaining dominant trees continue to grow.

The ecological significance of forest structure has been demonstrated through extensive research in the old-growth forests of the US Pacific Northwest (e.g., Franklin *et al.* 1981; Franklin and Spies 1991b; Carey 1998). Research in these forests has found that old-growth forests with high structural diversity also have high diversity of plant, vertebrate and invertebrate communities, increased richness and productivity of arboreal and understory plants, and high habitat diversity for particular vertebrate species (such as the spotted owl, *Strix occidentalis*).

Because structure in old-growth forests is closely related to functional and biological features that are inherently difficult to measure, emphasis has been placed on developing definitions of old growth in the US Pacific Northwest by quantifying the structural attributes of the forest (Franklin and Spies 1991a). Such definitions serve two purposes: firstly, they provide criteria to help in the mapping and inventory of old-growth forest areas; secondly, they are used by managers to assess the potential of younger stands to provide old-growth habitat (Wells *et al.* 1998). Two types of quantitative definitions have been developed, one based on a minimum set of criteria and another based on an index value representing a summation of scores for various criteria (Franklin and Spies 1991a). The interim definitions and index Franklin and Spies (1991a) developed for Douglas-fir forests in the US Pacific Northwest used the number of live trees and snags, canopy depth, and log mass. They cautioned that while these attributes were the most useful for the forests they studied, criteria would need to be adjusted to regional forest types to use these definitions elsewhere.

In a review of definitions of old growth and their applicability to British Columbia, Wells *et al.* (1998) concluded that few studies examining the characteristics of old-growth forests in British Columbia are available and that, consequently, the ability of managers to develop appropriate definitions for inventory and forest management purposes is limited. They found that studies comparing the structural characteristics of younger and older forests are even more limited. Arsenault and Bradfield (1995) have examined old and young forests in the wet Coastal Western Hemlock biogeoclimatic subzone (CWHvm: see Meidinger and Pojar [1991] for an explanation of biogeoclimatic classification) on the lower mainland of British Columbia. Kneeshaw and Burton (1998) have developed old-growth indices for the Sub-Boreal Spruce zone. Quesnel (1996) examined the characteristics of 26 old stands in southeastern British Columbia. Gulyas *et*

al. (1998) compiled structural data from forest cruise plots across British Columbia but has not used the data to develop old-growth definitions. The British Columbia Ministry of Forests (2001) has compiled DBH and average height as well as stems, volume, basal area and snags per hectare for individual site series across biogeoclimatic units using mensuration data from the provincial ecology program. To date, provincial inventories of old-growth forests have tended to use "working definitions" based on minimum age criteria below which forests are unlikely to be considered old growth (MacKinnon and Vold 1998). For western hemlock and Douglas-fir forests on coastal British Columbia, the minimum age for old growth is 150 years.

An opportunity to examine the overstory structure of coastal forests in British Columbia was created in 1992 with the establishment of chronosequence plots on southern Vancouver Island by the Canadian Forest Service. A chronosequence is an age sequence of forest stands selected such that all stands have had similar histories and growing conditions (Oliver 1982). Thus, space is substituted for time, allowing stand development patterns to be studied over a short time period (Norland and Hix 1996). The use of chronosequences to document changes during succession can be complicated by variations in soil, slope, aspect, vegetation, and history of disturbance between sites. Variation cannot be eliminated, but may be minimized by careful site selection (Crowell and Freedman 1994). Over the last 100 years harvesting and natural disturbances in British Columbia have created a mosaic of forests in varying successional stages. Often unharvested old-growth stands grow adjacent to younger stands. This mosaic of forests presents an opportunity to study both changes in stand structure during succession and the extent to which old-growth conditions are re-established in younger stands. Because old-growth stands change more slowly than younger stands, the old-growth stands serve as a control for between-site variability and are considered to represent conditions in the pre-harvest stand.

The chronosequence plots were established to examine the impacts of converting coastal old-growth forests to managed forests. Changes in mass, carbon, and nutrient distributions with secondary succession (Pollard and Trofymow 1993; Trofymow *et al.* 1997), and various biodiversity attributes of the forest, were measured (see papers in Trofymow and Mackinnon 1998). A previous report by Wells and Trofymow (1997) examined the abundance of downed coarse woody debris in these plots. The purpose of this study was two-fold: (i) to describe and quantify several physical attributes of the trees and snags of overstory species in these plots; and (ii) to examine trends in these attributes across the chronosequence plots. Two coastal forest types were studied, Douglas-fir–dominated stands on eastern Vancouver Island and western-hemlock-dominated stands on western Vancouver Island.

Methods

Site descriptions and plot layout

After examining 31 potential sites (Trofymow *et al.* 1997), a chronosequence of three post-harvest stands (regeneration, immature, and mature) and an old-growth control was selected at each of ten sites on Southern Vancouver Island (Figure 1). Five of these sites are located in the transition between the Coastal Western Hemlock submontane very wet biogeoclimatic variant (CWHvm1) and the Coastal Western Hemlock montane very wet biogeoclimatic variant (CWHvm2). Sites in the CWHvm were chosen to have western-hemlock–dominated stands although secondary components of amabilis fir (*Abies amabilis* (Dougl. ex Loud.) Dougl. ex J. Forbes), western redcedar, or Douglas-fir were acceptable, and a midslope position under 600 m in elevation. Although plot centers were located at all five CWHvm sites, limited funds resulted in only four sites being used – Renfrew (REN), Red/Granite creek (RGC), Nitinat (NIT), and Klanawa (KLA) (Table 1). The other five sites are located in the Coastal Western Hemlock very dry maritime biogeoclimatic subzone (CWHxm). Sites in the CWHxm were chosen to have Douglas-fir–dominated stands (small components of western hemlock or western redcedar were acceptable), and a midslope position under 600 m in elevation. Although plot centers were established at all five of the CWHxm sites, limited funds resulted in only four sites being used – Greater Victoria Watershed South (VWS), Greater Victoria Watershed North (VWN), Koksilah (KOK), and Nanaimo River (NAN) (Table 1).

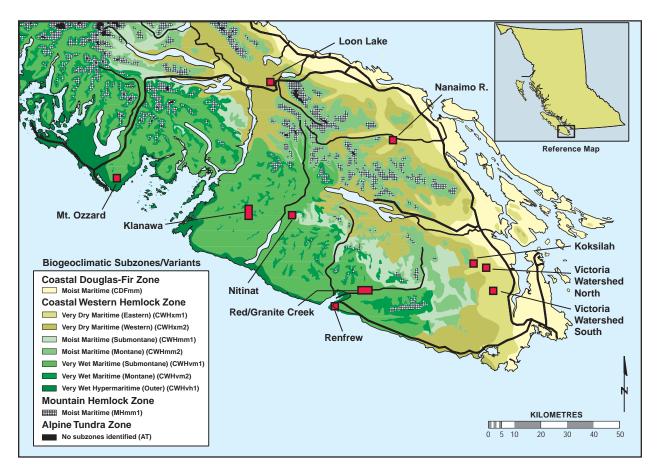


Figure 1. Locations of the ten Coastal Forest Chronosequences on southern Vancouver Island (from Trofymow et al. 1997).

Each chronosequence was within a 5×5 km or smaller area. Within a chronosequence, all of the plots were on similar slope, elevation (within 200 m) and aspect. Each chronosequence selected had stands in each of four age classes as of 1990: regeneration (3-8 years); immature (25-45 years); mature (65-86); and old growth (>200 years). These stands originated in the periods 1982-1987, 1945-1965, 1915-1925, and before 1790, respectively.

Most of the stands less than 90 years old were of harvest origin and had been burned. Two mature stands were of wildfire origin (KOK, KLA) and one (Mt. Ozzard; Figure 1) was of landslide origin. In those stands, plots were established to exclude residual veteran trees to more closely match initial conditions in the stands of harvest origin. Past disturbance and origin of the old-growth plots were unknown. All regeneration and immature stands had been planted, and none of the stands had been subject to any other silvicultural treatment (such as thinning).

A report by Trofymow *et al.* (1997) contains maps and descriptions of all chronosequence plots, including written directions and sketch maps of road access, forest cover maps, and basic site descriptions. Plot centers were located at least 80 m from the stand edge. Three subplot centers were positioned 30 m from the plot center, at the vertices of an equilateral triangle. The plot center and subplot centers were the center points of four circular subplots used to count and measure overstory tree species (Figure 2). Lines connecting the three subplot centers were used to measure coarse woody debris as described in the report by Wells and Trofymow (1997).

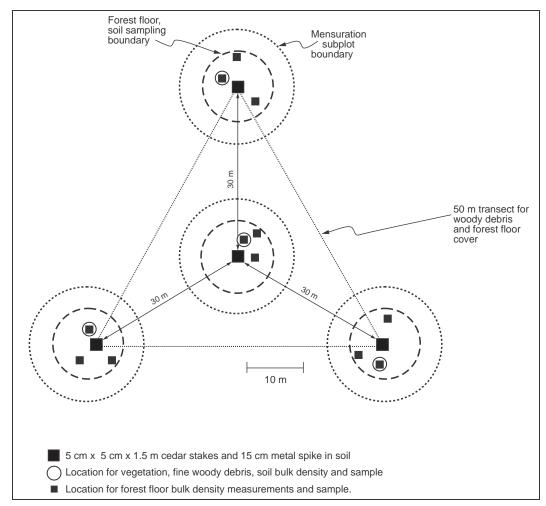


Figure 2. Example of triangular survey plot layout showing mensurational subplot and woody debris transects.

Field sampling

Measurements were made between May and September 1992. Total height, height to live crown and DBH (diameter at breast height) were measured for all living trees that were at least 3 m high, by species and crown class (suppressed, intermediate, codominant, and dominant) and for all dead trees (snags). In each plot, three of the four subplot centers were randomly chosen and trees measured in circular subplots of radius of 5 m or 10 m, depending on tree density. A 10-m plot was used if less than 10 trees were present in the 5-m plot. Total height and caliper at 5 cm from the base of the tree were measured for trees 0.1 to 3 m high in a 5-m plot. In each plot a minimum of five increment cores of dominant trees were collected to estimate years since stand establishment.

Data summary

Number of live stems per hectare (stand density) was summarized by diameter (DBH) class , height class and crown depth class. Diameter was divided into eleven 10-cm interval classes as follows: DBH class endpoints - 10; 20; 30; 40; 50, 60; 70; 80; 90; 100; >100 (any trees of DBH over 100 cm were included in the last class). Height was divided into twelve 5-m interval classes as follows: height class endpoints – 5 (0.1 - 5 m); 10; 15; 20; 25; 30; 35; 40; 45; 50; 55; >55 (any trees over 55 m in height were included in the last class). Crown depth in meters was divided into nine 5-m interval classes as follows: crown depth class endpoints - 5; 10; 15; 20; 25; 30; 35; 40; >40 (any crown depth over 40 m was included in the last class). Basal area per hectare (in m²) was calculated by summing the individual tree basal areas from each of the three circular subplots; basal area was allocated into the same eleven DBH classes used for live stems per hectare.

Number of snags per hectare, snag mass and stem biomass were summarized by diameter-based size classes (Class 1 = 1.1 - 12 cm; 2 = 12.1 - 29.9 cm; 3 = 30.0 - 59.9 cm and; 4 = 59.9 + cm) corresponding to size classes used in the downed coarse woody debris study (Wells and Trofymow 1997). Snags were defined as any standing dead tree greater than 3 m in height and more than 2 cm in diameter. Stem biomass was determined for all live trees measured in each plot using published regression equations (Standish *et al.* 1985; Gohlz *et al.* 1979; Feller and Blackwell 1989) that relate stem mass to tree DBH and height (Table 2). Snag mass was calculated as a cylinder using DBH and total snag height and using the relative wood densities by species for downed decay class III logs (Wells and Trofymow 1997).

Statistical analysis

A two-way analysis of variance (ANOVA) was used (SYSTAT [Wilkinson 1988]) to determine the effects of age class and subzone on: i) stand density, stem basal area, snag density; ii) stem biomass and snag mass for all trees and for each of the four size classes; and iii) percentage species composition by basal area and stand density.

Differences in species composition within subzone and age class were examined for the most common species including Douglas-fir, western hemlock, western redcedar, amabilis fir, and red alder (*Alnus rubra* (Bong.)), with minor species such as western yew (*Taxus brevifolia* Nutt.), western white pine (*Pinus monticola* Dougl. ex D. Don), Sitka spruce (*Picea sitchensis* (Bong.) Carrière), and grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.) assigned to an "other" group. In addition to testing for relative differences in species abundance by comparing the percentage of each species by basal area and stand density, a separate ANOVA was completed for each variable of each species to test for absolute differences in abundance.

For the analysis of variance the assumption of normality could not be tested because of the limited number of data points. To test the assumption of homogeneity of variance, the residuals were plotted

Variable	degrees of freedom
Subzone	2 - 1 = 1
Age class	4 - 1 = 3
Subzone \times age class	(2 - 1)(4 - 1) = 3
Experimental error	$(2 \times 4)(4 - 1) = 24$
Total	32 - 1 = 31

against estimated values to determine if the data exhibited heteroscedasticity (Miller 1986). The following ANOVA model was used for all analyses:

Significant differences among age class means were distinguished using Tukey s HSD multiple comparison test (Zar 1984).

To examine how the stand density and basal area distributions varied with age class and subzone, the stand densities and basal areas were expressed on a percentage basis and a Weibull function (Clutter *et al.* 1983) fitted:

$$F(x) = (c/b)(x/b)^{c-1}e^{-(x/b)^{c}}$$

where x is the DBH class, height class or crown depth class; F(x) the density or basal area in decimal percent; b the scale parameter; and c the shape parameter. As the function requires at least four classes to fit a distribution, only data for the immature, mature and old-growth plots could be used; regeneration plots contained only one or at most two classes. To allow for comparison of distributions among plots within the same age class and subzone, Weibull functions were fit to data from individual plots (24 functions – 3 age classes, 4 sites, 2 subzones). To compare distributions amongst subzones and age classes, functions were fit to the combined data (6 functions - 3 age classes, 2 subzones). Scale (b) and shape (c) parameter values plus standard errors and R^2 were calculated for each function using SYSTAT (Wilkinson 1988). Scale and shape parameters for all fitted variables are shown in Appendix I.

Results and Discussion

The results of the ANOVA for the number of live stems, stem biomass, number of snags, snag mass, stem basal area, and percentage species composition by basal area and stand density are summarized in Table 3.

Stand density - total number of live trees per hectare

In both subzones, stand density differed significantly with age class (Table 3) and although immature plots were always greater than old growth (Table 4), the ranking of all age classes weakly varied (P = 0.07) with subzone. In the CWHxm age classes ranked by stand density followed the order *immature* > *mature* > *re*generation > old growth while in the CWHvm age classes were ranked regeneration > immature > mature > old growth (Table 5). Total number of stems per hectare in the CWHxm (2494) significantly (p < 0.05) exceeded (Table 3) that of the CWHvm (1541) (Table 5). With the exception of regeneration plots, stand density was greater in CWHxm than in the CWHvm for each age class (Table 5). Although regeneration and immature plots in both subzones were planted, substantial additional natural regeneration occurred in the CWHxm, significantly increasing the overall stand density in the immature and mature plots. In contrast, although regeneration stands in the CWHvm had initially higher densities than in the CWHxm, density continued to decline with increasing stand age. These differences between subzones likely arise from differences in the onset of crown closure and early vegetative competition. In the wet CWHvm, understory vegetation develops more rapidly following clearfelling, as trees grow more rapidly and crown closure occurs sooner than in the drier CWHxm. Thus, in the CWHvm the time available for establishment of natural regeneration is less, and suppression of the smaller trees occurs earlier in stand development than in the CWHxm.

Stem diameters and stand density distributions

Stand density distributions by DBH class widens with stand age due to stand differentiation (Oliver and Larson 1990). Over time, some trees overtop others, resulting in crown stratification. The range of diameters observed in this study increased with age class. In regeneration plots, stems occurred in only one DBH class, while in the old-growth plots stems were present in all 11 DBH classes (Figure 3; Appendix II, Figures II-1, II-2). Mean and maximum DBH was 0.3 cm and 8.3 cm in regeneration stands, 9.8 cm and 51.1 cm in immature stands, 19.9 cm and 97.2 cm in mature stands, and 27.9 cm and 275.0 cm in old growth, respectively. Trees less than 1.0 cm DBH were found in almost all plots. These results were consistent with Franklin and Spies (1991b) who found that old-growth stands in the US Pacific Northwest had a much wider range in tree size than other structural stages.

Franklin and Spies (1991a) examined defining criteria of old-growth forests on Western Hemlock Series stands in the US Pacific Northwest. They suggested that a previous interim definition which required more than 20 stems per hectare with DBH greater than 80 cm be replaced by the criterion of 10 stems per hectare with a DBH greater than 100 cm. In this study, all old-growth plots in CWHvm and one of four plots in CWHxm (Appendix II, Figures II-1, II-2) had more than ten trees per hectare with DBH of 100 cm. All old-growth plots in CWHvm and three of the four old-growth CWHxm plots had more than 20 trees per hectare with DBH over 80 cm.

Parameter values from the fitted Weibull functions clearly differentiated (based on error bar separation) stands of different age classes (immature, mature, and old growth) and subzones (Figure 4, Appendix I). The scale parameter (b), which reflects the relative peak height of the distribution, accounted for most of the differences. With stand age, diameter distributions widened and more trees were in larger DBH classes and fewer in the smallest DBH class (Figure 3). The shape parameter (c) showed little variation among

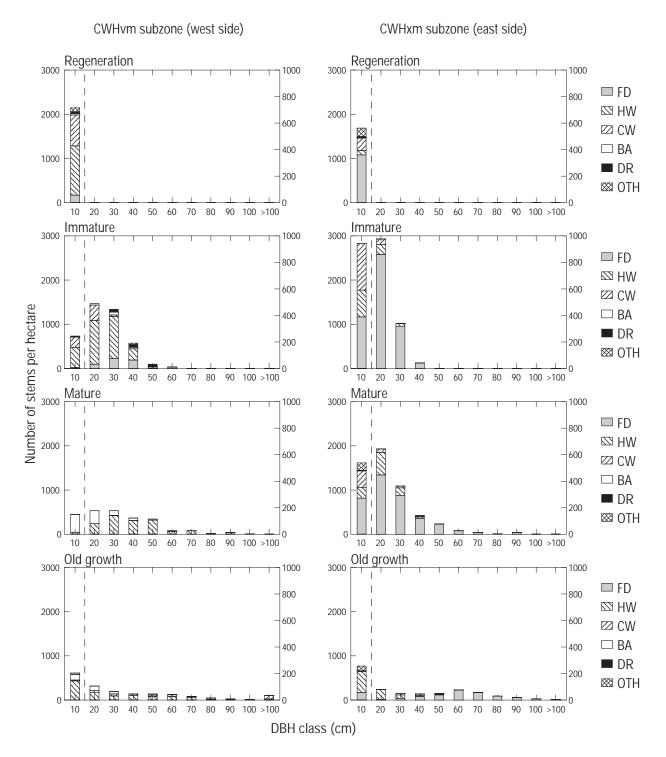


Figure 3. Mean number of stems per hectare of species within diameter (DBH) class by age class within biogeoclimatic subzone.

Frequencies of stems less than 10 cm DBH are represented on the left axis, all other classes are represented on the right axis. Diameter classes (cm) are : Class 10 = 0 - 10; 20 = 10 - 20; 30 = 20 - 30; 40 = 30 - 40; 50 = 40 - 50; 60 = 50 - 60; 70 = 60 - 70; 80 = 70 - 80; 90 = 80 - 90; 100 = 90 - 100; > 100 = 100+. (Fd = Douglas-fir; Hw = western hemlock; Cw = western redcedar; Ba = amabilis fir; Dr = red alder; Oth = other)

stands. Only the immature stands in the CWHxm and old growth in the CWHvm differed, a reflection of the skewed distribution (peak in the smallest DBH class) versus the wider more even distribution in the CWHvm old-growth plots.

Other studies of temperate forests have noted that size class distributions are one of the characteristic features that distinguish older forests from younger forests. Tyrrell and Crow (1994) discuss basic patterns of diameter distribution common in old-growth temperate forests. These include negative exponential, bell shaped unimodal, and intermediate skewed unimodal distributions (shifted to smaller diameter classes). Arsenault and Bradfield (1995) found in a study of three age classes forests on the coastal British Columbia mainland that in old-growth stands a large number of individuals were in the smallest size class with a steep decline and subsequent flattening across larger size classes. They suggested that this distribution was a defining structural property of old-growth forests. In contrast, Frelich and Lorimer (1985) report bell shaped distributions for old-growth eastern hemlock (*Tsuga canadensis* (L.) Carrière) stands. They attributed the low numbers of eastern hemlock in small size classes to deer browsing although competition from other plant species may also contribute to such patterns. The diameter distributions of old-growth plots in both the CWHvm and CWHxm subzones in this study best fit the reverse-J distribution.

Tyrrell and Crow (1994) discuss two factors characterizing old-growth forests that are consistent with this study. Firstly, with increasing stand age, stem density decreases as more large trees dominate the stand. Secondly, there is a shift to more even distribution among all size classes after a stand reaches the threshold age of 275-300 years

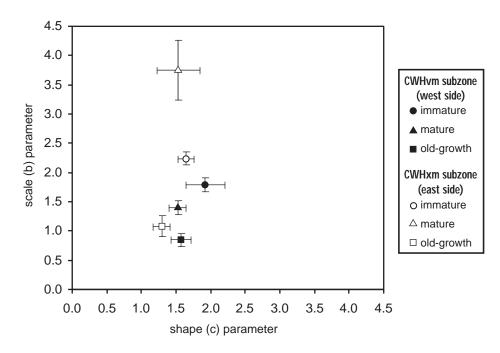


Figure 4. Weibull function parameters for stand density and diameter (DBH) by age class within subzone.

Bars depict the standard error for each parameter. Subzone: Open symbols = CWHxm, closed symbols = CWHvm. Age class: circle = immature, triangle = mature, square = old growth

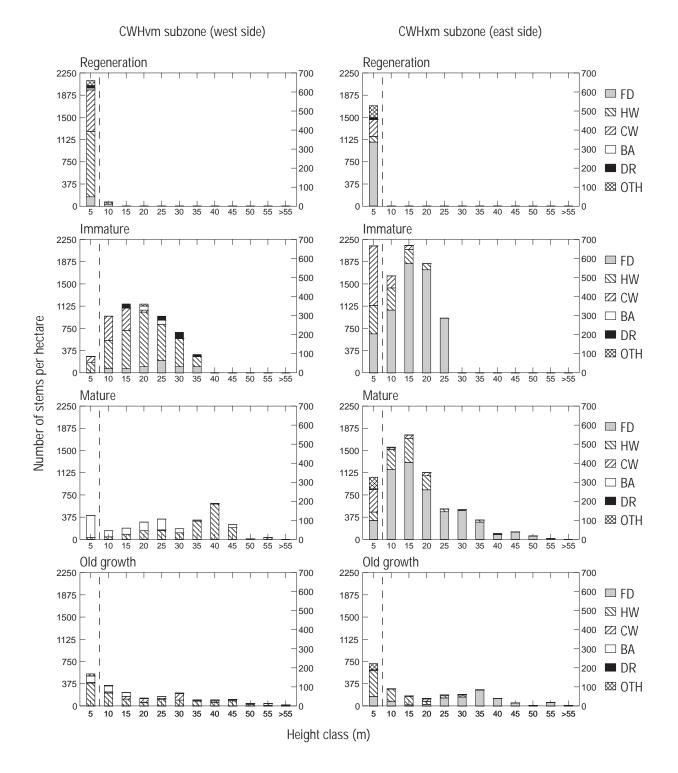


Figure 5. Mean number of stems per hectare of species within height class by age class and biogeoclimatic subzone.

Frequencies of stems in the height class 0.1-5 m are represented on the left axis, all other classes are represented on the right axis. Height classes (m) are: Class 5 = 0 - 5; 10 = 5 - 10; 15 = 10 - 15; 20 = 15 - 20; 25 = 20 - 25; 30 = 25 - 30; 35 = 30 - 35; 40 = 35 - 40; 45 = 40 - 45; 50 = 45 - 50; 55 = 50 - 55; >55 = 55+. (Fd = Douglas-fir; Hw = western hemlock; Cw = western redcedar; Ba = amabilis fir; Dr = red alder; Oth = other)

Stem heights and stand density distributions

Table 1 reports the mean, minimum and maximum tree height for all chronosequence plots. When data from both subzones are combined, mean and maximum heights were, respectively, 1.2 m and 6.8 m in regeneration plots, 10.1 m and 34.9 m in immature plots, 17.9 and 50.2 m in mature plots, and 16.1 and 58.7 m in old-growth plots. Stand density by height class for individual plots is shown in Appendix III.

In all plots trees less than 5 m tall made up a large fraction of all trees, more than 50% in the regeneration and old-growth stands (Figure 5). Almost all trees in regeneration plots were less than 5 m tall, though a few stems from 5 to 10 m in height occurred in one regeneration plot only in the CWHvm subzone (RGC, Figure III-2). Most trees in the immature plots were from 10 to 35 m in height; age classes ranked by stand density followed the order immature > mature > old growth (Figure 5). Trees more than 35 m tall were found only in mature and old-growth plots (Figure 5). The number of trees more than 35 m tall in mature and old-growth plots combined was greater in the CWHvm (94 stems/ha) than the CWHxm (42 stems/ha)but only a single individual in the top height class (i.e., over 55 m in height) occurred in each subzone. This trend occured in the mature plots alone; there were 140 stems/ha in the CWHvm over 35 m tall, compared to 42 stems/ha in the CWHxm. Old-growth plots followed this same trend, although there was less differentiation between the CWHvm and CWHxm (49 stems/ha versus 40 stems/ha, respectively, over 35 m tall).

Parameter values of the fit of the Weibull function by height class were similar for all age classes in the CWHxm (Figure 6) with old growth separated from mature and immature plots on the basis of the scale parameter. The mature and immature plots had high numbers of trees in the 5-m to 25-m height classes, while trees in old-growth plots cover the complete range of height classes (Figure 5). In contrast to the CWHxm, height distributions in the CWHvm varied among all age classes, differing in both scale and shape parameters (Figure 6). The immature plots in the CWHvm were unique in that height class 1 did not dominate (only two of the four plots had stems in height class 1, Appendix III Figure III-3) and had

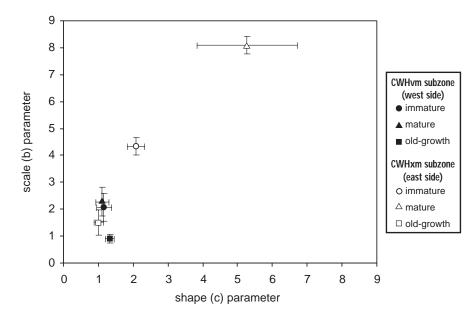


Figure 6. Weibull function parameters for stand density and height by age class within subzone.

Bars depict the standard error for each parameter. Subzone: Open symbols = CWHxm, closed symbols = CWHvm. Age class: circle = immature, triangle = mature, square = old growth

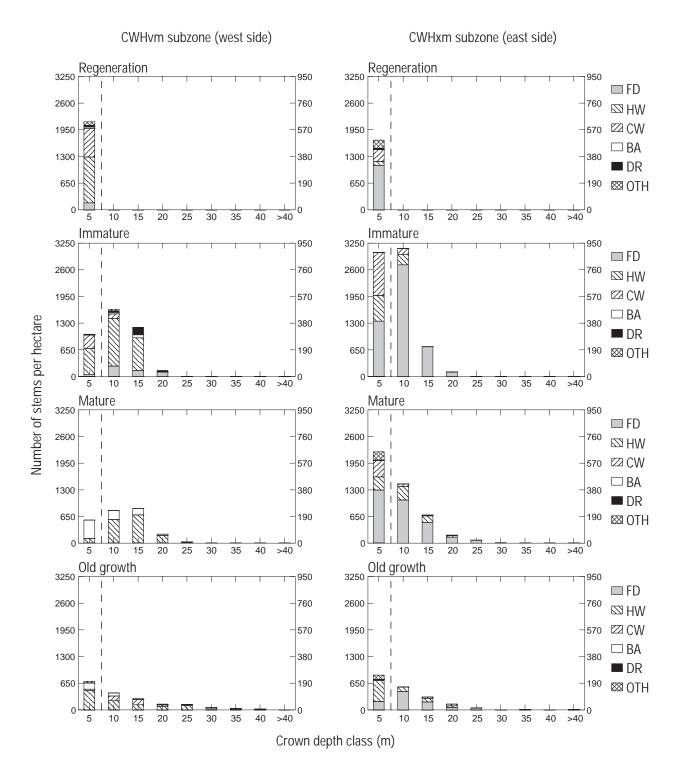


Figure 7. Mean number of stems per hectare of species within crown depth class by age class and biogeoclimatic subzone.

Frequencies of crowns less than 5 m deep (class 5) are represented on the left axis, all other classes are represented on the right axis. Crown depth (m) classes are: Class 5 = 0 - 5; 10 = 5 - 10; 15 = 10 - 15; 20 = 15 - 20; 25 = 20 - 25; 30 = 25 - 30; 35 = 30 - 35; 40 = 35 - 40; > 40 = 40+. (Fd = Douglas-fir; Hw = western hemlock; Cw = western redcedar; Ba = amabilis fir; Dr = red alder; Oth = other)

a unimodal distribution centered on height class 4 (Figure 5). Mature plots in the CWHvm had a much wider distribution and higher numbers of stems in the 35-m to 40-m height classes than in the CWHxm (Figure 5). The CWHvm old-growth stands had a wider distribution of heights compared to the mature or immature stands and a distribution most similar to the CWHxm old-growth stands (Figure 5). Old-growth height distributions did differ between subzones (Figure 6), the CWHvm having fewer trees in class 1 and more in classes 10 and 12 than the CWHxm.

The changes in height class distribution with age were similar to those observed for diameter class distributions, i.e., distributions widen with increasing age. Old-growth plots had trees in all height classes, thus forming a multi-storied canopy. Multiple canopy layers have been identified as a stand structural feature of old-growth forests (Franklin and Spies 1991a). In contrast, the regeneration and immature stands had a limited range of height classes, indicating a more uniform canopy structure. Mature stands in both subzones had trees across all height classes. Mature stands in the CWHxm subzone still had a high percentage of stems in the smaller height classes than in the CWHvm, suggesting that old-growth characteristics may develop more quickly in the CWHvm subzone.

Crown depths and stand density distributions

The mean and maximum crown depths were, respectively, 3.7 m and 19.6 m for the immature plots, 5.7 m and 25.2 m for the mature plots, and 6.4 m and 40.2 m for the old-growth plots. Crown depth for each plot is summarized in Table 1 and graphs of stand density by crown depth class for each plot are in Appendix IV.

Distributions of stem density by crown depth class were similar to those for DBH and height class, i.e., most stems (and all stems in regeneration plots) were in the <5 m class regardless of age class or subzone (Figure 7). The majority of stems in the immature and mature plots had crown depths from 5 to 15 m. The old-growth plots had the widest range of crown depth classes. Stems with crown depths over 20 m were only found in mature and old-growth plots, representing 1% and 4% of stems, respectively (Figure 7).

Fits of the Weibull function of stand density and crown depth class (Figure 8) confirmed the differences in crown depth distribution among age classes and further indicated differences in distributions with subzone. Age classes in the CWHxm did not differ in the shape parameter (Figure 8) reflecting the influence of the large proportion of stems with crown depths under 5 m in all age classes (Figure 7). The CWHxm immature and mature plots differed in the scale parameter (old-growth plots had an intermediate value), which reflects increasing crown depth with age. All age classes in the CWHvm differed from each other in the scale parameter (Figure 8) reflecting the wider range of crown depths with stand age. Within the same age class, subzones differed. The high proportion of stems with crown depths under 5 m in immature and mature stands in the CWHxm compared to the CWHvm (Figure 7) resulted in steeper skewed distribution curves and thus a significant difference in the shape parameter (Figure 8). The old-growth stand crown depth distributions were similar in the CWHxm and CWHvm – their shape and scale parameter values overlapped (Figure 8).

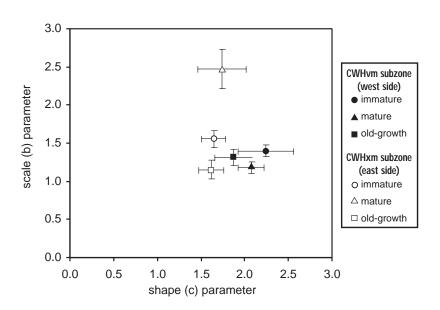


Figure 8. Weibull function parameters for stand density and crown depth by age class within subzone.

Bars depict the standard error for each parameter. Subzone: Open symbols = CWHxm, closed symbols = CWHvm. Age class: circle = immature, triangle = mature, square = old growth

Stem biomass and its distribution by size class

Stem biomass for each plot is reported in Table 4. With the exception of the Renfrew site, stem biomass significantly (p < 0.05) increased with stand age (Table 3) and within the same age class tended (Table 6) to be greater in the CWHvm than in the CWHxm, although this result was not statistically significant (Table 3).

Most of the major species examined (Douglas-fir, western hemlock, and western redcedar) had significant subzone by age class interaction, although the interaction for all species combined was not significant (Table 3). Douglas-fir biomass increased across all four age classes in the CWHxm and was only present at lower levels in the regeneration and immature plots in the CWHvm (Table 6). Within the same age-class, western hemlock stem biomass was much higher in the CWHvm than CWHxm, and in both subzones biomass increased from regeneration to mature stands and then remained constant or slightly decreased in old-growth stands (Table 6). Western redcedar stem biomass in the CWHxm was at low levels across all age classes while in the CWHvm, biomass was greatest in the old-growth plots (325 Mg/ha), intermediate in immature plots (9.4 Mg/ha), and lowest in the mature and regeneration plots (0.3 and 0.2 Mg/ha) (Table 6). The dominance of western redcedar biomass in the CWHvm old-growth plots compared to the mature plots could be due to the long lifespan of western redcedar and limited stand disturbance in the CWHvm. With time, western redcedar would become a more significant stand component than the shorter-lived western hemlock (Burns and Honkala 1990). Long intervals between major disturbances give rise to a forest whose composition is controlled by gap dynamics and favours shade-tolerant trees (Lertzman and Krebs 1991; Lertzman 1992). Amabilis fir (absent in the CWHxm) biomass in the CWHvm, while lower than that of hemlock, followed a similar pattern to hemlock with age class, i.e., it increased from regeneration to immature and was slightly lower in old growth (Table 6).

Stem biomass by size class for individual plots and a summary table of biomass by age class are presented in Appendix V. Biomass in the immature stands primarily occurred in size class 2 in the CHWxm, in classes 2 and 3 in the CWHvm, and was absent from class 4 (Figure 9). Across subzones, approximately 81% of stem biomass was in classes 3 (47%) and 4 (34%) in mature stands, and 78% in class 4 in oldgrowth stands. There was more stem biomass in size class 4 in CWHvm old-growth plots compared to those

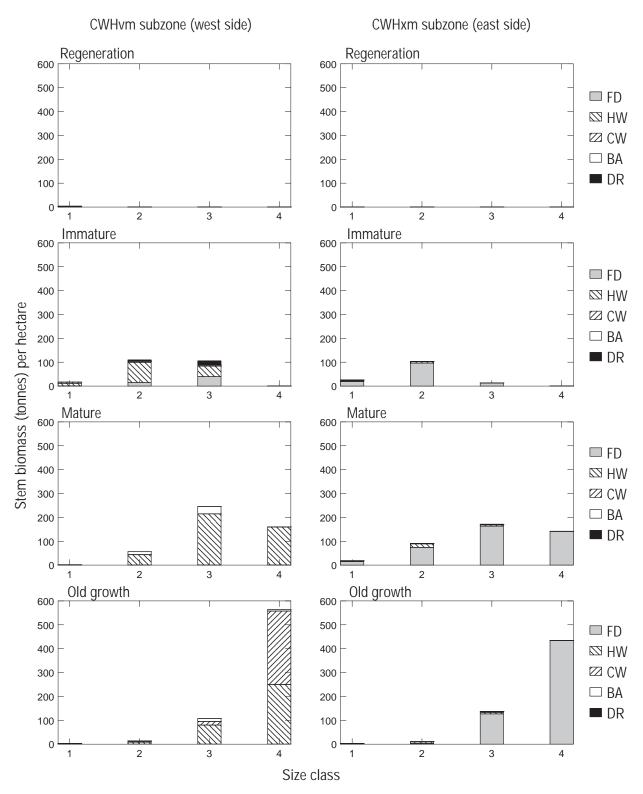


Figure 9. Mean stem biomass (Mg) per hectare of species within size class by age class and biogeoclimatic subzone.

Size (cm DBH) classes are: Class 1 = 1.1 - 12; 2 = 12.1 - 29.9; 3 = 30.0 - 59.9, and; 4 = 59.9 + . (Fd = Douglas-fir; Hw = western hemlock; Cw = western redcedar; Ba = amabilis fir; Dr = red alder)

in the CWHxm; this was primarily a function of the old-growth Klanawa plot (Figure V-2) which contained large western redcedar trees resulting in size class 4 biomass of over 1200 Mg/ha. In the CWHvm subzone, western hemlock, western redcedar and a few amabilis firs contributed to size class 4. Western hemlock dominated (Figure 9), accounting for 54, 76, and 74 % of the biomass in size classes 1 - 3, respectively, with Douglas-fir, western redcedar, and amabilis fir present in minor amounts. In the CWHxm, Douglas-fir dominated all size classes (Figure 9), contributing 72, 85, 94 and 100 % of the stem biomass in size classes 1, 2, 3 and 4, respectively.

Snag density and its distribution by size class

Snags originate episodically or continuously, as a result of fire, weather, insects, disease, or canopy suppression. Rates of tree death (recruitment), decay, and tree fall (Timoney and Robinson 1996) control the number of snags present. Snag recruitment rates vary with species, diameter, height, cause of death, and wind exposure (Timoney and Robinson 1996). In coastal forests, large snags are often residuals from previous stands disturbed naturally or by logging.

Numbers of snags per hectare in each plot are reported in Table 4. Across subzone, snags per hectare varied significantly with age class (Table 3) and their densities were highest in immature (801 snags/ha), intermediate in immature (475 snags/ha) and lowest in old growth (475 snags/ha) stands. No snags were present in any of the regeneration plots as all of these plots originated following clearcutting. The abundance of snags in immature and mature stands is due to natural thinning with stand development. Snag density peaked in the immature plots of the CWHvm subzone and in the mature plots of CWHxm (Table 7), which is probably related to the different patterns of regeneration and stand development of two dominant tree species, western hemlock (CWHvm) and Douglas-fir (CWHxm). Western hemlock has a light and prolific seed habit which typically results in greater numbers of established seedlings. High initial stem densities and more rapid tree growth in the CWHvm results in increased inter-tree competition and early mortality in western hemlock-dominated stands, thus the peak in snag density in immature stands. Douglas-fir seeds are distributed less prolifically and tree growth in the CWHxm is slower, so inter-tree competition occurs later and the snag density peak in mature stands. Species distributions of snags were similar to those of live stems per hectare; snags in the CWHxm were dominated by Douglas-fir and lower numbers of western hemlock and snags in the CWHvm were dominated by western hemlock and western redcedar (Table 7, Figure 10). Red alder snags were present in low numbers in both subzones.

Snag density by size class for individual plots and a summary table by subzone and age-class are presented in Appendix VI. Less than 3% of all snags were more than 60 cm in DBH (class 4) (Figure 10). The majority fell within size class 1 – 84% in CWHxm and 75% in the CWHvm subzones, respectively. In the immature plots in both subzones most snags were in size class 1, with much lower numbers in classes 2 and 3, and none in class 4 (Figure 10). In the mature plots, snags in size class 1 and 2 dominated in the CWHvm subzone (37% and 51% of all the snags, respectively) while mature plots in the CWHxm had more snags in size class 1 than 2 (82% and 17%, respectively) (Figure 10, Table 7). Snags in the old-growth plots were more evenly distributed among size classes. In the CWHvm, 15% of the snags were in size class 1, 27% in class 2, 45% class 3, and 13% in class 4. In the CWHxm, 58% of the snags were in size class 1, 28% in class 2, 11% in class 3, and 3% in class 4 (Figure 10, Table 7).

According to the definition of Franklin and Spies (1991a), old growth has at least 4 snags per hectare greater than 5 m tall and 50 cm in DBH. All four old-growth plots in the CWHvm and two of four in the CWHxm met these criteria. All old-growth and mature plots met the interim definition criteria which requires more than10 snags per hectare (Franklin and Spies 1991a). In British Columbia, Wells *et al.* (1998) suggested that quantitative development of old-growth definitions requires establishment of categories of forest development along a continuum of successional development. They suggested that threshold values

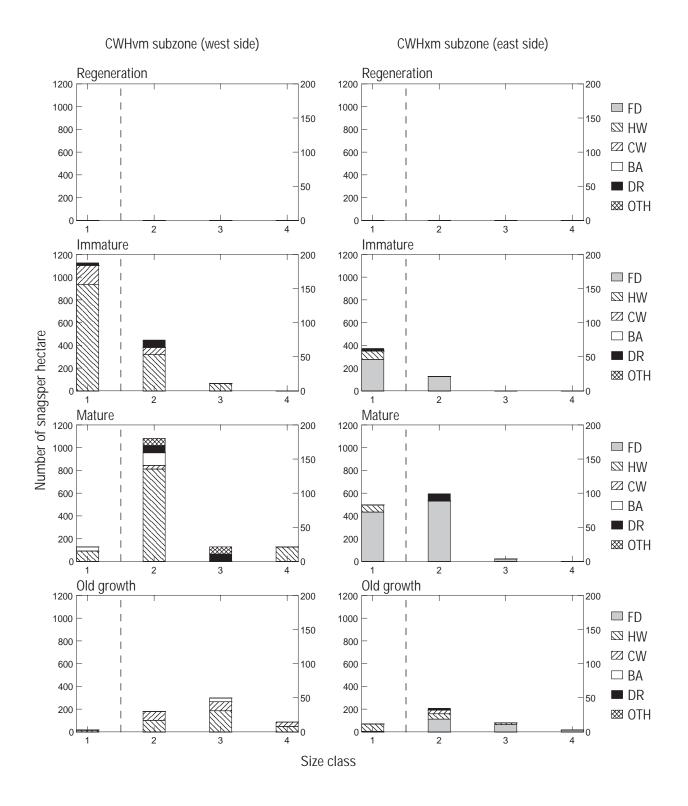


Figure 10. Mean number of snags per hectare of species within size class by age class and biogeoclimatic subzone.

Class 1 frequencies are represented on the left axis, all other classes are represented on the right axis. Size (cm DBH) classes are: Class 1 = 1.1 - 12; 2 = 12.1 - 29.9; 3 = 30.0 - 59.9, and; 4 = 59.9 + . (Fd = Douglas-fir; Hw = western hemlock; Cw = western redcedar; Ba = amabilis fir; Dr = red alder; Oth = other) of old-growth attributes, such as the number of snags per hectare, must be chosen to separate one forest stage from another. They were cautious to point out that when lines are drawn at specific points along this continuum, there are inevitable regions of overlap among stages of forest development.

Arsenault and Bradfield (1995) found that, in coastal forests, old growth has fewer snags than younger stands as a result of reduced self-thinning. Furthermore, snags in old growth were more evenly distributed across all size classes.

Timoney and Robinson (1996) found that, following natural disturbance (fire and flood), snag numbers increase with age. They observed that in stands disturbed by fire (even low to moderate intensity fire) most snags soon blow down, leaving, at stand origin, low densities of snags with high log diameters. Fire origin snags tend to fall sooner than snags of non-fire origin, perhaps due to weakening of the tree base or to greater wind exposure in large burned areas (Morrison and Raphael 1993; Timoney and Robinson 1996). Smaller-diameter snags tend to rot more quickly and fall over (Morrison and Raphael 1993), leading to an increase in median snag diameter over time (Timoney and Robinson 1996). This is consistent with our results from old-growth plots where large-diameter snags (class 3 and 4) accounted for the majority of snags present (Figure 10).

Snag mass and its distribution by size class

Snag mass per hectare in each plot is shown in Table 4. Across age classes, snag mass tended (Table 3) to be greater in the CWHvm (20 Mg/ha) than in the CWHxm (9 Mg/ha) (Table 8). Lower snag numbers and mass in the CWHxm may be due to the greater frequency of stand-replacing fires and surface fires, which remove large trees that could become snags. There was a weak tendency for snag mass to vary with age class (Table 3). Snags were absent in regeneration plots and snag mass tended to be highest in mature plots in the CWHvm and mature and old-growth plots in the CWHxm subzone (Table 8). In the CWHxm, Douglas-fir comprised 89% of snag mass while in the CWHvm subzone western hemlock snags were most common, comprising 76% the snag mass (Table 8). Western redcedar was present in both subzones but was less than 1% of the total snag mass in the CWHvm.

Snag mass by size class for individual plots and a summary table by subzone and age class are presented in Appendix VII. As with many of the other stand variables, snag mass distribution by size class changed with stand age (Table 8, Figure 11). For immature plots in both subzones, size class 1 contained most of the mass and class 2 contained a lesser fraction. Significant snag mass in size class 3 occurred in the CWHvm, though this occurred in only one plot (the immature plot at Renfrew; plot 52). Compared to immature plots, mature plots in both subzones had increased snag mass in size class 2, and lesser amounts in classes 1 and 3. The CWHvm mature plots also had a large amount of snag mass in class 4, even more than that in the old-growth plots (Figure 11). This was entirely due to a few large snags in the Klanawa mature plot (plot 83) which are likely residuals as this stand was of fire (or insect and fire) and not harvest origin. Most of the snag mass in the old-growth plots was in the largest size classes (3 and 4) in the CWHvm and in class 4 in the CWHxm subzone. Snag mass was composed of species that also dominated the live stem biomass, western hemlock and western redcedar in the CWHvm, and Douglas-fir in the CWHxm. Although red alder was only a very minor portion of the live stem biomass in any size or age class (Figure 9) it was a larger fraction of the snag mass, especially in the mature plots (Figure 11). This is likely due to red alder s relatively short life span; it initiates early in stand development and then dies out as the longer-lived species come to dominate the stand.

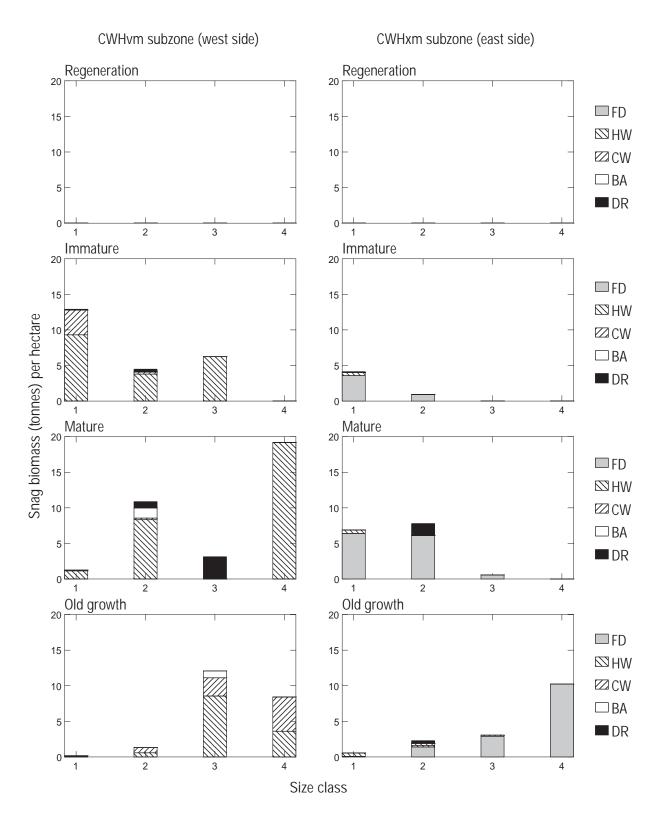


Figure 11. Mean snag mass (Mg) per hectare of species within size class by age class and biogeoclimatic subzone.

Size (cm DBH) classes are: Class 1 = 1.1 - 12; 2 = 12.1 - 29.9; 3 = 30.0 - 59.9, and; 4 = 59.9 + . (Fd = Douglas-fir; Hw = western hemlock; Cw = western redcedar; Ba = amabilis fir; Dr = red alder)

Stem basal area and its distribution by diameter class

Stem basal area per hectare in each plot is presented in Table 4. The significant differences in basal area with subzone or age class were similar to those noted for stem biomass (Table 3). For both subzones combined, when ranked by basal area, the order was *old growth* > *mature* > *immature* > *regeneration* (Table 9). These differences in age class were significant (p < 0.05) (Table 3). Basal area in each age class in the CWHvm tended to be greater than that in the CWHvm (Table 9) although differences between subzone were not significant (Table 3).

Stem basal area of western hemlock in both subzones and amabilis fir in the CHWvm subzone was greatest in mature plots, intermediate in immature and old-growth plots, and lowest in regeneration plots (Table 9). As discussed for stem biomass, this may be related to the increase in mortality of western hemlock and amabilis fir with increasing stand age. Douglas-fir basal area in the CWHxm subzone increased with increasing age class. Western redcedar basal area in the CWHxm subzone, though a minor component of the basal area of the total stand, increased with increasing age class. The pattern differed in the CWHvm subzone (Table 9) where western redcedar basal area was lowest in regeneration plots, was still quite low in immature and mature plots, and was very high in the old-growth plots (Table 9).

Stem basal area by diameter class for individual plots and a summary table by size class, subzone, and age class are presented in Appendix VIII. Weibull functions were distinct for each age class within a subzone and differed from each other primarily on the basis of the scale parameter (Figure 12). The CWHvm old growth differed the most amongst all age classes and subzones due to an outlier at the Klanawa site which had a high basal area in trees of DBH over100 cm. Within any age class, the stem basal area distribution Weibull scale parameter in the CWHvm subzone was greater than that in the CWHxm (Figure 12), indicating that stem basal area increases more rapidly with age in the CWHvm than the CWHxm subzone (Figure 13). The changes in basal area distribution with age class were similar to those noted for other variable distributions, i.e., the distribution widened with stand age (Figure 13). The basal area curve shape did differ from other variables in that most basal area curves were unimodal bell-shaped rather than negative exponential or reverse J-shaped.

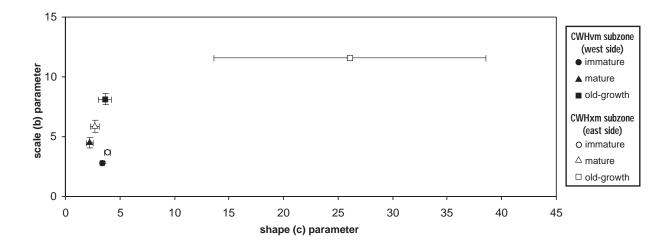


Figure 12. Weibull function parameters for basal area and diameter (DBH) by age class within subzone.

Bars depict the standard error for each parameter.Subzone: Open symbols = CWHxm, closed symbols = CWHvm. Age class: circle = immature, triangle = mature, square = old growth

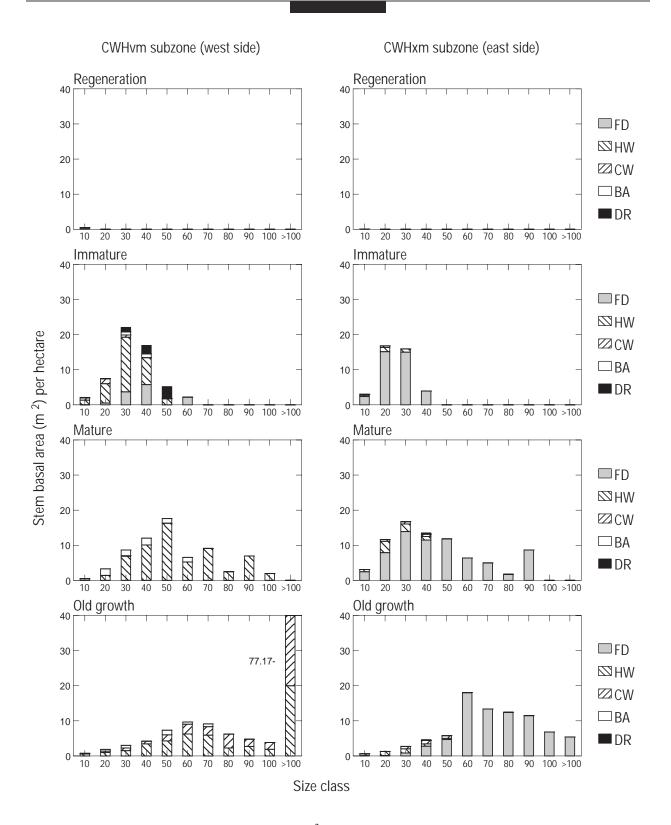


Figure 13. Mean stem basal area (m^2 / ha) of species within diameter (DBH) class by age class within biogeoclimatic subzone.

Diameter classes (cm) are : Class 10=0 - 10; 20=10 - 20; 30=20 - 40; 40=30 - 40; 50=40 - 50; 60=50 - 60; 70=60 - 70; 80=70 - 80; 90=80 - 90; 100=90 - 100; >100 = 100+`. (Fd = Douglas-fir; Hw = western hemlock; Cw = western redcedar; Ba = amabilis fir; Dr = red alder)

The old-growth basal area criterion defined by Spies and Franklin (1991) for Douglas-fir is 69 (\pm 5) m²/ha. Three of four mature plots in both the CWHvm and CWHxm subzones met this criterion (Table 4), with means of 69 m²/ha and 79 m²/ha, respectively (Table 9). All old-growth plots in both CWHvm and CWHxm subzones met the criterion, with means of 128 m²/ha and 83 m²/ha, respectively. That basal area in the CWHvm old-growth plots was 85% greater than the Spies and Franklin (1991) criterion is due to the difference in forest types. The CWHvm western hemlock and western redcedar forests are likely in a higher precipitation regime and more productive than the forest types used by Spies and Franklin (1991) to develop their criteria.

Species composition by stand density and basal area

Species composition, both by numbers of stems and by basal area (Tables 10 and 11), was as expected for the two biogeoclimatic subzones, which primarily reflect variation in climate (Green and Klinka 1994). Subzone effects were significant for both the percentage of basal area and the percentage of stems for Douglas-fir, western hemlock, and amabilis fir, but for western redcedar subzone effects were significant for basal area only (Table 3).

Douglas-fir dominated all age classes in the CWHxm subzone, comprising more than 90% of the basal area and over 50% of the stems, with the percentage stems lowest in the old-growth plots. In contrast, in the CWHvm subzone Douglas-fir comprised only 5% of the stems and 15% of the basal area, and this species was absent from the mature and old-growth stands (Table 10 and 11). For western hemlock in the CWHxm subzone this trend was reversed; this species comprised 19% of the stems, 5% of the basal area, was present in almost all age classes, and the percentage of stems was highest (40%) in the old-growth plots. Stems of western hemlock represented only 5% of the basal area, indicating it was in smaller size classes only (Table 10 and 11). In the CWHvm subzone, western hemlock comprised more than 50% of the stems or basal area in all age classes and its percentage was highest in mature plots (87% of basal area, 73% of stems), intermediate in immature plots, and lowest in regeneration plots (Table 10 and 11).

Western redcedar comprised about 16% of the stems in both subzones and did not significantly vary with stand age, though the percentage of stems tended to be highest in regeneration plots (Table 3 and 10). In the CWHvm subzone, the percentage of basal area in western redcedar varied with stand age, peaking at 52% in old-growth plots, while in the CWHxm subzone it remained at low levels (0 - 3%) in all age classes (Table 11). Amabilis fir was only present in the CWHvm subzone, in which mature stands tended to be the age class with the highest percentage of basal area and stems in this species. Red alder comprised less than 2% of the stems in both subzones, was absent in mature and old-growth plots, and did not contribute measurable basal area to any of the plots in the CWHxm subzone.

Other species contributed fewer than 5% of the stems and less than 1% of the basal area in both subzones (Table 10 and 11) and neither variable differed with stand age (Table 3). Western white pine and grand fir comprised only 5% and 1% of the stems in the CWHxm, respectively, and were not present in the CWHvm plots. Sitka spruce and western yew each comprised 1% of the stems in the CWHvm and were not present in CWHxm plots. All these species were too scarce to draw any conclusions about differences among age classes.

The results from this study are consistent with those reported by Norland and Hix (1996) who observed that species composition varied across age classes. Stand succession involved major changes in density, basal area, and species composition. Species composition in this study was similar to that reported by Arsenault and Bradfield (1995) who found western hemlock to be the dominant species in young forests, followed by amabilis fir and western redcedar. Arsenault and Bradfield (1995) reported that mature forests were characterized by regeneration of western hemlock and western redcedar in the smallest diameter class and more Douglas-fir in the intermediate diameter classes. Regeneration of western hemlock and western

redcedar in the smallest size classes was common in the CWHvm subzone in this study; however, there was no increase of Douglas-fir in intermediate diameter classes. The contribution of Douglas-fir was probably reduced in the CWHvm forests of this study due to the influence of the maritime climate on west coast of Vancouver Island; Arsenault and Bradfield conducted their study on the mainland British Columbia coast where the climate is more submaritime.

The relative abundance of a tree species may have a profound influence on the growth and development on the other tree species in a stand. Cobb *et al.* (1993) found that growth and development of lodgepole pine and Douglas-fir are apparently strongly affected by the presence or absence of other species, their density, and their times of establishment. Although Cobb *et al.* (1993) considered how species composition, density of stems, and time of establishment may have affected stand development, other factors could be important. In this study it appears that factors such as regional climate, climatic fluctuations, fire history, and or species-specific insect or disease attacks may provide a temporary competitive advantage to one species over another leading to long-term changes in species composition and stand structure.

Conclusions

Few studies have tried to characterize overstory structure both between and within different biogeoclimatic subzones of coastal British Columbia. Measurement of chronosequence plots located on eastern and western Vancouver Island has clearly demonstrated that the regional climate associated with the CWHxm and the CWHvm subzones has significantly influenced overstory structure. The CWHvm is more structurally diverse than the CWHxm, primarily due to higher levels of precipitation and differences in the levels of disturbance by fire, forest health agents, wind, and other site conditions. Our data supports the contention of both Franklin and Spies (1991b) and Timoney and Robinson (1996) that old-growth structure is a function of local and regional conditions. The results also show that overstory structure and diversity in coastal forests increases as a function of stand age. Additionally, we found that, at the stand level, overstory structure is highly variable in forests of the same age and within the same biogeoclimatic subzone.

Overstory structure attributes collected for Vancouver Island forests in the CWHxm and CWHvm subzones compare favorably to those of others in the Pacific Northwest (Table 12). Most structural attributes showed their greatest change early in stand succession followed by no change, a slow rise, or slow decline through later stages. All old-growth plots in the CWHvm of this study met the minimum age and structural criteria developed by Franklin and Spies (1991a) to define old growth (Table 12). Old-growth plots in the CWHxm subzone exceeded the minimum age criteria and met the minimum for some attributes for old growth in the US Pacific Northwest, although none of the plots met all attributes. That some of these plots did not meet these criteria indicates that i) new criteria would be needed for the CWHxm, or ii) stands over 300 years old should be defined as old growth regardless of structure, or both. Local site conditions and regional climate are likely to significantly influence overstory structure. Therefore structural comparisons with sites in geographical locations outside British Columbia are not ideal. Lower fit of coastal forest chronosequence old-growth plots to US Pacific Northwest definitions of old-growth Douglas-fir may be due to regional differences in climate or to differences in site quality (most coastal forest chronosequences were on medium to poor sites).

Robust definitions of old growth in British Columbia are hindered by a lack of research describing structural, compositional, and functional characteristics of old growth (Hamilton, E.; Nicholson, A. 1991. Defining British Columbia s old-growth forests: discussion paper. B.C. Ministry of Forests, Research Branch, Victoria, BC. Draft paper.). This study provides some data on which to base such definitions, and our results support the suggestion by Wells *et al.* (1998) that definitions of old growth need to be based on

fundamental ecological and physical characteristics to be useful for forest management and conservation. Although overstory attribute summaries from this study provide some direction for defining old-growth characteristics, the variability of many of these attributes is such that more data is required to rationalize a rigorous definition that will withstand scientific and operational scrutiny.

Forest type, species composition, site conditions and stand disturbance history influence stand development and the age at which old-growth attributes develop (Franklin and Spies 1991b). Low diversity of structure and species composition in the CWHxm, compared to the CWHvm, may be due to differences in disturbance regimes, i.e., to more frequent stand-replacing fires in the CWHxm (Beese and Sanford 1992). Disturbance in the CWHvm subzone is less severe, which leaves remnants of stands or creates more gaps in stands. Spies and Franklin (1991) state that low to moderate disturbances during the development of a stand have an important influence on structure in old growth.

Environmental and social concerns have raised awareness about the maintenance of forest structure and composition. Society is questioning the impacts of past forest management practices on coastal forests of British Columbia. Kimmins (1997) pointed out that forest management has the potential to change biological diversity and that it is therefore important to understand these changes in relation to forest health and ecosystem integrity. These are fundamental questions in the debate over forest sustainability and certification.

The results of this study indicate that past practices have not measurably impacted tree species diversity. Clear-cut harvesting and burning at the eight chronosequence sites has reduced overstory structural diversity in both biogeoclimatic subzones (CWHxm and CWHym). Typically there has been a decrease in the range of tree size (both diameter and height), a short- to mid-term increase in the number of trees, and a decrease in the number and biomass of large snags when comparisons are made to old-growth plots. These findings are not surprising, nor are they unique to this study. The more interesting consideration is the length of time that may be required for these sites to acquire structural attributes similar to those measured in oldgrowth plots. There is some overlap between mature and old-growth plots for a number of the measured attributes. However, it appears that wide variation in many of these attributes (tree diameter, crown depth, basal area, and the number and biomass of snags) does not begin to develop within the stand for at least 65 years. On low-productivity sites this time may be even greater. Reduction in structural diversity is not considered permanent; however, the time required to acquire structural diversity may be beyond the timelines established for plantation forestry. Minimum harvest age and piece size often drive merchantability and the available wood supply. As harvest constraints increase, the minimum harvest age on the coast has declined from 120 years to as low as 40 years in some coastal timber supply areas. This reduction in harvest age has led to harvest of smaller materials and in many cases it has not provided the time required to recreate the structural diversity that was once present in old-growth forest stands. Adoption of the British Columbia Forest Practices Code (which includes biodiversity guidelines) and the application of variable retention and non-clearcut silvicultural systems has provided more emphasis on the maintenance of forest structure in coastal British Columbia. More research is required to determine if these approaches appropriately mimic natural stand succession and overstory structure development. There are a number of unanswered questions related to the spatial and temporal distribution of the structures retained in these types of silviculture systems and whether they adequately mimic those present in undisturbed old growth.

Literature Cited

- Arsenault, A.; Bradfield, G. E. 1995. Structural-compositional variation in three age-classes of temperate rainforests in southern coastal British Columbia. Canadian Journal of Botany 73:54-64.
- Baskerville, G.L. 1972. Use of logarithmic regression in the estimation of plant biomass. Canadian Journal of Forest Research 2:49-53.
- Beese, W.J.; Sanford, J.S. 1992 Age of old-growth forests on Vancouver Island. Contract Report. B.C. Ministry of Forests. 29 p.
- Bingham, B.B.; Sawyer, J.O. Jr. 1991. Distinctive features and definitions of young, mature, and old-growth douglas-fir/hardwood forests. pages 363-378 *in* Leonard F. Ruggiero, Keith B. Aubry, Andrew B. Carey, and Mark H. Huff, tech. eds. Wildlife and vegetation of unmanaged Douglas-fir forests. USDA Forest Service, Pacific Northwest Research Station, Portland, OR, General Technical Report PNW-GTR-285.
- British Columbia Ministry of Forests, 2001. Mensuration data from the provincial ecology program. For. Sci. Prog., B.C. Min. For., Victoria, B.C. Work. Pap. 62/2001.Burns, R.M.; Honkala, B.H.. 1990. Silvics of North America. Volume 1, Conifers. USDA Forest Service. Agriculture Handbook 654. 675 p.
- Carey, A.B. 1998. Ecological foundations of biodiversity: Lessons from natural and managed forests of the Pacific Northwest. Northwest Science (Special issue) 72(2): 127-133.
- Clutter, J.L.; Fortson, J.C.; Pienaar, L.V.; Bristar, G.H.; Bailey, R.L. 1983. Timber management: A quantitative approach. John Wiley & Sons, Inc., New York.
- Cobb, D.F.; O Hara, K.L.; Oliver, C.D. 1993. Effects of variations in stand structure on development of mixed-species stands in eastern Washington. Canadian Journal of Forest Research 23: 545-552.
- Crowell, M.; Freedman, B. 1994. Vegetation development in a hardwood-forest chronosequence in Nova Scotia. Canadian Journal of Forest Research 24: 260-271.
- Feller, M.C.; Blackwell, B.A. 1989. The conversion of multistoried brush fields to coniferous plantations

 a benchmark evaluation of alternative silvicultural treatments. FRDA 2.6 Prescribed fire and soil studies. Final Report. Faculty of Forestry, University of British Columbia, Vancouver.
- Franklin, J. F.; Spies, T.A. 1991a. Ecological definitions of old-growth Douglas-fire forests. pages 61-69 in Leonard F. Ruggiero, Keith B. Aubry, Andrew B. Carey, and Mark H. Huff, tech. eds. Wildlife and vegetation of unmanaged Douglas-fir forests. USDA Forest Service, Pacific Northwest Research Station, Portland, OR, General Technical Report PNW-GTR-285
- Franklin, J. F.; Spies, T.A. 1991b. Composition, function, and structure of old-growth Douglas-fir forests. pages 71-82 *in* Leonard F. Ruggiero, Keith B. Aubry, Andrew B. Carey, and Mark H. Huff, tech. eds. Wildlife and vegetation of unmanaged Douglas-fir forests. USDA Forest Service, Pacific Northwest Research Station, Portland, OR, General Technical Report PNW-GTR-285
- Franklin, J.F.; Cromack, K.; Denison, W.; Mckee, A.; Maser, C.; Sedell, J.; Swanson, F.; Juday; G. 1981. Ecological characteristics of old-growth Douglas-fir forests. USDA Forest Service, Pacific Northwest Research Station, Portland, OR, General Technical Report PNW-118.
- Frelich, L.E.; Lorimer, C.G. 1985. Current and predicted long-term effects of deer browsing in hemlock forests in Michigan, USA. Biological Conservation 34: 99-120.

- Gholz, H.L.; Grier, C.C.; Campbell, A.G.; Brown, A.T. 1979. Equations for estimating biomass and leaf area of plants in the Pacific Northwest. Oregon State University, Forest Research Laboratory, Research Paper 41.
- Goebel, P.C.; Hix, D.M. 1996. Development of mixed-oak forests in southeastern Ohio: a comparison of second-growth and old-growth forests. Forest Ecology and Management 84: 1-21.
- Green, R.N.; Klinka, K. 1994. A field guide for site identification and interpretation for the Vancouver Forest Region.British Columbia Ministry of Forests, Land Management Handbook 28. Victoria, B.C.
- Gulyas, G.; Elm, T.J; Akhurst, P. 1998. Structural attributes of forest stands. Contract report prepared for Forest Practices Branch. B.C. Ministry of Forests. Simon Reid Collins, Vancouver, B.C.
- Kimmins, J.P. 1997. Biodiversity and its relationship to ecosystem health and integrity. Forestry Chronicle 73(2): 229-232
- Kneeshaw, D.; Burton, P. 1998. Assessment of functional old growth status: a case study in the Sub-Boreal Spruce zone of British Columbia, Canada. Natural Areas Journal 18: 293-308.
- Lertzman, K.P. 1992. Patterns of gap-phase replacement in subalpine, old-growth forest. Ecology 73: 657-669.
- Lertzman, K.P.; Krebs, C.J. 1991. Gap-phase structure of subalpine old-growth forest. Canadian Journal of Forest Research 21: 1730-1741.
- MacKinnon, A.; Vold, T. 1998. Old-growth forests inventory for British Columbia, Canada. Natural Areas Journal 18: 309-318.
- Meidinger, D.; Pojar, J. (eds.) 1991. Ecosystems of British Columbia. Special Report, Series 6. B.C. Ministry of Forests. Research Branch. Victoria, B.C.
- Miller, R.G., Jr. 1986. Beyond ANOVA, basics of applied statistics. John Wiley & Sons, New York.
- Morrison, M.L.; Raphael, M.G. 1993. Modeling the dynamics of snags. Ecological Applications 3: 322-330.
- Norland, E.R.; Hix, D.M. 1996. Composition and structure of a chronosequence of young, mixed-species forests in southeastern Ohio, USA. Vegetation 125:11-30.
- Oliver, C.D. 1982. Stand development–its uses and methods of study. Pages 197-200 *in* J. E. Mean, ed. Forest Succession and Stand Development Research in the Northwest. Symposium proceedings. Oregon State University, Corvallis, Oregon.
- Oliver, C.D.; Larson, B.C. 1990. Forest stand dynamics. McGraw-Hill, Inc. New York.
- Pollard, D.F.W.; Trofymow, J.A. 1993. An introduction to the coastal forest chronosequences. pages 5-7 *in* V. Marshall, compiler. Proceedings of the Forest Ecosystem Dynamics Workshop. Feb. 10 11, 1993.
 FRDA Rep. 210. Forestry Canada and British Columbia Ministry of Forests, Victoria.
- Quesnel, H. 1996. Assessment and characterization of old-growth stands in the Nelson Forest Region. Technical Report TR-013. B.C. Ministry Forests, Forest Sciences Section, Nelson Forest Region. Nelson, B.C.
- Spies, T.A.; Franklin, J.F. 1988. Old-growth and forest dynamics in the Douglas-fir forests region of western Oregon and Washington. Natural Areas Journal 8: 190-201.

- Spies, T.A.; Franklin, J.F. 1991. The structure of natural young, mature and old-growth Douglas-fir forests in Oregon and Washington. Pages 91-109 *in* Leonard F. Ruggiero, Keith B. Aubry, Andrew B. Carey, and Mark H. Huff, tech. eds. Wildlife and vegetation of unmanaged Douglas-fir forests. USDA Forest Service, Pacific Northwest Research Station, Portland, OR, General Technical Report PNW-GTR-285
- Standish, J.T.; Manning, G.H.; Demaerschalk, J.P. 1985. Development of biomass equations for British Columbia tree species.. Agriculture Canada, Ministry of State for Forestry, Pacific Forestry Centre, Victoria, B.C. Information Report BC-X-264. 47 p.
- Timoney, P.K.; Robinson, A.L. 1996. Old-growth white spruce and balsam poplar forests of the Peace River Lowlands, Wood Buffalo National Park, Canada: development, structure, and diversity. Forest Ecology and Management 81:179-196.
- Trofymow, J.A. and A. MacKinnon (ed.). Structure, Process, and Diversity in Successional Forests of Coastal British Columbia: Proceedings of a Workshop. Feb. 17 - 19, 1998. Victoria, B.C. Northwest Science. Vol. 72 Special Issue No. 2
- Trofymow, J.A.; Porter, G.L.; Blackwell, B.A.; Marshall, V.; Arskey, R.; Pollard, D. 1997. Chronosequences selected for research into the effects of converting coastal British Columbia old-growth forest to managed forests: An establishment report. Canadian Forest Service, Pacific Forestry Centre, Victoria, B.C., Information Report BC-X-374. 137 p.
- Tyrrell,L.E.; Crow, T.R., 1994. Structural characteristics of old-growth hemlock-hardwood forests in relation to age. Ecology 75: 370-386.
- Wells, R.W.; Lertzman, K.P.; Saunders, S.C. 1998. Old growth definitions for forests of British Columbia, Canada. Natural Areas Journal 18:279-292.
- Wells R.W.; Trofymow, J.A. 1997. Coarse woody debris in chronosequences of forests on southern Vancouver Island. Canadian Forest Service, Pacific Forestry Centre, Victoria, B.C., Information Report BC-X-375. 35 p.
- Wilkinson, L. 1988. SYSTAT: the system for the statistics. SYSTAT Inc., Evanston, Ill.
- Zar, J.H. 1984. Biostatistical analysis. 2nd ed. Prentice-Hall Inc., Englewood Cliffs, N.J.

Site	Plot no.	Age ^a class	Age	Tree d	liameter	(cm) ^b	Tre	e height	(m)	Crow	wn depth	(m)
				Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
						С	WHxm su	bzone (e	ast side)			
Victoria Watershed South	1	R	4	<1.0	<1.0	<1.0	0.9	0.2	3.7	na ^c	na	na
	2	I	32	7.8	<1.0	36.6	8.3	1.8	22.6	3.6	<1.0	19.6
	5	M	99	24.6	<1.0	83.3	21.7	0.4	50.1	7.1	<1.0	25.2
	6	O	245	28.8	<1.0	119.8	19.4	0.6	58.4	7.7	<1.0	33.5
Victoria Watershed North	11	R	6	<1.0	<1.0	<1.0	1.2	0.4	2.6	na	na	na
	12	I	42	16.4	5.2	29.4	18.2	9.0	23.5	5.8	0.4	11.6
	13	M	93	19.0	<1.0	55.0	17.6	1.4	37.6	5.8	<1.0	17.4
	15	O	316	35.2	<1.0	92.2	22.3	0.6	47.4	5.2	<1.0	19.1
Koksilah	21	R	5	<1.0	<1.0	<1.0	0.4	0.2	0.6	na	na	na
	22	I	43	6.2	<1.0	32.6	6.7	0.3	20.8	2.3	<1.0	12.2
	23	M	77	13.7	3.6	35.7	12.8	3.7	27.3	3.3	<1.0	11.2
	24	O	288	37.0	<1.0	89.3	19.4	1.4	35.9	6.3	<1.0	14.5
Nanaimo River	31 35 33 34	R I M O	10 39 68 330	0.2 4.3 11.1 14.2	<1.0 <1.0 <1.0 <1.0	5.6 29.5 89.8 95.2	1.0 4.8 9.1 7.7	$0.1 < 1.0 \\ 0.7 \\ 1.0$	3.5 22.8 41.5 38.8	na 2.1 3.6 3.9	na <1.0 <1.0 <1.0	na 14.1 20.1 40.2
						C	WHvm su	bzone (v	vest side)			
Renfrew	51	R	4	0.4	<1.0	5.2	1.9	0.3	4.3	na	na	na
	52	I	42	17.2	5.0	35.6	19.7	8.1	32.4	5.7	0.5	13.7
	53	M	66	37.9	14.5	97.2	35.2	15.4	46.0	11.2	3.0	21.3
	54	O	255	32.0	<1.0	118.0	18.7	1.0	33.1	7.4	<1.0	17.3
Red/Granite Creek	61	R	9	1.7	<1.0	8.3	2.4	0.4	6.8	na	na	na
	62	I	43	15.9	5.7	49.9	15.4	5.3	31.4	5.5	0.9	18.9
	63	M	76	31.4	11.1	46.2	33.1	11.3	42.7	9.5	0.3	18.1
	64	O	176	25.9	<1.0	211.0	15.5	1.6	58.8	7.0	<1.0	35.2
Nitinat	71	R	9	0.4	<1.0	5.2	1.2	0.1	4.4	na	na	na
	72	I	39	13.6	<1.0	51.1	12.2	0.9	34.9	5.3	<1.0	17.3
	73	M	70	30.9	<1.0	82.0	25.5	1.5	44.7	8.2	<1.0	22.7
	74	O	270	19.3	<1.0	119.0	13.3	0.4	52.1	6.4	<1.0	37.9
Klanawa	81	R	3	<1.0	<1.0	<1.0	0.3	0.2	0.5	na	na	na
	82	I	32	17.4	<1.0	45.7	15.9	0.9	26.2	6.2	<1.0	14.9
	83	M	69	10.2	<1.0	81.6	9.2	0.7	50.2	3.0	<1.0	14.2
	84	O	445	47.3	4.6	275.0	19.4	3.2	53.3	9.3	<1.0	33.6

Table 1. Names, numbers, ages and tree characteristics of the Canadian Forest Service Coastal Forest Chronosequences plots studied.

^a Age class: R = regeneration, I = immature, M = mature, O = old growth

^b Tree diameters are at DBH (1.3 m height)

^c na - tree crown depths were not measured in regeneration plots

Tree species/component	Tree diameter	Regression equation ^a	n	r^2	I^2
Douglas-fir ^b	DBH (4.5-66 cm)	2			
Stemwood		$mass = 10.3 + 110.4 (DBH_2)Ht$	49	0.99	
Stembark		mass = $3.1 + 15.6 (DBH^2)Ht$	49	0.98	
Douglas-fir ^C	DBH (> 66.0 cm)				
Stemwood		mass = -3.0396 + 2.5951 ln (DBH)	99		0.99
Stembark		mass = -4.3103 + 2.4300 ln (DBH)	99		0.99
Western redcedar ^b	DBH (3.8 - 68.9 cm)	1			
Stemwood	· · · · · · · · · · · · · · · · · · ·	$mass = 17.5 + 68.4 (DBH_2^2)Ht$	70	0.95	
Stembark		mass = $3.3 + 9.0 (DBH^2)Ht$	70	0.83	
Western hemlock ^b	DBH (3.1 - 70.5 cm)				
Stemwood	(**** , **** ****)	$mass = 5.5 + 123.3 (DBH_{2}^{2})Ht$	70	0.99	
Stembark		mass = 3.0 + 16.0 (DBH2)Ht	70	0.92	
Amabilis fir ^b	DBH (4.5-30.4 cm)				
Stemwood	(Mass = $1.4 + 122.9 (DBH^2)Ht$	45	0.96	
Stembark		Mass = $1.0 + 15.6 (DBH^2)$ Ht	45	0.94	
Grand fir ^b	DBH (4.6-43.9cm)				
Stemwood		Mass = $5.9 + 105.7 (DBH^2)Ht$	40	0.95	
Stembark		Mass = 0.6 + 16.4 (DBH2)Ht	40	0.79	
Red alder ^d	DBH (0-30 cm)				
Stemwood	() = 0 = 0 = 0 = 0 = 0 = 0 = 0 = 0 = 0 =	$Mass = -2.020 + 2.125 \ln (DBH)$	11		0.96
Stembark		$Mass = -3.755 + 1.917 \ln (DBH)$	11		0.93

Table 2.Regression equations used to estimate stem biomass (Mg ha⁻¹).

^a All logarithmic equations have been corrected for logarithmic bias according to the method of Baskerville (1972). Variables are as follows: n= number of data points used to develop the equation; $r^2 = coefficient$ of determination; $I^2 = index$ of fit.; DBH= diameter at breast height in meters for linear equations and centimeters for logarithmic equations.; Ht. = tree height in meters.

^b Equations obtained from Standish *et al.* (1985).

^c Equations obtained from Gohlz *et al.* (1979).

^d Equations obtained from Feller and Blackwell (1989).

		Live ste hect	1	Stem bio per heo		Snags hecta	1	Snag : per he		Stem I area hecta	per	Spec compo by basa	sition	Spec compo by st den	osition tand
		F-		F-		F-		F-		F-		F-		F-	
Species	Source	Ratio	P ^d	Ratio	Р	Ratio	Р	Ratio	Р	Ratio	Р	Ratio	Р	Ratio	Р
All	Subzonea	5.89	0.02	0.90	0.35	0.56	0.46	2.72	0.11	1.60	0.22	-	-	-	-
	Age Class ^b	4.15	0.02	20.33	0.00	3.76	0.02	2.58	0.08	17.48	0.00	-	-	-	-
	$S \times AC$	2.75	0.07	0.14	0.94	1.55	0.23	0.52	0.67	1.28	0.30	-	-	-	-
Douglas-fir	Subzone	27.40	0.00	95.20	0.00	7.38	0.01	11.46	0.00	51.80	0.00	85.051	0.000	36.905	0.000
	Age Class	3.18	0.04	21.49	0.00	2.41	0.09	2.15	0.12	24.77	0.00	1.957	0.153	0.257	0.855
	$S \times AC$	2.50	0.08	25.44	0.00	2.41	0.09	2.15	0.12	28.26	0.00	1.063	0.387	0.187	0.904
Western hemlock	Subzone	4.65	0.04	71.66	0.00	3.03	0.10	7.33	0.01	61.59	0.00	37.027	0.000	26.032	0.000
	Age Class	1.01	0.41	15.74	0.00	2.28	0.11	1.26	0.31	12.69	0.00	2.350	0.103	1.204	0.330
	$S \times AC$	1.38	0.27	12.84	0.00	1.94	0.15	1.19	0.34	8.31	0.00	1.678	0.204	0.754	0.531
Western redcedar	Subzone	0.51	0.48	3.28	0.08	7.47	0.01	3.64	0.07	4.12	0.05	10.214	0.005	0.001	0.970
	Age Class	1.55	0.23	3.36	0.04	4.54	0.01	1.61	0.21	4.46	0.01	11.650	0.000	1.029	0.397
	$S \times AC$	1.24	0.32	3.24	0.04	4.62	0.01	1.41	0.26	4.10	0.02	10.573	0.000	0.524	0.670
Amabilis fir	Subzone	2.20	0.15	6.13	0.02	2.28	0.14	3.06	0.09	6.31	0.02	3.039	0.097	4.189	0.052
	Age Class	0.86	0.48	1.67	0.20	1.80	0.17	1.12	0.36	1.54	0.23	1.106	0.370	1.159	0.346
	$S \times AC$	0.79	0.51	1.67	0.20	1.80	0.17	1.12	0.36	1.54	0.23	1.106	0.370	1.118	0.361
Red alder	Subzone	1.24	0.28	0.88	0.36	0.17	0.68	0.29	0.60	0.89	0.36			0.078	0.408
	Age Class	1.22	0.32	0.98	0.42	1.26	0.31	1.50	0.24	0.99	0.42	0.611	0.616	1.126	0.358
	$S \times AC$	1.11	0.37	1.09	0.37	0.10	0.96	0.30	0.83	1.10	0.37	0.678	0.576	1.077	0.378
Other (Western yew,	Subzone	2.59	0.12	-	-	1.00	0.33	-	-	0.95	0.34	0.575	0.457	1.136	0.354
western white pine,	Age Class	1.11	0.37	-	-	1.00	0.41	-	-	0.96	0.43	0.760	0.530	1.844	0.187
Sitka spruce, and grand fir),	$S \times AC$	0.53	0.67	-	-	1.00	0.41	-	-	1.02	0.40	0.789	0.514	0.412	0.746
Western yew	Subzone	2.24	0.15	-	-	-	-	-	-	1.00	0.33	0.588	0.452	3.085	0.092
	Age Class	0.87	0.47	-	-	-	-	-	-	1.00	0.41	0.782	0.518	1.203	0.330
	$S \times AC$	0.87	0.47	-	-	-	-	-	-	1.00	0.41	0.782	0.518	1.203	0.330
Western white pine	Subzone	5.67	0.03	-	-	-	-	-	-	2.61	0.12	1.176	0.291	3.728	0.065
-	Age Class	0.77	0.53	-	-	-	-	-	-	0.89	0.46	0.453	0.718	0.724	0.548
	$S \times AC$	0.77	0.53	-	-	-	-	-	-	0.89	0.46	0.453	0.718	0.724	0.548
Sitka spruce	Subzone	1.20	0.29	-	-	-	-	-	-	1.00	0.33	0.588	0.452	1.357	0.256
	Age Class	0.85	0.48	-	-	-	-	-	-	1.00	0.41	0.782	0.518	0.813	0.499
	$S \times AC$	0.93	0.44	-	-	-	-	-	-	1.00	0.41	0.782	0.518	0.881	0.465
Grand fir	Subzone	1.60	0.22	-	-	-	-	-	-	-	-			1.479	0.236
	Age Class	0.80	0.51	-	-	-	-	-	-	-	-			0.840	0.485
	$S \times AC$	0.80	0.51	-	-	-	-	-	-	-	-			0.840	0.485

Table 3.Summary of F statistics and probability values for the effect of subzone and age class on
number of live stems per hectare, stem biomass, snags per hectare, snag mass, stem basal area
and % species composition by basal area and stand density.

^a Subzone = CWHxm, CWHvm

^b Age Class (AC) = Regeneration, Immature, Mature, Old growth.

^c Probability values < 0.05 are in boldface; those < 0.10 are underlined.

Degrees of freedom: subzone = 1, age class = 3, subzone \times age class = 3, error = 24.

Site	Plot	Age class	Live stems per ha	Stem biomass in Mg ha ⁻¹	Snags per ha	Snag mass in Mg ha ⁻¹	Stem basal area in m ² ha ⁻¹
				CWHx	am subzone	(east side)	
Victoria Watershed							
South	1	Regeneration	1428	0.0	0	0.00	0
	2	Immature	2688	106.5	714	6.58	29
	5	Mature	2689	610.3	210	18.90	86
	6	Old growth	1080	741.0	242	45.33	79
Victoria Watershed							
North	11	Regeneration	1008	0.0	0	0.00	0
	12	Immature	2058	181.5	504	8.96	49
	13	Mature	1407	333.9	357	8.04	64
	15	Old growth	815	537.0	66	4.93	89
Koksilah							
	21	Regeneration	756	0.0	0	0.00	0
	22	Immature	5964	162.6	42	0.61	41
	23	Mature	3318	220.0	1386	20.82	57
	24	Old growth	550	528.8	55	10.86	86
Nanaimo River							
	31	Regeneration	3528	2.4	0	0.00	0
	35	Immature	5838	117.3	294	4.13	29
	33	Mature	4200	526.8	420	13.28	92
	34	Old growth	2254	537.0	126	3.35	69
				CWHv	m subzone	(west side)	
Renfrew						· /	
	51	Regeneration	2184	2.1	0	0.00	0
	52	Immature	1512	209.8	3108	64.75	40
	53	Mature	539	498.0	429	16.41	74
	54	Old growth	644	275.0	280	53.68	85
Red/Granite Creek		See Stowald		2.0.0	_00		
	61	Regeneration	1806	8.3	0	0.00	0
	62	Immature	1806	188.6	882	12.17	48
	63	Mature	882	512.9	504	39.52	76
	64	Old growth	594	635.8	33	8.51	90
Nitinat		U					
	71	Regeneration	1848	2.9	0	0.00	0
	72	Immature	2394	278.7	0	0.00	64
	73	Mature	561	432.1	99	3.13	63
	74	Old growth	2309	523.0	88	15.34	78
Klanawa							
	81	Regeneration	2646	0.0	0	0.00	0
	82	Immature	1806	251.6	798	17.56	63
	83	Mature	2478	411.7	378	78.69	66
					44		
	84	Old growth	517	1315.3	44	10.36	248

Table 4.	Numbers of live stems per hectare, stem biomass, snags per hectare, snag mass, and stem
	basal area in each plot.

	С	WHvm su	bzone (we	est side)			CWHxr	n subzone (east side)	
		Age cl	ass ^a				Age	class ^a		
Species	R	Ι	М	0	Mean	R	Ι	М	0	Mean
Douglas-fir	170 (104)	202 (150)	0 (0)	0 (0)	93 (34)	1082 (626)	2387 (516)	1814 (592)	431 (34)	1429 (208)
Western hemlock	1114	1199	544	650	877	95	700	474	580	462
	(234)	(115)	(123)	(291)	(83)	(95)	(383)	(424)	(295)	(111)
Western redcedar	700	361	3	132	299	286	1093	426	47	463
	(467)	(106)	(3)	(68)	(90)	(191)	(657)	(377)	(25)	(142)
Amabilis fir	32	42	568	187	207	0	0	11	0	3
	(0)	(0)	(728)	(141)	(96)	0)	(0)	na	(0)	(2)
Red alder	42	85	0	0	32	32	0	4	3	10
	(0)	(60)	(0)	(0)	(13)	(0)	(0)	(0)	(0)	(6)
Other	85	11	0	38	33	202	0	202	106	117
	(60)	(0)	(0)	(44)	(13)	(105)	(0)	(15)	(0)	(34)
Total	2143	1899	1114	1006	1541	1697	4180	2930	1166	2494
	(196)	(187)	(471)	(433)	(142)		(638)	(1038)	(593)	(386)

Table 5Mean stems per hectare of tree species within and across age class for the CWHvm and
CWHxm subzones. Standard errors are given in parentheses.

^aAge classes: R = Regeneration; I = Immature; M = Mature; O = Old growth.

Table 6Mean stem biomass per hectare of tree species within and across age class for the
CWHvm and CWHxm subzones. Standard errors are given in parentheses. Stem biomass
was calculated for major species only for stems of DBH greater than 1.0 cm.

		CWHvm s	ubzone (v	west side)			CWHxm	subzone (e	east side)	
		Age	class ^a				Age	class ^a		
Species	R	Ι	М	0	Mean	R	Ι	М	0	Mean
Douglas-fir	1.8 (1.4)	54.5 (46.6)	0.0 (0.0)	0.0 (0.0)	14.1 (8.5)	0.6 (0.6)	129.3 (21.6)	393.3 (79.0)	565.1 (47.9)	272.1 (43.0)
Western hemlock	1.3	139.2	419.4	340.3	225.0	0.0	9.0	23.8	14.4	11.8
	(0.5)	(40.4)	(36.5)	(81.2)	(33.8)	(0.0)	(6.6)	(23.1)	(4.9)	(4.2)
Western redcedar	0.2	9.4	0.3	325.0	83.8	0.0	3.7	4.6	5.8	3.5
	(0.2)	(2.7)	(0.3)	(177.1)	(37.8)	(0.0)	(3.4)	(2.5)	(2.9)	(0.9)
Amabilis fir	0.0	7.9	44.0	22.0	18.58	0.0	0.0	0.0	0.0	0.0
	(0.0)	(7.9)	(26.2)	(11.8)	(5.6)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)
Red alder	0.1	21.0	0.0	0.0	5.3	0.0	0.0	1.0	0.6	0.4
	(0.1)	(20.6)	(0.0)	(0.0)	(3.7)	(0.0)	(0.0)	(1.0)	(0.6)	(0.2)
Total	3.3	232.2	463.7	687.2	346.6	0.6	142.0	422.8	585.9	287.8
	(1.8)	(20.3)	(24.7)	(222.5)	(58.6)	(0.6)	(17.9)	(89.0)	(51.7)	(45.1)

^aAge classes: R = Regeneration; I = Immature; M = Mature; O = Old growth.

	C	WHvm sub	zone (we	st side)			CWHxm	subzone (e	east side)		
		Age cla	ss ^a				Age class ^a				
Species	R	Ι	М	0	Mean	R	Ι	М	0	Mean	
Douglas-fir	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	297 (114)	525 (295)	37 (9)	215 (63)	
Western hemlock	0	997	247	69	328	0	74	64	74	53	
	(0)	(618)	(80)	(34)	(123)	(0)	(61)	(64)	(50)	(17)	
Western redcedar	0	180	5	36	56	0	0	0	5	1	
	(0)	(74)	(5)	(27)	(18)	(0)	(0)	(0)	(5)	(1)	
Amabilis fir	0	0	56	5	15	0	0	0	0	0	
	(0)	(0)	(40)	(5)	(8)	(0)	(0)	(0)	(0)	(0)	
Red alder	0	32	21	0	13	0	21	11	3	9	
	(0)	(32)	(21)	(0)	(7)	(0)	(21)	(11)	(3)	(4)	
Other	0	0	21	0	5	0	0	0	0	0	
	(0)	(0)	(21)	(0)	(4)	(0)	(0)	(0)	(0)	(0)	
Total	0	1210	350	111	418	0	393	599	119	278	
	(0)	(674)	(89)	(59)	(138)		(0)	(145)	(271)	(41)	

Table 7Mean number of snags per hectare of tree species within and across age class for the
CWHvm and CWHxm subzones. Standard errors are given in parentheses.

^aAge classes: R = Regeneration; I = Immature; M = Mature; O = Old growth.

Table 8	Mean snag mass per hectare of tree species within and across age class for the CWHvm
	and CWHxm subzones. Standard errors are given in parentheses. Snag mass was
	calculated for major species only for snags of DBH greater than 1.0 cm.

	C	WHvm su	bzone (we	est side)			CWHxm	subzone (e	ast side)	
		Age cl	ass ^a				Age o	class ^a		
Species	R	Ι	М	0	Mean	R	Ι	М	0	Mean
Douglas-fir	0.0	0.0	0.0	0.0	0.0	0.0	4.5	13.1	14.6	8.1
	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(1.7)	(2.7)	(8.9)	(1.9)
Western hemlock	0.0	19.3	28.7	12.8	15.2	0.0	0.5	0.5	0.9	0.5
	(0.0)	(13.1)	(16.7)	(5.1)	(3.9)	(0.0)	(0.4)	(0.5)	(0.7)	(0.2)
Western redcedar	0.0	3.8	0.2	8.2	3.0	0.0	0.0	0.0	0.3	0.1
	(0.0)	(1.5)	(0.2)	(6.0)	(1.2)	(0.0)	(0.0)	(0.0)	(0.3)	(0.1)
Amabilis fir	0.0	0.0	1.5	1.0	0.6	0.0	0.0	0.0	0.0	0.0
	(0.0)	(0.0)	(1.1)	(1.0)	(0.3)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)
Red alder	0.0	0.5	4.0	0.0	1.1	0.0	0.1	1.7	0.4	0.5
	(0.0)	(0.5)	(4.0)	(0.0)	(0.7)	(0.0)	(0.1)	(1.7)	(0.4)	(0.3)
Total	0.0	23.6	34.4	22.0	20.0	0.0	5.1	15.3	16.1	9.1
	(0.0)	(14.2)	(16.6)	(10.7)	(4.5)	(0.0)	(1.8)	(2.9)	(9.9)	(2.1)

^aAge classes: R = Regeneration; I = Immature; M = Mature; O = Old growth.

		CWHvm	subzone ((west side)			subzone (east side)		
		Age	class ^a				Age	class ^a		
Species	R	Ι	М	0	Mean	R	Ι	М	0	Mean
Douglas-fir	0.30	12.18	0.00	0.00	3.12	0.05	36.41	69.28	75.96	45.43
	(0.26)	(10.42)	(0.00)	(0.00)	(1.90)	(0.05)	(5.63)	(4.28)	(5.48)	(5.69)
Western hemlock	0.12	31.77	60.48	49.79	35.54	0.00	2.50	7.03	3.88	3.35
	(0.05)	(8.73)	(6.41)	(10.00)	(4.78)	(0.00)	(1.80)	(6.84)	(1.32)	(1.23)
Western redcedar	0.01	2.68	0.14	73.90	19.18	0.00	0.75	1.88	2.45	1.27
	(0.01)	(0.90)	(0.14)	(35.25)	(8.02)	(0.00)	(0.73)	(1.02)	(1.17)	(0.32)
Amabilis fir	0.00	2.07	8.52	4.18	3.69	0.00	0.00	0.00	0.00	0.00
	(0.00)	(2.07)	(5.03)	(2.23)	(1.09)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)
Red alder	0.02	7.28	0.00	0.00	1.83	0.00	0.00	0.36	0.22	0.15
	(0.02)	(7.11)	(0.00)	(0.00)	(1.26)	(0.00)	(0.00)	(0.36)	(0.22)	(0.07)
Other	0.00	1.02	0.00	0.02	0.26	0.00	0.00	0.02	0.02	0.01
	(0.00)	(1.02)	(0.00)	(0.02)	(0.18)	(0.00)	(0.00)	(0.01)	(0.02)	(0.00)
Total	0.45	57.01	69.13	127.88	63.62	0.05	39.66	78.57	82.54	50.20
	(0.29)	(4.60)	(2.99)	(40.76)	(10.52)		(0.05)	(4.76)	(8.15)	(4.57)

Table 9Mean stem basal area (m²) per hectare of tree species within and across age class for the
CWHvm and CWHxm subzones. Standard errors are given in parentheses. Basal area
was calculated using DBH measurements for stems of DBH greater than 1.0 cm.

^aAge classes: R = Regeneration; I = Immature; M = Mature; O = Old growth.

Table 10Mean stand-density-based percent tree species composition within and across age class
for the CWHvm and CWHxm subzones. Standard errors are given in parentheses.

	C	WHvm su	ıbzone (w	est side)		CWHxm subzone (east side)							
		Age cl	ass ^a				Age	class ^a					
Species	R	Ι	М	0	Mean	R	Ι	М	0	Mean			
Douglas-fir	9 (6)	9 (6)	0 (0)	0 (0)	5 (2)	58 (19)	62 (13)	66 (19)	50 (17)	59 (8)			
Western hemlock	54	65	73	64	64	3	20	12	40	19			
	(12)	(9)	(20)	(12)	(7)	(3)	(14)	(10)	(13)	(6)			
Western redcedar	29	18	1	18	17	26	18	16	5	16			
	(17)	(4)	(1)	(11)	(5)	(19)	(11)	(14)	(3)	(6)			
Amabilis fir	2	2	27	15	11	0	0	0	0	0			
	(2)	(2)	(20)	(8)	(6)	(0)	(0)	(0)	(0)	(0)			
Red alder	2	4	0	0	2	2	0	0	0	1			
	(2)	(3)	(0)	(0)	(1)	(2)	(0)	(0)	(0)	(1)			
Other	4	1	0	2	1	11	0	б	5	5			
	(3)	(1)	(0)	(1)	(1)	(9)	(0)	(4)	(5)	(3)			
Total	100	100	100	100	100	100	100	100	100	100			

^aAge classes: R = Regeneration; I = Immature; M = Mature; O = Old growth.

		CWHvm su	ıbzone (w	/est side)			CWHxm	subzone (e	east side)	
		Age cla	ass ^a							
Species	R	Ι	М	0	Mean	R	Ι	М	0	Mean
Douglas-fir	49	19	0	0	15	100	91	90	92	92
	(25)	(16)	(0)	(0)	(8)	na	(6)	(7)	(3)	(3)
Western hemlock	36	57	87	45	58	0	8	7	5	6
	(16)	(16)	(8)	(11)	(8)	(0)	(6)	(7)	(2)	(3)
Western redcedar	4	5	0	52	16	0	2	2	3	2
	(4)	(2)	(0)	(12)	(7)	(0)	(2)	(1)	(1)	(1)
Amabilis fir	0	3	13	3	5	0	0	0	0	0
	(0)	(3)	(7)	(2)	(2)	(0)	(0)	(0)	(0)	(0)
Red alder	11	14	0	0	5	0	0	0	0	0
	(11)	(13)	(0)	(0)	(4)	(0)	(0)	(0)	(0)	(0)
Other	0	2	0	0	1	0	0	0	0	0
	(0)	(2)	(0)	(0)	(1)	(0)	(0)	(0)	(0)	(0)
Total	100	100	100	100	100	100	100	100	100	100

Table 11Mean basal-area-based percent tree species composition within and across age class for
the CWHvm and CWHxm subzones. Standard errors are given in parentheses.

^a Age classes: R = Regeneration; I = Immature; M = Mature; O = Old growth.

Old-growth attribute	Washington/Oregon	California	CWHvm	CWHxm	CWHvm
Number live stems by DBH class	All species > 100 cm DBH (> 10 stems/ha)	Douglas-fir >90 cm DBH (29 ± 3 stems/ha)	All species >100 cm (average 23.8 stems/ha)	One of four old-growth plots met criteria by Franklin and Spies (1991)	All four old-growth plots met criteria by Franklin and Spies (1991)
Number live stems by height class	Multilayered Canopy	Multilayered Canopy	NA	All old-growth plots met criteria by Franklin and Spies (1991)	All old-growth plots met criteria by Franklin and Spies (1991)
Number of snags/ha	> 4 snags/ha (> 5 m tall) (>50 cm DBH)	> 5 ± 2 snags/ha (>4 m tall) (>40 cm DBH)	> 10 snags/ha (>50 cm DBH)	All old-growth plots met criteria by Franklin and Spies (1991)	All old-growth plots met criteria by Franklin and Spies (1991)
Biomass of snags Mg/ha	NA	10 to 110	NA	22 Mg/ha	16.1 Mg/ha
Basal area m ² /ha	Old growth $69(\pm 5)m^2/ha$ Mature $34(\pm 5)m^2/ha$	NA NA	83 m²/ha NA	128 m ² /ha 79 m ² /ha	83 m²/ha 69 m²/ha

 Table 12.
 Comparison of structural attributes from old growth definitions for Washington/Oregon, California, and British Columbia with attributes of old-growth chronosequence plots in the CWHxm and CWHvm.

Note: Structural attributes for Washington and Oregon are summarized from Spies and Franklin (1988) and from Franklin and Spies (1991). Structural attributes for California are summarized from Bingham and Sawyer (1991) Structural attributes from British Columbia from MacKinnon (2001) Criteria by Franklin and Spies (1991) refer to criteria for old-growth definitions.

Appendix I

Weibull function parameters and R^2 for stand density by diameter, height, or crown depth and for basal area (m²) by diameter (DBH)

		Density b DBH cla	5			Density by height class		Density by crown depth class			Basal area by DBH class		
Subzone Age class	R ²	Ca	B ^b	R ²	C	В	R ²	C	В	R ²	С	В	
CWHxm Immature	0.736	1.924	1.794	0.445	1.160	2.073	0.873	2.240	1.399	0.848	3.390	2.811	
		(0.277)	(0.118)		(0.207)	(0.528)		(0.318)	(0.074)		(0.215)	(0.072)	
CWHxm Mature	0.834	1.523	1.393	0.458	1.108	2.274	0.927	2.074	1.178	0.335	2.216	4.467	
		(0.128)	(0.122)		(0.192)	(0.528)		(0.148)	(0.073)		(0.340)	(0.440)	
CWHxm Old growth	0.737	1.573	0.844	0.615	1.330	0.905	0.822	1.874	1.314	0.271	3.639	8.135	
		(0.146)	(0.108)		(0.136)	(0.154)		(0.219)	(0.109)		(0.591)	(0.490)	
CWHvm Immature	0.868	1.639	2.240	0.490	2.082	4.341	0.866	1.645	1.556	0.852	3.860	3.678	
		(0.115)	(0.113)		(0.261)	(0.316)		(0.136)	(0.110)		(0.244)	(0.075)	
CWHvm Mature	0.343	1.535	3.745	0.073	5.275	8.100	0.565	1.744	2.472	0.280	2.691	5.890	
		(0.304)	(0.513)		(1.435)	(0.330)		(0.278)	(0.256)		(0.418)	(0.502)	
CWHvm old-growth	0.700	1.292	1.061	0.499	1.005	1.509	0.808	1.619	1.154	0.426	26.070	11.615	
		(0.120)	(0.177)		(0.139)	(0.457)		(0.144)	(0.128)		(12.466)	(0.085)	

Table I-1.Weibull function parameters and R2 for stand density (stem/ha) by diameter (DBH),
height or crown depth class and for basal area (m2) by diameter (DBH) class. Functions
fit for each age class within a subzone.

Standard error in parentheses, n=4

^a C= scale parameter

^b B = shape parameter

Appendix II

Stems per hectare of species within diameter (DBH) class, for each plot

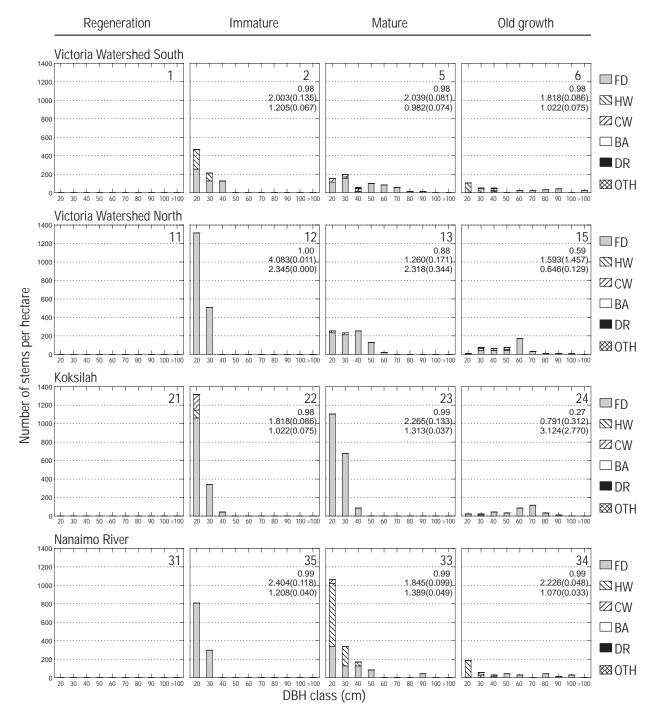


Figure II-1. Stems per hectare of species within diameter (DBH) classes 20-100 by age class within CWHxm sites. (all larger diameter stems are in the ">100" class)

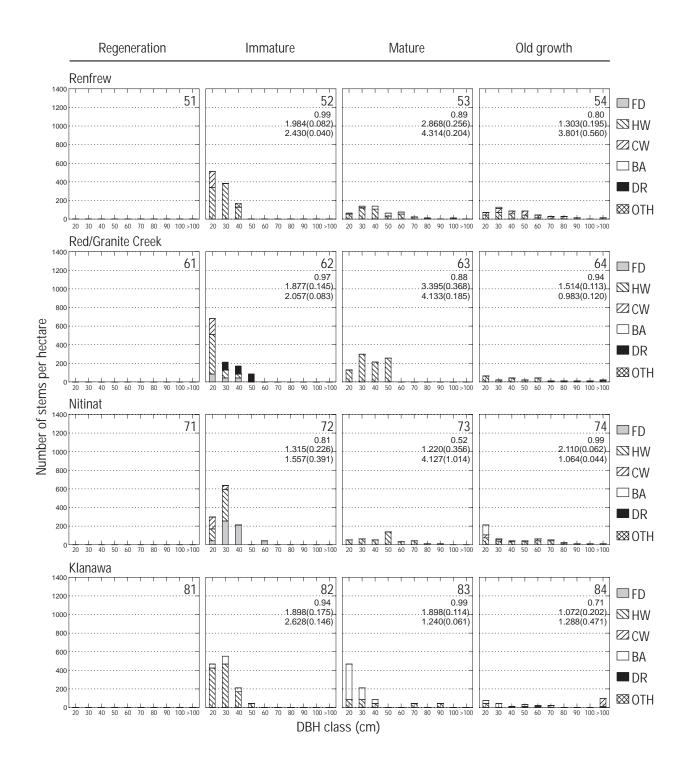


Figure II-2. Stems per hectare of species within diameter (DBH) classes 20-100 by age class within CWHvm sites. (all larger diameter stems are in the ">100" class)

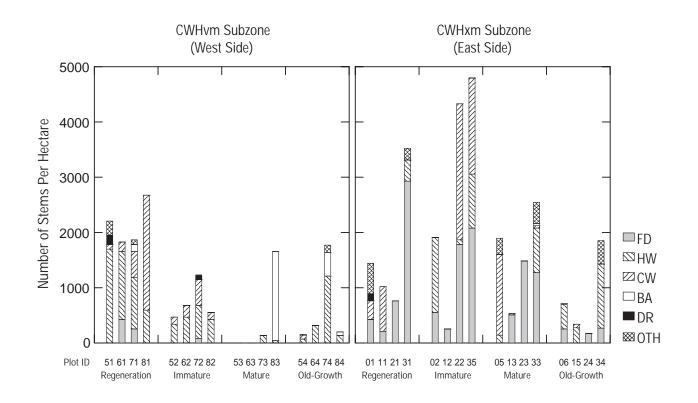


Figure II-3. Stems per hectare of species within diameter (DBH) class 10, by age class within subzone.

(Fd = Douglas-fir; Hw = western hemlock; Cw = western redcedar; Ba = amabilis fir; Dr = red alder; Oth = other)

Appendix III



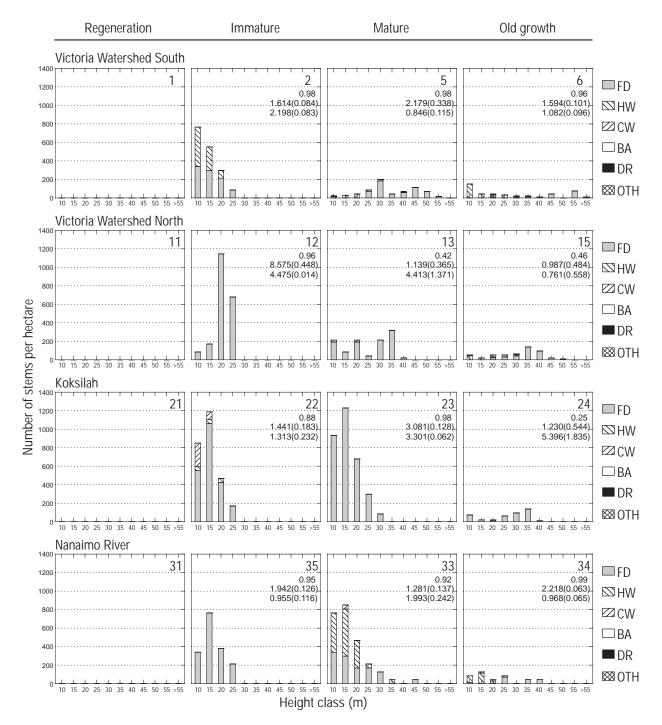


Figure III-1. Stems per hectare of species within height classes 10 - 55 by age class, within CWHxm sites (all stems over 55 m in height are in the ">55" class)

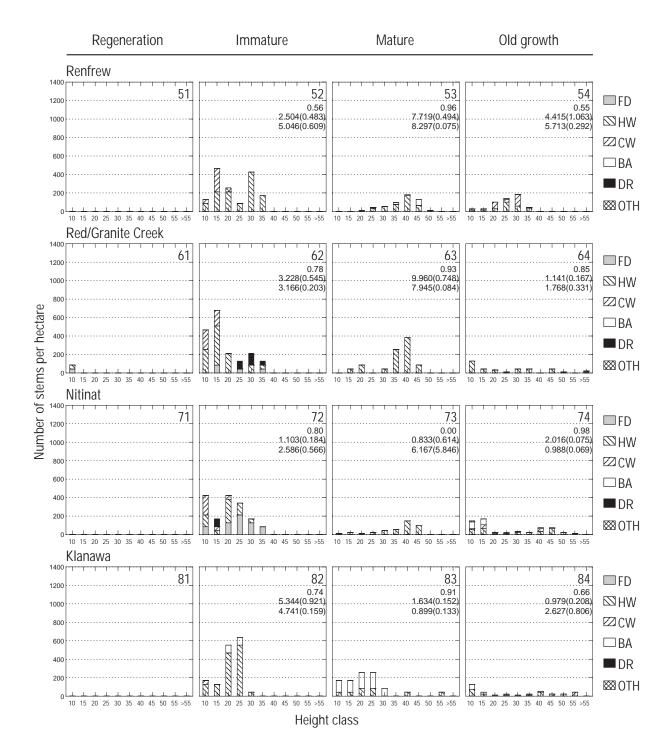
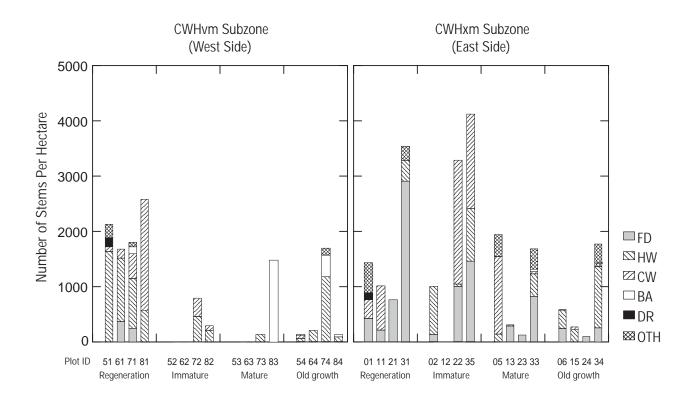


Figure III-2. Stems per hectare of species within classes 10 - 55 by age class, within CWHvm sites. (all stems over 55 m in height are in the ">55" class)





(Fd = Douglas-fir; Hw = western hemlock; Cw = western redcedar; Ba = amabilis fir; Dr = red alder; Oth = other)

Appendix IV

Stems per hectare of species within crown depth class, for each plot.

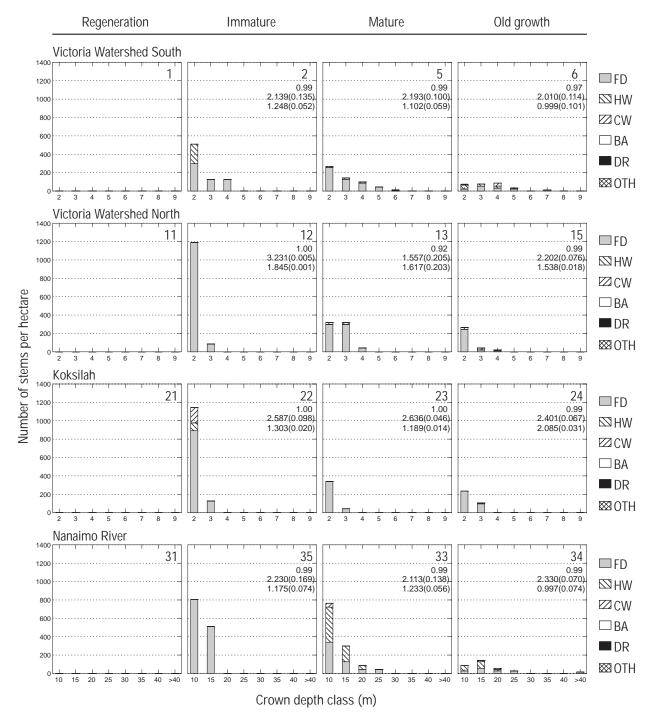


Figure IV-1. Stems per hectare of species within crown depth classes 10 - 40 by age class within CWHxm sites. (all stems with crown depth over 40 m are in the ">40" class)

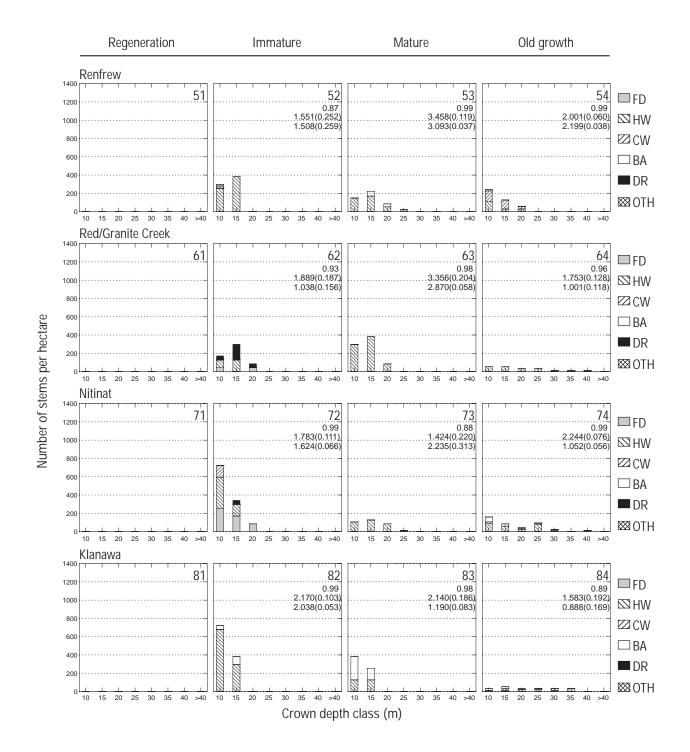


Figure IV-2. Stems per hectare of species within crown depth Classes 10 - 40 by age class within CWHvm sites. (all stems with crown depth over 40 m are in the ">40" class)

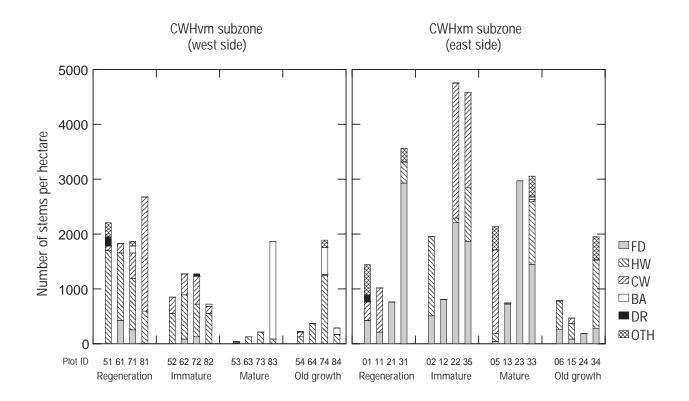


Figure IV-3. Stems per hectare of species within crown depth class 5 by age class within subzone.

(Fd = Douglas-fir; Hw = western hemlock; Cw = western redcedar; Ba = amabilis fir; Dr = red alder; Oth = other)

Appendix V

Stem biomass per hectare of species within size class, for each plot

С	WHvm sub	zone (wes	st side)		(CWHxm subzone (east side)					
		Age	class ^b			Age class ^b					
Size class ^a	R	Ι	М	0	Size Class	R	Ι	М	0		
1	3.3	16.5	1.8	3.0	1	0.6	25.5	18.4	3.4		
	(1.8)	(2.9)	(1.1)	(0.5)		(0.6)	(6.4)	(8.6)	(1.3)		
2	0.0	109.9	56.3	13.8	2	0.0	103.1	91.3	10.5		
	(0.0)	(17.6)	(15.5)	(4.4)		(0.0)	(25.5)	(22.1)	(2.4)		
3	0.0	105.8	245.3	107.0	3	0.0	13.4	171.5	137.5		
	(0.0)	(15.5)	(79.9)	(16.3)		(0.0)	(9.8)	(56.0)	(56.1)		
4	0.0	0.0	160.3	563.4	4	0.0	0.0	141.6	434.6		
	(0.0)	(0.0)	(62.6)	(239.6)		(0.0)	(0.0)	(82.0)	(91.6)		
Total	3.3	232.2	463.7	687.2	Total	0.6	142.0	422.8	585.9		
	(1.8)	(20.3)	(24.7)	(222.5)		(0.6)	(17.9)	(89.0)	(51.7)		

Table V.	Mean (and standard error) stem biomass per hectare by size class within age class for the
	CWHvm and CWHxm subzones.

^a Size classes defined by DBH: Class 1 = 1.1 to 12 cm; Class 2 = 12.1 to 29.9 cm; Class 3 = 30 to 59.9 cm, and; Class 4 = 59.9+ cm.

^b Age classes: R = Regeneration; I = Immature; M = Mature, and; O = Old growth.

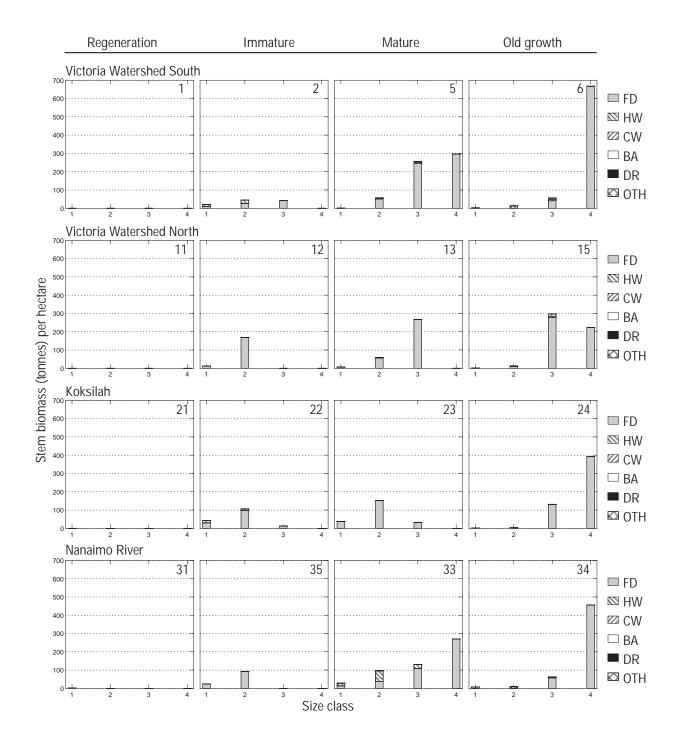


Figure V-1. Stem biomass (Mg) per hectare of species within size (DBH) class by age class within CWHxm sites.

(Class 1 = 1.1 to 12 cm; Class 2 = 12.1 to 29.9 cm; Class 3 = 30 to 59.9 cm, and; Class 4 = 59.9 + cm) (Fd = Douglas-fir; Hw = western hemlock; Cw = western redcedar; Ba = amabilis fir; Dr = red alder; Oth = other)

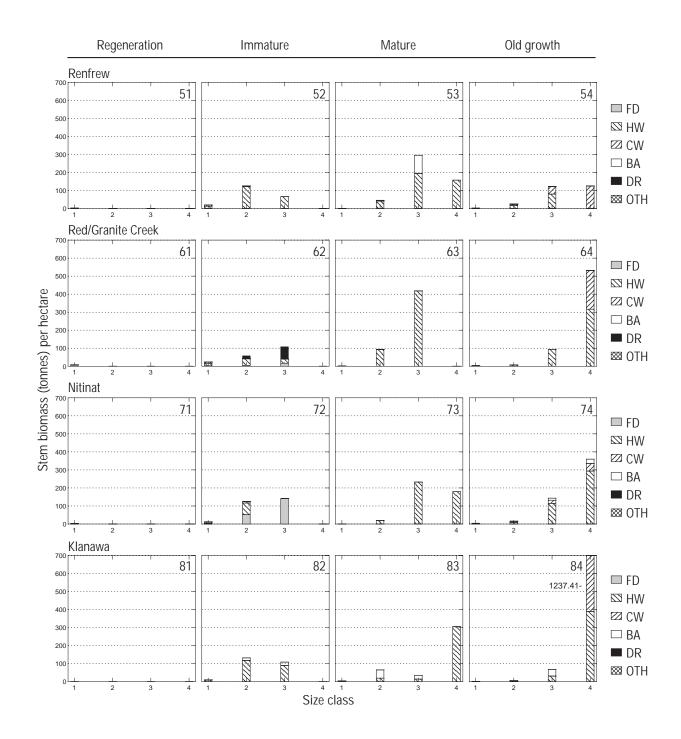


Figure V-2. Stem biomass (Mg) per hectare of species within size (DBH) class by age class within CWHvm sites.

(Class 1 = 1.1 to 12 cm; Class 2 = 12.1 to 29.9 cm; Class 3 = 30 to 59.9 cm, and; Class 4 = 59.9 + cm) (Fd = Douglas-fir; Hw = western hemlock; Cw = western redcedar; Ba = amabilis fir; Dr = red alder; Oth = other)

Appendix VI

Snags per hectare of species within size class, for each plot

C	WHvm s	ubzone (we	est side)		(east side)			
		Age c	lass ^b				Age	class	
Size class ^a	R	Ι	М	0	Size Class	R	Ι	М	0
1	0	1125	127	17	1	0	371	497	69
	(0)	(642)	(30)	(13)		(0)	(145)	(296)	(38)
2	0	74	180	30	2	0	21	99	34
	(0)	(32)	(68)	(24)		(0)	(12)	(30)	(5)
3	0	11	21	50	3	0	0	4	13
	(0)	(11)	(12)	(24)		(0)	(0)	(4)	(5)
4	0	0	21	14	4	0	0	0	3
	(0)	(0)	(21)	(3)		(0)	(0)	(0)	(3)
Total	0	1210	350	111	Total	0	393	599	119
	(0)	(674)	(89)	(59)		(0)	(145)	(271)	(41)

Table VI.Mean (and standard error) number of snags per hectare by size class within age class for
the CWHvm and CWHxm subzones.

^a Size classes defined by DBH: Class 1 = 1.1 to 12 cm; Class 2 = 12.1 to 29.9 cm; Class 3 = 30 to 59.9 cm, and; Class 4 = 59.9+ cm.

^b Age classes: R = Regeneration; I = Immature; M = Mature, and; O = Old growth.

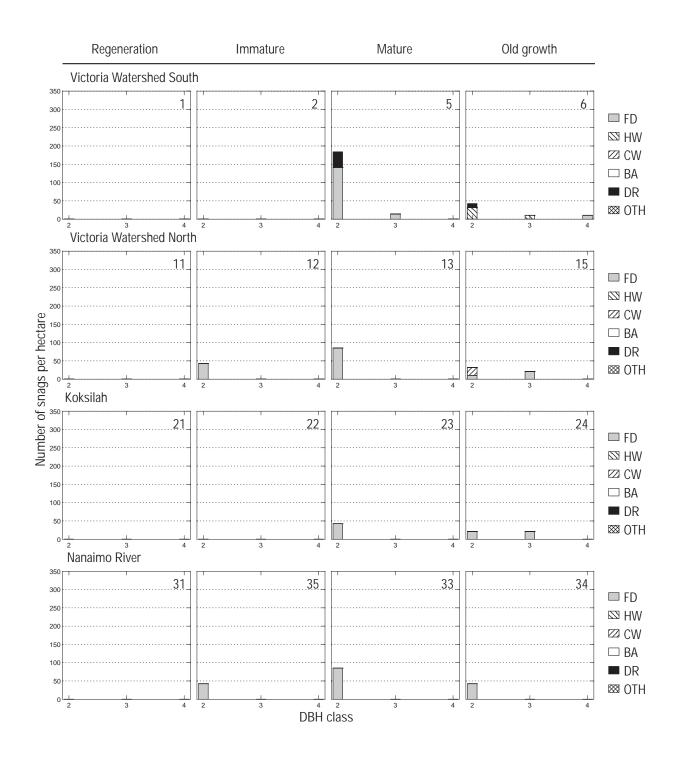


Figure VI-1. Snags per hectare of species within size (DBH) classes by age class within CWHxm sites.

(Class 2 = 12.1 to 29.9 cm; Class 3 = 30 to 59.9 cm, and; Class 4 = 59.9+ cm) (Fd = Douglas-fir; Hw = western hemlock; Cw = western redcedar; Ba = amabilis fir; Dr = red alder; Oth = other)

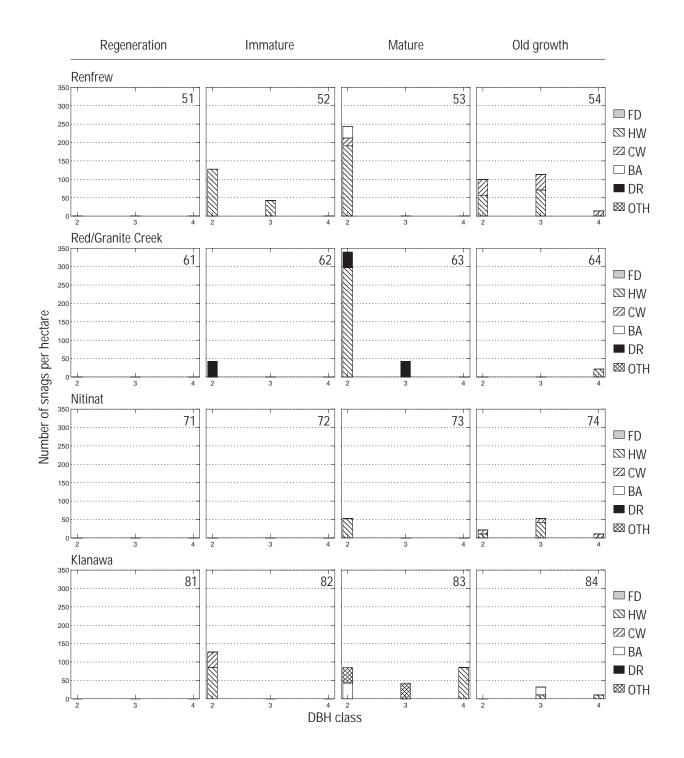


Figure V1-2. Snags per hectare of species within size (DBH) classes by age class within CWHvm sites.

(Class 2 = 12.1 to 29.9 cm; Class 3 = 30 to 59.9 cm, and; Class 4 = 59.9+ cm) (Fd = Douglas-fir; Hw = western hemlock; Cw = western redcedar; Ba = amabilis fir; Dr = red alder; Oth = other)

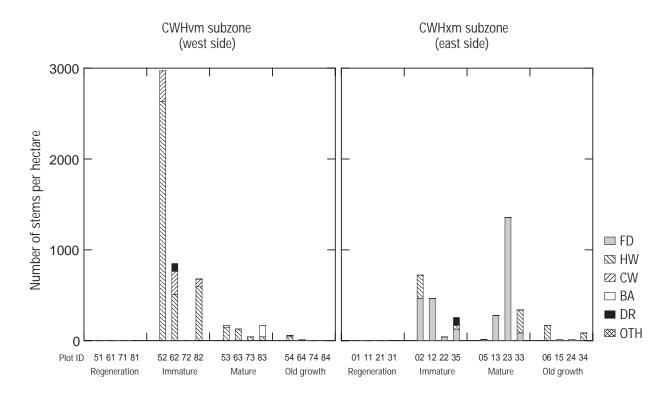


Figure VI-3. Snags per hectare of species within size class 1 by age class within subzone.

(Fd = Douglas-fir; Hw = western hemlock; Cw = western redcedar; Ba = amabilis fir; Dr = red alder; Oth = other)

Appendix VII

Snag mass (Mg) per hectare of species within size class, for each plot

Table VII.	Mean (and standard error) snag mass per hectare by size class within age class for the
	CWHvm and CWHxm subzones.

(CWHvm su	bzone (we	est side)			CWHxm s	ubzone (ea	ast side)			
		Age c	lass ^b			Age class					
Size class ^a	R	Ι	М	0	Size class	R	Ι	М	0		
1	0.0	12.9	1.3	0.2	1	0.0	4.1	6.9	0.6		
	(0.0)	(7.3)	(0.4)	(0.1)		(0.0)	(1.6)	(4.3)	(0.3)		
2	0.0	4.5	10.9	1.3	2	0.0	0.9	7.8	2.3		
	(0.0)	(2.3)	(5.7)	(0.8)		(0.0)	(0.5)	(3.4)	(0.5)		
3	0.0	6.2	3.1	12.1	3	0.0	0.0	0.6	3.0		
	(0.0)	(6.2)	(3.1)	(8.3)		(0.0)	(0.0)	(0.6)	(2.3)		
4	0.0	0.0	19.2	8.4	4	0.0	0.0	0.0	10.2		
	(0.0)	(0.0)	(19.2)	(1.7)		(0.0)	(0.0)	(0.0)	(10.2)		
Total	0.0	23.6	34.4	22.0	Total	0.0	5.1	15.3	16.1		
	(0.0)	(14.2)	(16.6)	(10.7)		(0.0)	(1.8)	(2.9)	(9.9)		

^a Size classes defined by DBH diameters: Class 1 = 1.1 to 12 cm; Class 2 = 12.1 to 29.9 cm; Class 3 = 30 to 59.9 cm, and; Class 4 = 59.9+ cm.

^b Age classes: R = Regeneration; I = Immature; M = Mature, and; O = Old growth.

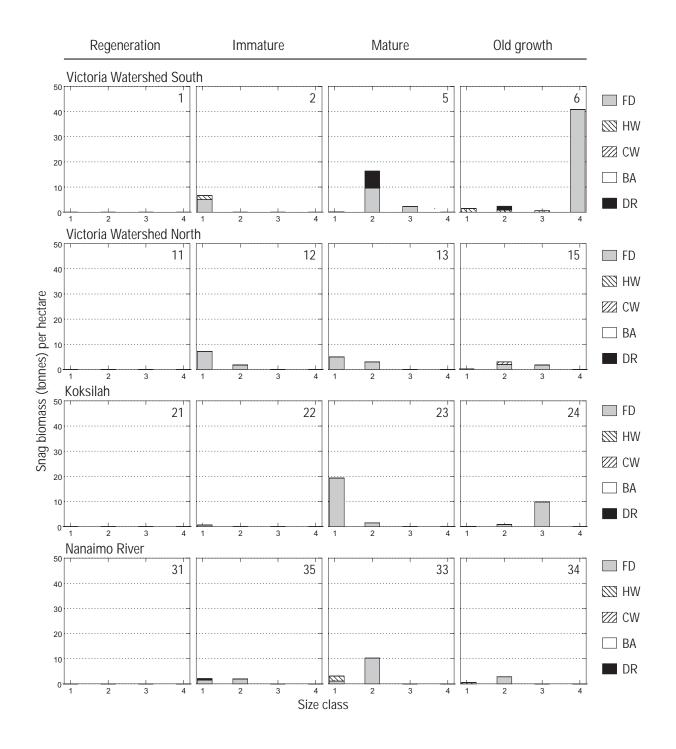
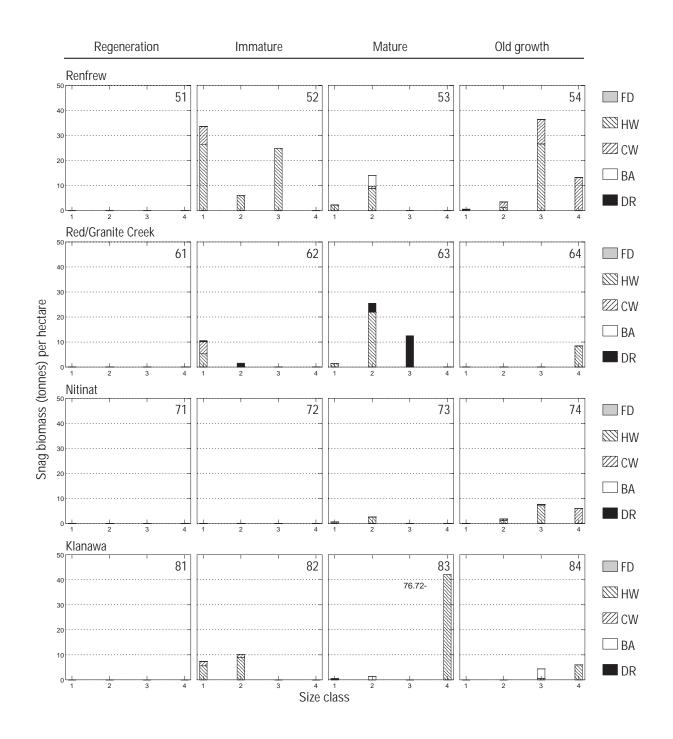
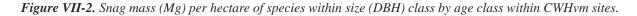


Figure VII-1. Snag mass (Mg) per hectare of species within size (DBH) class by age class within CWHxm sites.

(Class 1 = 1.1 to 12 cm; Class 2 = 12.1 to 29.9 cm; Class 3 = 30 to 59.9 cm, and; Class 4 = 59.9 + cm), (Fd = Douglas-fir; Hw = western hemlock; Cw = western redcedar; Ba = amabilis fir; Dr = red alder)





(Class 1 = 1.1 to 12 cm; Class 2 = 12.1 to 29.9 cm; Class 3 = 30 to 59.9 cm, and; Class 4 = 59.9+ cm) (Fd = Douglas-fir; Hw = western hemlock; Cw = western redcedar; Ba = amabilis fir; Dr = red alder)

Appendix VIII

Stem basal area (m²) per hectare of species within size class, for each plot

	CWHvm su	ıbzone (w	est side)			CWHxm subzone (east side)				
		Age	class ^b				Age c	lass		
Size class ^a	R	Ι	М	0	Size class	R	Ι	М	0	
1	0.45	4.02	0.80	0.95	1	0.05	5.40	4.40	0.78	
	(0.29)	(0.91)	(0.57)	(0.23)		(0.05)	(1.45)	(2.14)	(0.25)	
2	0.00	27.69	11.64	4.69	2	0.00	30.34	26.71	3.66	
	(0.00)	(4.35)	(3.27)	(1.28)		(0.00)	(6.46)	(7.83)	(0.74)	
3	0.00	25.30	36.16	21.18	3	0.00	3.92	32.11	28.61	
	(0.00)	(3.34)	(10.83)	(4.43)		(0.00)	(2.86)	(9.19)	(10.58)	
4	0.00	0.00	20.52	101.06	4	0.00	0.00	15.36	49.49	
	(0.00)	(0.00)	(7.82)	(45.02)		(0.00)	(0.00)	(9.00)	(8.52)	
Total	0.45	57.01	69.13	127.88	Total	0.05	39.66	78.57	82.54	
	(0.29)	(4.60)	(2.99)	(40.76)		(0.05)	(4.76)	(8.15)	(4.57)	

Table VIII.Mean (and standard error) stem basal area per hectare by size class within age class for
the CWHvm and CWHxm subzones.

^a Size classes defined by DBH diameters: Class 1 = 1.1 to 12 cm; Class 2 = 12.1 to 29.9 cm; Class 3 = 30 to 59.9 cm, and; Class 4 = 59.9 + cm.

^b Age classes: R = Regeneration; I = Immature; M = Mature, and; O = Old growth.

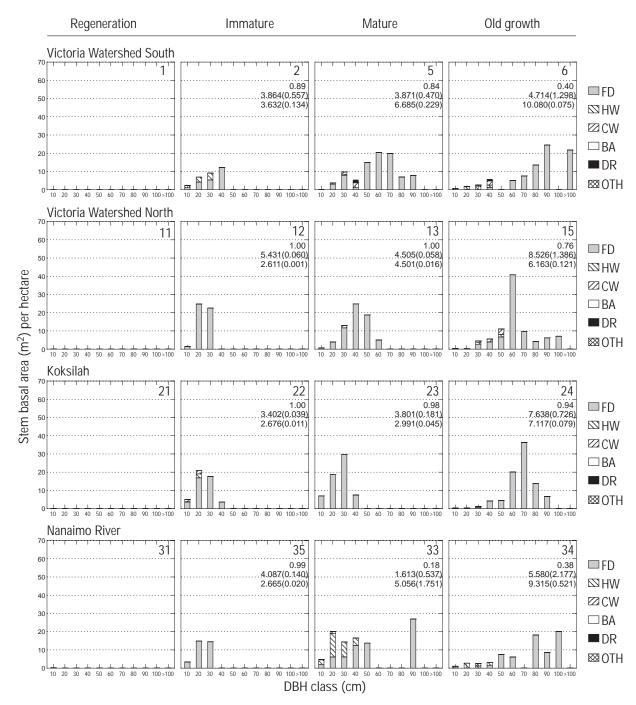


Figure VIII-1. Stem basal area (m²) per hectare of species within diameter (DBH) classes 10-100 by age class within CWHxm sites. (All larger diameter stems are in the ">100" class.)

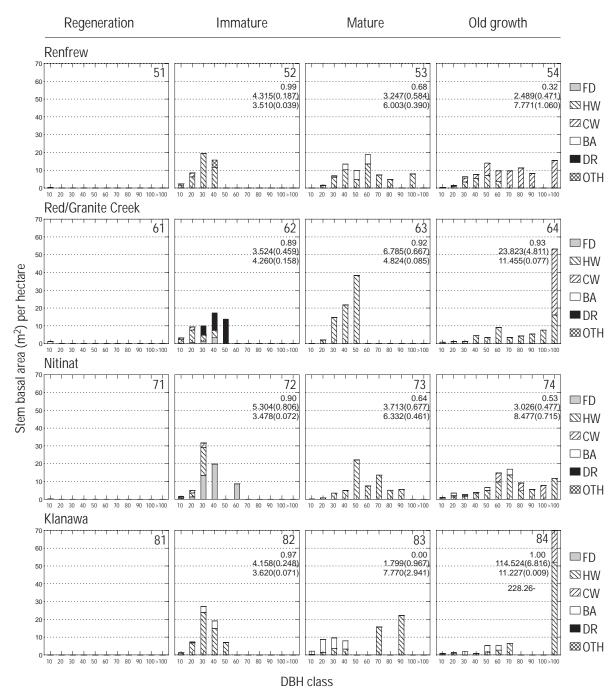
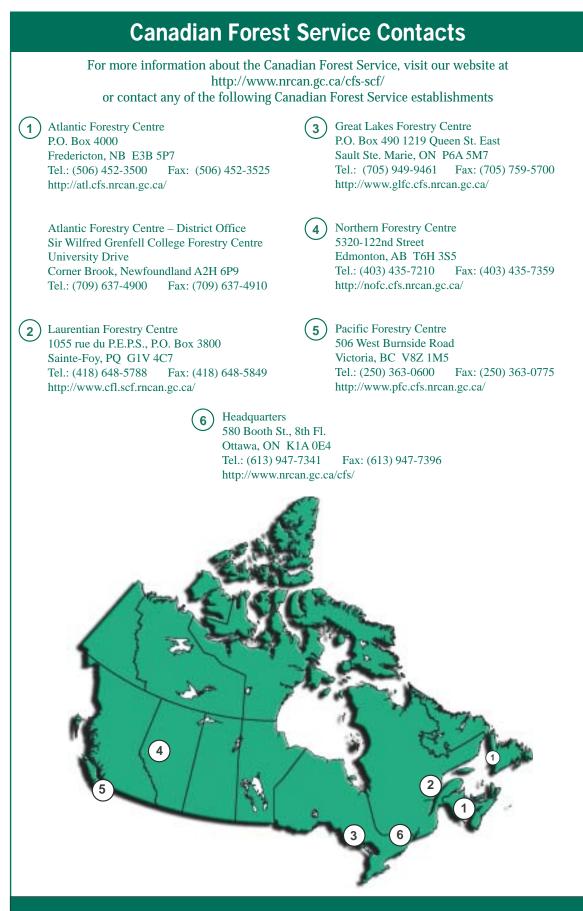


Figure VIII-2. Stem basal area (m²) per hectare of species within diameter (DBH) classes 10-100 by age class within CWHvm sites. (All larger diameter stems are in the ">100" class.)



To order publications on-line, visit the Canadian Forest Service Bookstore at: bookstore.cfs.nrcan.gc.ca