

# Attributes and indicators of old-growth and successional Douglas-fir forests on Vancouver Island<sup>1</sup>

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**Abstract:** The Douglas-fir forests of coastal British Columbia are within the most heavily modified forest ecosystem types in coastal BC and local land managers are developing new forestry practices to retain elements of old growth within the managed forest area. To determine how successful these practices are requires the selection and monitoring of appropriate attributes and knowledge on how they change with stand development. In this paper we summarize previously published results from an extensive data set on four Douglas-fir dominated sites located on eastern Vancouver Island. Data were collected as part of the Coastal Forest Chronosequences project which was addressing questions on (1) how does conversion to managed forests impact species and forest structural diversity and (2) how does this diversity recover in older second-growth stands. Each site contained four stands, a postharvest chronosequence: regeneration (R, 5–10 years), immature (I, 25–45 years), and maturing (M, 75–95 years) stands, and an old growth (O, >240 years) control stand. Over 20 attributes are summarized including structural attributes, and at three sites, detailed biodiversity and process attributes. All old-growth plots exceeded the minimum age criteria and some but not all of the minimum structural attribute criteria for old-growth Douglas-fir forests in the US Pacific Northwest, reflecting regional or site type differences. Most structural attributes showed their greatest change within the first 100 years, although older stands (M and O) still differed based on tree and snag sizes and tree mass or basal area. Most species abundance and richness attributes and process attributes clearly differentiated R from the forested stages but were of less value for differentiating among older (M and O) stands. Arboreal lichen abundance and species richness; the abundance of cryptogams, achlorophyllus plants, litter collembola, and specific species of fungi and carabids; litter fall and gap fraction were the exception, these attributes clearly differentiating M from O stands. In postharvest stands, the overall pattern of change with succession for most attributes, as

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inferred from the chronosequence, was confirmed to be very different from a previously published conceptual model for post-fire succession. Compared to the post-fire model, the greatest changes in the postharvest stands occurred early in stand development, associated with canopy closure. Although stand structural attributes can clearly be used to distinguish old-growth features in managed forest stands, none-the-less it is important to monitor and demonstrate, at least for a selection of nonstructural attributes, that forestry practices are effective in maintaining biodiversity and associated processes of old-growth forests in the managed forest area.

*Key words:* old-growth forest, succession, Douglas-fir forest, criteria and indicators, biodiversity, managed forest.

**Résumé :** Les forêts de douglas comptent parmi les types d'écosystèmes forestiers les plus fortement modifiés dans les zones côtières de la Colombie-Britannique, et les aménagistes forestiers locaux mettent au point de nouvelles pratiques forestières pour conserver des éléments de forêt ancienne dans la forêt aménagée. Pour déterminer l'efficacité de ces pratiques, il faut bien choisir et surveiller des attributs de forêt ancienne, et savoir comment ils évoluent au cours du développement d'un peuplement. Dans cet article, nous résumons des résultats déjà publiés provenant d'une vaste base de données, sur quatre sites dominés par le douglas, dans l'est de l'île de Vancouver. Les données ont été recueillies dans le cadre du projet sur les chronoséquences des forêts côtières, lequel abordait notamment les questions suivantes : (1) Quel est l'effet de l'aménagement des forêts sur la diversité des espèces et sur la structure des forêts? (2) Comment cette diversité se rétablit-elle dans les peuplements plus âgés de seconde venue? Chaque site comprenait quatre peuplements constituant une chronoséquence post-récolte : un peuplement en régénération (R, de 5 à 10 ans), un peuplement immature (I, de 25 à 45 ans), un peuplement en cours de maturation (M, de 75 à 95 ans) et un peuplement ancien servant de témoin (O pour « old growth », plus de 240 ans). Nous résumons plus de 20 attributs, notamment des attributs structuraux et, pour trois sites, des attributs détaillés liés à la biodiversité et aux processus. Toutes les placettes d'étude dans les peuplements anciens satisfaisaient au critère d'âge et à certains des critères d'attributs structuraux établis pour les forêts anciennes de douglas, dans les États du nord-ouest des États-Unis donnant sur le Pacifique, ce qui reflète des différences régionales ou liées au type de site. Pour la plupart des attributs structuraux, le changement maximal se produit au cours des 100 premières années, quoique les stades M et O se distinguent toujours sur les plans de la taille des arbres et des chicots, ainsi que de la masse ou de la surface terrière des arbres. La plupart des attributs d'abondance et de richesse en espèces et des attributs de processus différenciaient clairement les peuplements R des autres, mais sont apparus moins utiles pour différencier les peuplements plus âgés (M et O). L'abondance et la richesse en espèces des lichens corticoles, l'abondance des cryptogames, des plantes sans chlorophylle, des collemboles de la litière et d'espèces particulières de champignons et de carabidés, ainsi que la chute de litière et la fraction de trouées faisaient exception : ces attributs différenciaient clairement les peuplements M et O. Dans les peuplements établis après une récolte, le patron général des changements successionnels pour la plupart des attributs, d'après la chronoséquence, s'est avéré très différent d'un modèle conceptuel de la succession après incendie, lequel a fait l'objet d'une publication. Par comparaison à ce modèle, les changements les plus importants dans les peuplements, après récolte, se produisent au début du développement des peuplements, en association avec la fermeture du couvert. Bien qu'il soit évident que des attributs structuraux des peuplements peuvent servir à distinguer des caractéristiques de forêt ancienne dans les peuplements aménagés, il est important de faire un suivi et de montrer, au moins pour certains attributs non structuraux, que les pratiques forestières permettent de maintenir la biodiversité et les processus connexes des forêts anciennes sur le territoire forestier aménagé.

*Mots clés :* forêt ancienne, succession, forêts de douglas, critères et indicateurs, biodiversité, forêt aménagée.

## Introduction

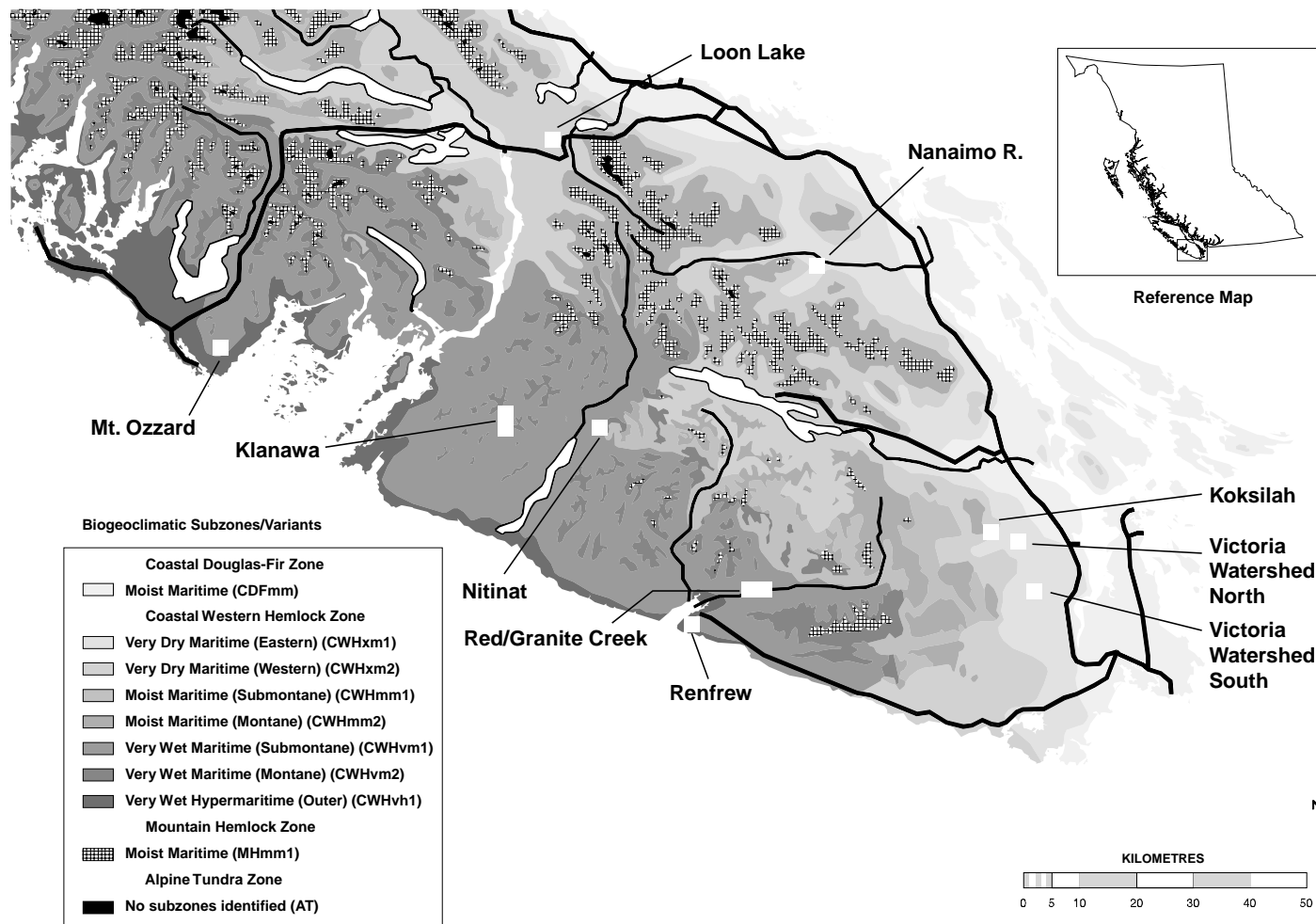
Changes caused by the conversion of old-growth coastal forests to managed forests raise concerns that have important implications for the forest industry because they have the potential to affect sales of forest products in international markets and the ability of Canada to meet obligations under sustainable forestry and biodiversity conventions. The effects of conversion are perhaps of greatest concern in the Pacific maritime coast region Douglas-fir forests of British Columbia (B.C.), which have been logged since the mid 1800s (see MacKinnon 2003). As of 1995, about 2% of the 123 600 ha in the Coastal Douglas Fir (CDF) biogeoclimatic zone and 6% of the 637 200 ha in the dry Coastal Western Hemlock (CWHxm) subzone of Vancouver Island remained as old forests. The rest of the area was either immature forest of logging origin (54% CDF, 85% CWHxm) or had been developed (44% CDF, 9% CWHxm). Only about 0.6% of the CDF and 2.2% of the CWHxm area was in parks (MacKinnon and Eng 1995). As old growth is limited and most of these forests are on privately owned land, implementation of park-based conservation or restoration strategies for old growth will be difficult, if not impossible, and will depend on local land managers developing forestry practices to retain elements of old growth within the managed forest area. To determine how successful these practices are in retaining these elements requires the selection and monitoring of the attributes and indicators of old-growth forests and knowledge of how they change with stand development.

In 1992, the Canadian Forest Service (CFS) established the Coastal Forest Chronosequences (CFC) project to examine the impacts of old-growth conversion by studying differences in carbon and nutrient distributions, carbon cycling, ecosystem structure, and biodiversity at four sites in the drier (east Vancouver Island Douglas-fir, CWHxm) and four sites in the wetter (west island western hemlock – red cedar, CWHvm) coastal forest subzones (Trofymow et al. 1997; Trofymow and Porter 1998) (Fig. 1). Questions addressed included: (1) how does conversion to managed forests impact species and forest structural diversity and (2) how does this diversity recover in older second-growth stands. Each site contained four stands, a postharvest chronosequence: regeneration (R, 5–10 years), immature (I, 25–45 years), and maturing (M, 75–95 years) postharvest stands, and an old-growth stand (O, >240 years). Stands ranged in size from 5–50 ha. Further details on site locations and stand conditions have been published (Trofymow et al. 1997) and are available online ([www.pfc.cfs.nrcan.gc.ca/ecology/chrono](http://www.pfc.cfs.nrcan.gc.ca/ecology/chrono)). Old-growth stands at each site serve as a control reference against which attributes of the postharvest stands can be compared. Implicit assumptions with this approach include changes in the old-growth stands with time have been much less than in the postharvest stands, stands are well matched within a site (i.e., they are all on similar site associations), the preharvest stands were similar to the old-growth stand, and the harvested stands were disturbed in similar ways when harvested. Although care was taken to find suites of stands at a site on similar slope, elevation, and aspect, it is realized that variation existed and that all assumptions were likely not met. This problem is inherent in the chronosequence approach and has been recognized previously in ecosystem process (Cole and van Miegroet 1989) and biodiversity studies (Kremsater and Bunnell 1998).

Most of the research on biodiversity and ecosystem processes in the CFC project from 1993 to 1998 was conducted on the dry, east island forest (CWHxm subzone). Therefore, this paper will focus on the results from studies of the four Douglas-fir chronosequences (VWS, Victoria Watershed South; VWN, Victoria Watershed North; KOK, Koksilah; NAN, Nanaimo River) for which the greatest number of attributes have been measured. In this paper, we present a synopsis of the studies conducted within the CFC project. We then examine how the attributes of the old-growth stands at each site compared with definitions proposed for old-growth Douglas-fir forests in the US Pacific Northwest (US PNW) (Spies and Franklin 1988; Franklin and Spies 1991a). We then describe a conceptual model of patterns of change in ecosystem attributes with succession developed for the US PNW (Spies and Franklin 1988; Franklin and Spies 1991a, 1991b) and compare it with the patterns of change for a suite of structural, biodiversity and process attributes measured as part of the CFC project. We conclude with

**Fig. 1.** Locations of the ten Coastal Forest Chronosequences sites on southern Vancouver Island in relation to Biogeoclimatic subzones on southern Vancouver Island. Sites at Loon Lake and Mt. Ozzard were not sampled. Map prepared by CFS, NFI from 1: 250 000 biogeoclimatic ecosystem classification maps by B.C. Ministry of Forests. (From Trofymow et al. 1997).

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a discussion of the potential usefulness of the different attributes as indicators for monitoring purposes in ecosystem-based forestry and adaptive management.

### **Synopsis of attributes measured in individual studies**

A variety of forest structural, biodiversity, and ecosystem process attributes were measured on the southeast Vancouver Island Douglas-fir dominated chronosequences. The synopsis for each study below describes how measurements were made, the number of sites measured, the results of the study concentrating on the significant effects of stand age on the variables measured, and references to sources of the detailed results. Unless otherwise noted, all four stands at a site (three plots in the postharvest chronosequence and the old-growth control) were measured once. Several of the biodiversity and process studies included repeated samples over more than 1 year.

#### **Structure**

##### ***Overstorey trees***

Mensurational measurements of overstorey trees were made at four sites. With increasing stand age, the number of live stems decreased while stem biomass and basal area, and the number of diameter classes, height classes, and crown depth classes, increased (Hedberg and Blackwell 1998; Blackwell et al. 2002).

##### ***Snags***

Snags were only present in the three forested stands (I, M, O) at the four sites. Although snag size increased with stand age, snag biomass was lowest in I and similar in M and O plots. Snag density was highest in M and I plots and lowest in O plots (Hedberg and Blackwell 1998; Blackwell et al. 2002).

##### ***Canopy gaps***

Hemispherical canopy photography and LAI2000 readings were used to measure gap fraction and effective leaf area index in the forested stands at four sites. Gap fraction increased and effective leaf area index decreased with increasing stand age. Within-stand variability of these attributes also increased with stand age, indicating that O stands had more heterogeneous canopy structure (Frazer et al. 1997, 1998, 2000).

##### ***Downed coarse woody debris***

Downed coarse woody debris (CWD) was measured and density samples taken along a line intercept (150 m) at four sites. Total mass or volume was greatest in M plots, intermediate in R and O, and least in I plots. Coarse woody debris distributions were skewed to smaller size classes and lower decay classes in young stands and more uniformly distributed in older stands (Wells and Trofymow 1997, 1998).

##### ***Forest floor mass***

Forest floor cover and depth were measured and bulk density samples taken along line intercepts at four sites. Forest floor mass was greatest in R and O plots and lowest in I and M plots (Trofymow and Blackwell 1998).

#### **Biodiversity**

Biodiversity studies were focused on groups of organisms with low dispersal abilities, so that the forest stand being studied would represent the main habitat for the organism and not simply a patch in their environment. For each group of organisms, the effects of stand age could be assessed by measuring abundance, species richness, diversity indices, and multivariate analysis (e.g., canonical correspondence

analysis) for the entire group, and by identification of species that were restricted to one or more age classes.

#### ***Collembola in forest floor litter***

Surface soil cores were sampled annually for 4 years at three sites. A total of 75 species were identified. Abundance was greatest in O, intermediate in I and M, and least in R plots. Species richness (number) was similar amongst O, M, and I and less in R plots. Multivariate analysis found that O differed from M. No restricted species were found (Addison et al. 1998, 2003).

#### ***Collembola in decaying stumps***

Core samples from decaying stumps of similar stages of decay were taken three times in 1 year at three sites. Seventy-two species were identified. Abundance and species richness were lowest in R plots, higher and similar in I, M, and O plots. Similarity indices showed R fauna differed the most from I, M, and O. Multivariate analysis indicated fauna were clustered into seral communities (Setälä and Marshall 1994; Setälä et al. 1995; Marshall et al. 1998).

#### ***Carabid beetles on the forest floor***

Pitfall traps were placed at two sites and sampled monthly for a 16-month period. Twenty-eight species were identified. Carabid abundance was lowest in R stands, intermediate in I, and highest in M and O stands, and species richness was highest in R plots and lower and no different in the forested stands. Two species were restricted to O seral stages (Craig 1995; Brumwell et al. 1998).

#### ***Spiders on the forest floor***

A total of 32 species of litter dwelling spiders were collected from the pitfall traps also used for carabid sampling. Spider abundance and richness were highest in R plots and declined or were no different in any of the forested (I, M, and O) plots. Five species preferred R stages, and one species I and M stages. No species were restricted to the O stage (Brumwell 1996; Brumwell et al. 1998).

#### ***Soil nematodes in salal rhizospheres***

Soil cores were taken in summer and winter for 1 year at three sites from within patches of salal, an understorey ericaceous indicator plant ubiquitous to all plots. A total of 40 species or species groups were identified. Abundance increased with stand age: R lowest, I and M intermediate, and O highest. Similarity indices did not differ with age. Although the greatest number of species were found in O plots, all species in O plots were also found in plots of one or more of the younger seral stages. Two species were restricted to O and M seral stages (Panesar et al. 1998, 2001).

#### ***Salamanders***

As part of a larger study, time-constrained searches and artificial cover objects were used in a weekly survey conducted over 2 years at one site. Four species were found. Salamander abundance was lower in R plots but was no different in any of the forested plots. (Davis 1996, 1998).

#### ***Plants***

Plant percent cover was measured once at three sites. A total of 244 species, comprising 12 tree, 18 shrub, 107 herb, and 107 cryptogam species, was recorded. More species were in R plots, although these were mostly invasive herbaceous and grass species. Cryptogam abundance and diversity was greatest in M and O plots. Species of achlorophyllous plants were restricted to M and O plots and might serve as good indicators in an old-growth index (Ryan et al. 1998).

### ***Lichens in the upper canopy***

Branch samples from the upper canopy were collected once from four sites, supplemented by a sampling at one site of windfallen branches following a severe windstorm. Thirty-eight species or species groups were identified. Lichen abundance per branch increased with increasing stand age. The R and I plots had half the number of species found in the M and O plots. Five species of lichen were restricted to the O stands, and all species in the R and I were found in the M or O stands (Enns 1998; Enns et al. 1999).

### ***Macrofungi sporocarps***

The percent occurrence of sporocarps on transects of quadrats was measured monthly over 2 years at three sites. A total of 384 species was recorded within four guilds; mycorrhizal, litter decay, wood decay, and general saprobes. Species richness and total frequency (proxy for abundance) was least in R plots, greater in the forested plots, and tended to be greatest in I plots. Species richness and total frequency in the litter decay, general saprobe, and mycorrhizal guilds were similar to those for all species, although the mycorrhizal species richness tended to be highest in the O plots. Wood decay fungi richness and frequency was lowest in O plots and greatest in I plots. The frequencies of 58 species varied with stand age. Some were restricted to the R stage, with most species returning by the I stage and the rest by the M stage. Some species of *Russula* remained less frequent in M than O plots. One species may be restricted to O, but was too infrequent to tell (Countess et al. 1998; Countess 2001).

### ***Ectomycorrhizae***

Over a 2-year period, the abundance and types of ectomycorrhizal roots were measured from soil cores taken from adjacent M and O stands at two sites. A total of 69 types were found. The O and M stands showed almost no differences in richness, equitability, or diversity of types. There was no evidence of types restricted to either M or O stands (Goodman 1995; Goodman and Trofymow 1998a, 1998b, 1998c).

## **Processes**

### ***Detrital C fluxes***

Rates of overstorey litter fall, litter, and wood block decomposition, soil respiration, and soil microbial activity were measured seasonally at three sites over a 3-year period. Surface litter and wood decay, respiration, and microbial activity were lower in R plots than the forested plots, with no differences among the I, M, or O plots. Buried wood decay was higher in R plots than in the forested plots. Litter fall was lowest in I, intermediate in M, and highest in O plots. (Trofymow 1998)

### ***Soil chemistry and nutrient concentrations***

Mineral soils were sampled at three depths at four sites. Total cations and cation exchange capacity decreased with increasing stand age. No other effects of stand age were found (Trofymow et al. 1997; Trofymow and Porter 1998; Blackwell and Trofymow 1998)

### ***Soil P chemistry***

Mineral soils were sampled at three depths at 4 sites and concentration and forms of soil P were analysed. Over 85% of the NaOH-extractable P was orthophosphate, as determined by <sup>31</sup>P nuclear magnetic resonance (NMR) spectroscopy. Total available and extractable P declined with depth, but no effect of seral stage was found (Preston and Trofymow 1998, 2000).

**Table 1.** Comparison of CFC old-growth plot attributes to B.C. working and US PNW interim definitions of old-growth coastal Douglas-fir forests.

Attribute	Minimum	VWS	VWN	KOK	NAN	Reference
Stand age	150 year	245	316	288	330	BCMOF 1992
All species trees > 100 cm DBH	≥10/ha	21	11	0 <sup>1</sup>	28	Franklin and Spies 1991a
Shade species >40 cm DBH	≥10/ha	0	32	0	0	Franklin and Spies 1991a
Snags >50 cm DBH, >5 m tall	≥4/ha	17	10	11	0 <sup>2</sup>	Franklin and Spies 1991a
Log biomass <sup>3</sup>	30 Mg/ha	15	17	24	61	Franklin and Spies 1991a

Notes: DBH, diameter at breast height.

<sup>1</sup>KOK: 11/ha, 90cm DBH.

<sup>2</sup>NAN: 42/ha, 12–30cm DBH.

<sup>3</sup>diameters ≥12cm.

### *Soil organic matter chemistry*

At all four sites, five soil organic matter types were characterized: fine woody debris, forest floor, fine roots from forest floor, and two water-floatable size fractions (2–8 mm and <2 mm) from the 10–30 cm mineral soil. There were no significant effects on C or N concentrations due to seral stage and carbon-13 NMR spectroscopy showed little harvesting effect on organic composition. Heterogeneity was due to small-scale variation of inputs of CWD high in lignin, vs. high-tannin litter and roots and presence of char was detected in some samples (Preston et al. 1998b, 2002).

### *Downed coarse woody debris properties*

The physical and chemical properties of samples taken during the field measurements of CWD were examined. Increases in decay class (I to V, assigned in the field) were associated with decreasing density and small increases in C, N, and P concentrations. NMR analysis of material <12 cm diameter showed a consistent pattern of initial nonselective mass loss (decay class I to III), followed by more rapid loss of polysaccharides and accumulation of lignin in decay classes IV and V. This pattern indicates that, for management purposes, a system with only two decay classes may suffice. The minimal effects of one harvest on soil organic matter and CWD were attributed to the large legacy effect, and can not be expected to persist through more harvesting cycles (Preston et al. 1998a, 1998b).

### **Definitions of old-growth Douglas-fir**

A premise of this project was that, in order to understand how conversion impacts forest attributes, the attributes of the postharvest chronosequence must be compared with a control, in this case the old-growth stand at each site. How then do we “know” that these stands are indeed old growth? Old-growth stands were initially selected simply if the age of the dominant trees, confirmed by increment cores, was greater than 200 years (Trofymow et al. 1997; Trofymow and Porter 1998). In B.C., the minimum age for coastal Douglas-fir stands to be considered old growth is 150 years (British Columbia Ministry of Forests (BCMOF) 1992; Wells et al. 1998). Through studies of old Douglas-fir forests in the US PNW, Spies and Franklin (1988) proposed an interim definition for old-growth forests based on several structural features, including tree, snag, and downed wood sizes and abundance from measurements in a large number of old stands in the US PNW (Table 1). They later extended the use of these structural features to develop an old-growth index by which the degree of development of old-growth features in individual stands could be assessed (Franklin and Spies 1991a). The US PNW definitions were developed for forest in the *Tsuga heterophylla* Zone, which covers a broad range of conditions and corresponds roughly with the wet to dry subzones of the CWH (MacKinnon and Trofymow 1998).



**Table 2.** Idealized patterns of change with succession in selected ecosystem attributes in post-fire Douglas-fir forests (after Spies and Franklin 1988, Spies 1998).

Attributes following U-shaped Curve 1	Attributes following sigmoidal S-shaped Curve 2
Amount of coarse woody debris	Average tree size
Number of large snags	Diversity of tree sizes
CWD as % of ecosystem biomass	Incidence of broken tops
Spatial heterogeneity of understorey	Surface area of boles and branches
Plant species diversity	Wood biomass
Vertebrate species diversity	Forest floor depth
Susceptibility to fire	Vertical foliage diversity

All old-growth stands at VWS, VWN, KOK, and NAN exceeded the minimum age criteria for B.C. However, they met some but not all of the minimum criteria for structural attributes from the US PNW interim definition (Table 2) (Blackwell et al. 2002). The lower fit of the old-growth Douglas-fir stands to the US PNW definition may be due to at least two reasons. Regional differences in disturbance history and intensity, and site and genetic growth potential between the US PNW and eastern Vancouver Island could mean that attributes of old-growth forests may develop more slowly in the B.C. stands. For example, the maximum site index for Douglas-fir on Weyerhaeuser lands in the US PNW is over 45, while on Weyerhaeuser lands in B.C., the highest is just over 35.<sup>3</sup> Alternatively the differences may be due to unavoidable bias in site selection of the chronosequences. All sites were on medium to poor site series (Trofymow and Porter 1998) as all high site stands in the region have been logged, and thus might develop old-growth attributes more slowly than the mean for Douglas-fir in this subzone.

### Conceptual model of patterns of change in attributes with succession

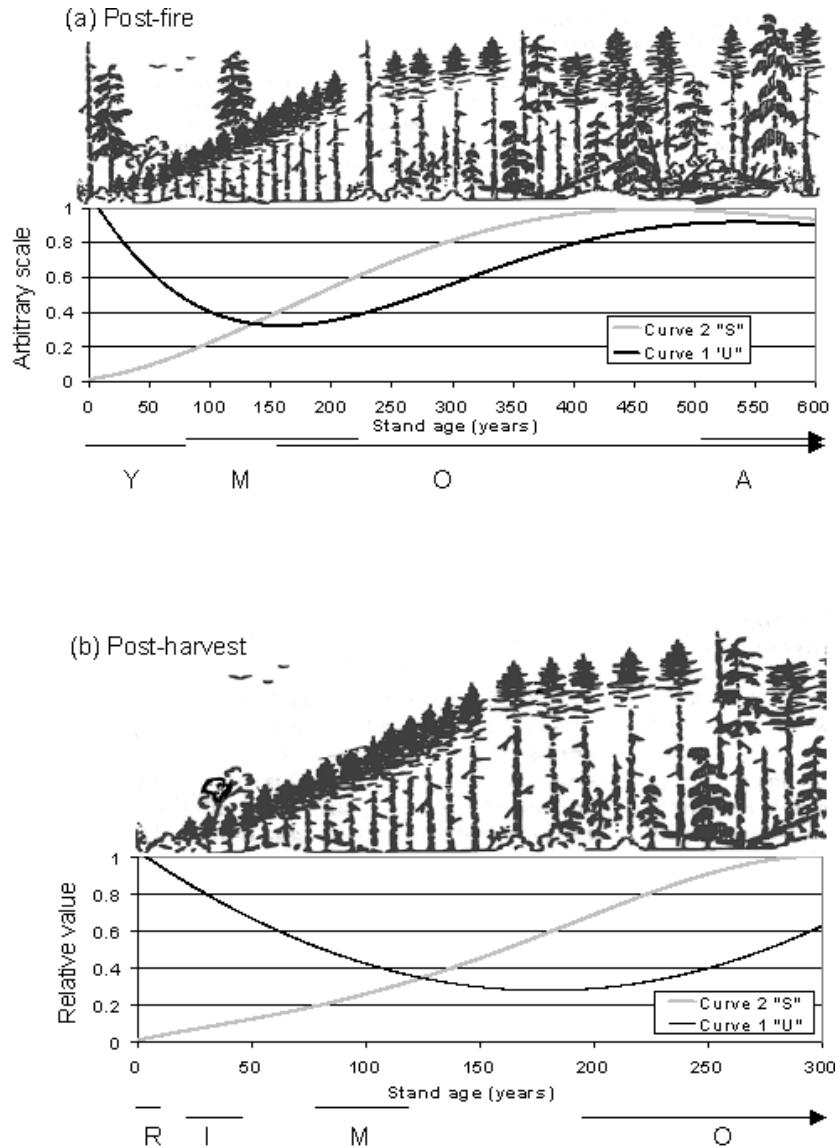
The synopsis described some of the differences in specific attributes of the four age classes in the Douglas-fir chronosequence. In this section, we explore the use of a conceptual model of stand development as a way to summarize and compare multiple attributes across all stand ages. Such an approach would help address the question, “how quickly during postharvest succession do attributes change and recover relative to those in the old growth.”

Spies and Franklin (1988) have proposed that ecological succession in Douglas-fir forests can be described by changes in abundance of structural attributes related to the dominant trees (Fig. 2a). They suggest that following a stand-replacing disturbance such as fire, the changes in structural and other attributes (as plotted on an arbitrary scale) follow two general pathways with time. The first pathway is a U-shaped curve with highest values in young stands immediately after disturbance, declining to low levels in mature stands and rising to high levels in old-growth stands. The second pathway is a sigmoidal S-shaped curve with values at low or null levels in young stands immediately after disturbance and then increasing with stand age to an asymptote later in succession in old growth. Attributes related to the amounts of dead wood and species diversity follow U-shaped curves, and attributes related to live biomass follow S-shaped curves (Table 2).

By graphing the curves from Spies and Franklin (1988) on the same time scale used for the chronosequences (Fig. 2b), the curves can serve as null hypotheses for testing whether the attributes in the postharvest chronosequence stands are following a successional pattern similar to that in post-fire stands. Caution must be used in this approach, as the successional pathway can only be inferred because data are from chronosequence of stands and not from a time series. The age ranges of seral stands used

<sup>3</sup>B. Beese. 2001. Weyerhaeuser, Coastal B.C. Group. Personal communication.

**Fig. 2.** Conceptual models of successional patterns of change in ecosystem attributes in Douglas-fir forests following (a) post-fire or (b) postharvest disturbances. Seral stages for the post-fire succession (Y, young; M, mature; O, Old-growth; A, Ancient) are after Spies and Franklin 1988, Franklin and Spies 1991*b*, and Wells et al. 1998. Seral stages for the postharvest succession (R, regeneration; I, immature, M, mature; O, old-growth) are those used in the Coastal Forest Chronosequence project (Trofymow et al. 1997). (Modified after Wells et al. (1998), drawing by Walter Wells. Used with permission of Natural Areas Journal and R.W. Wells.)



in this project were within the seral stage age ranges recognized for B.C. (Wells et al. 1998; Spies and Franklin 1988), other than that the “young” seral stage is separated into regeneration (R) and immature (I) stages. Thus, if the postharvest chronosequence stands are following a successional pathway similar to post-fire stands conceptualized by Spies and Franklin (1988) then, when attributes are graphed on a similar scale, the curve drawn through points from the chronosequence should be similar to generalized

curves from the conceptual model. Attributes following the U-shaped curve of post-fire stands should decline through R and I stand ages, reach a minimum in the M and show no change or increase slightly in the O stage. Attributes following the S-shaped curve for post-fire stands should increase continually from R to I to M to O stand ages (Fig. 2b).

To allow for the comparison of multiple attributes from the chronosequences with the generalized curves from the conceptual model, a relative value for each attribute was calculated (value in a seral stage/maximum value across all seral stages) and plotted on a relative scale. As the conceptual model was derived for post-fire stands, we would expect that the curves for the postharvest stands should differ as harvest and fire differ in their post-disturbance impact on stand attributes.

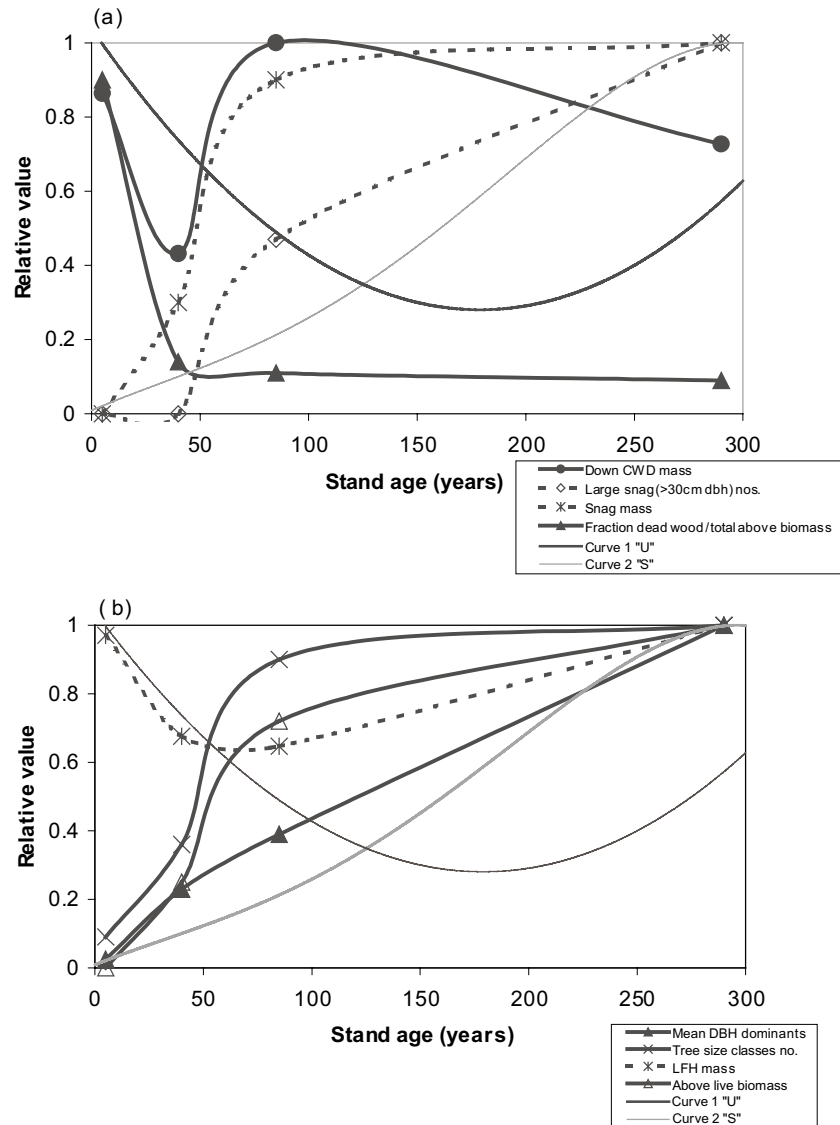
### Comparison of chronosequence results with the conceptual model

Initial comparisons were made for structural attributes that Spies and Franklin (1988) and Spies (1998) suggest should follow either the conceptual U-shaped or S curves (Table 2). None of the eight structural attributes from the postharvest chronosequence plots followed the broad U or low slope S curves suggested for the post-fire conceptual model (Fig. 3). Downed wood mass showed a narrow U curve within 100 years after harvest (Fig. 3a). Large snags and snag mass had increased the most within the first 100 years, although large snags were most abundant in O plots. The ratio of dead to live wood was highest in the R plots, then declined and was no different in any of the forested stages. Three of the live biomass structural attributes did follow sigmoidal curves, although only live biomass followed the low slope S curve of the conceptual model (Fig. 3b). Mean diameter at breast height (DBH) of dominants and number of tree size classes showed their greatest increase early in stand development with less change between the M and O stages. Forest floor mass followed a U-shaped curve, with a minimum in the I and M stages.

The patterns of change in the abundance and diversity of several groups of the litter and soil-dwelling mesofauna were examined next. Given the small size of many of the forest stands, particularly the old growth, effort had been concentrated on these groups of animals because of their limited range and dispersal capabilities and hence the likelihood of greater fidelity with a particular patch. None of the mesofaunal abundance or diversity attributes followed the low slope S or broad U curves of the post-fire conceptual model (Fig. 4). Carabid beetle and stump collembola had their greatest increase within the first 50–100 years with no change to the O stage (Fig. 4a). Litter collembola and soil nematodes increased more slowly in the first 50–100 years, with the larger increases to O stages giving overall curves close to the general S curve (Fig. 4a). Litter spider abundance was highest in R stages, then declined and was at low levels in all forested stages. Surprisingly, the relative changes with succession in mesofaunal group species numbers (Fig. 4a) were less than the changes in abundance for the same group (Fig. 4b). None showed patterns of change like the conceptual U or S curves (Fig. 4b). The numbers of species of all mesofauna groups remained relatively high soon after harvesting. Nematodes and litter and stump collembola species numbers increased within the first 50–100 years with no further change in the O stage. Carabid beetle and litter spider species numbers declined from the R to I stages with no changes in the rest of the forested stages. Some individual species were restricted to M or O stands and the abundance of those species more closely followed the S conceptual curve (e.g., the carabid *Z. matthewsii*, Fig. 4b).

The overall plant, fungal, or lichen species number curves were unlike either of the conceptual model U or S curves (Fig. 5). Plant species were highest in R plots and declined with stand age. Total fungal species peaked at the immature stage because of the continued presence of regeneration species and restoration of species from forested stages. Lichen species did increase with stand age with a sigmoidal curve with the greatest increase between I and M stages. The abundance of some restricted species or species groups more closely matched the slope of the conceptual S curve at later stages. For example the fungi *Russula xerampalina*, absent at the R stage and at intermediate levels at I and M stages, was at highest abundance in O stands. Species of achlorophyllus plants were absent in R

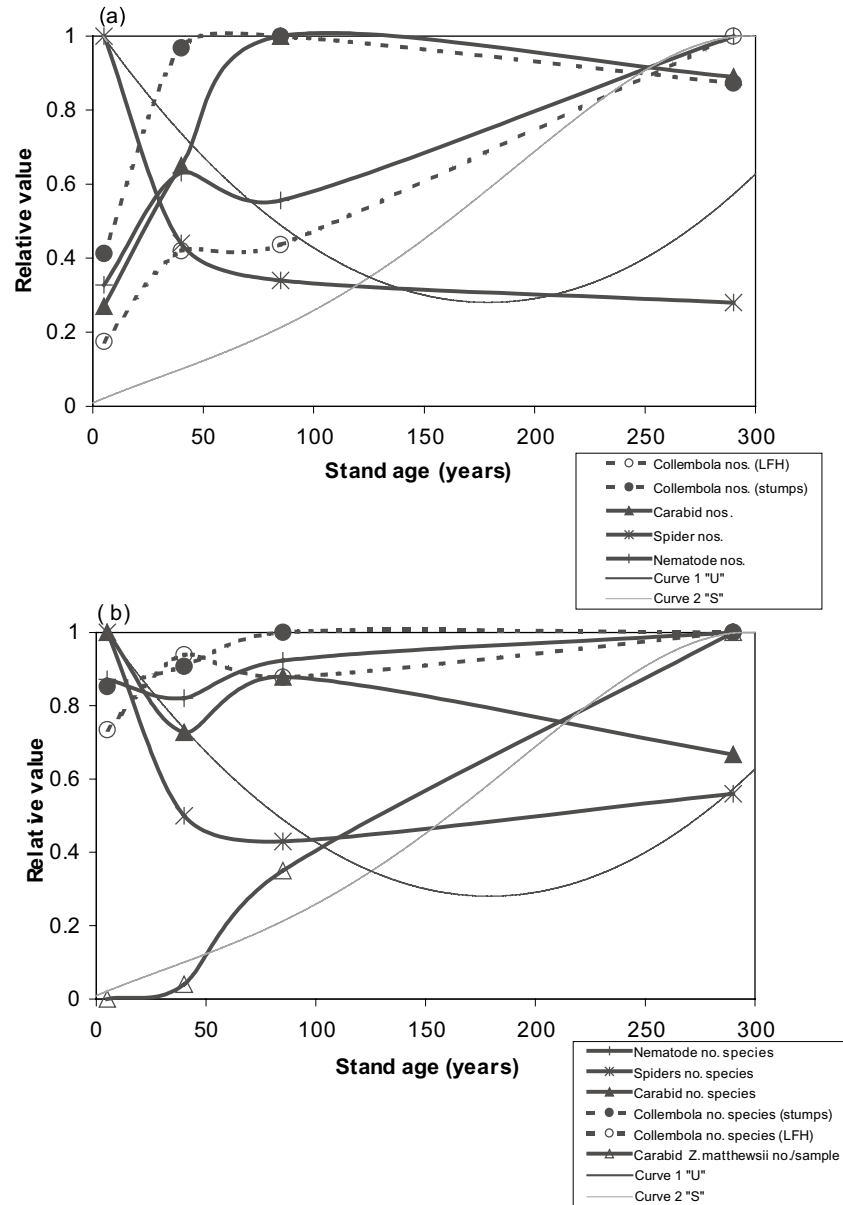
**Fig. 3.** Structural attributes in postharvest chronosequence plots expected to follow a (a) U-shaped curve (downed CWD mass, large snag density, snag mass, fraction of dead to total aboveground mass) or (b) S-shaped curve (dominant tree mean DBH, number of tree size classes, forest floor mass, aboveground live biomass) pattern of change.



and I stands and increased in abundance with increasing stand age. Many achlorophyllous plants are known to be epiparasitic on ectomycorrhizal fungal species. Thus it is interesting to speculate whether recovery of these plants in M stands follows the return of specific ectomycorrhizal fungal species such as *R. xerampalina* in the I stands.

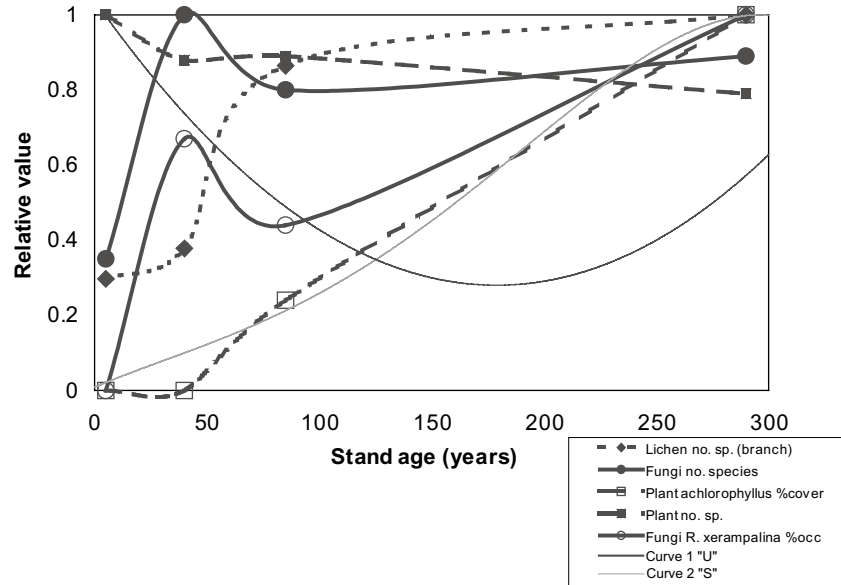
The pattern of change in process attributes was unlike either of the conceptual model U or S curves (Fig. 6). Depending upon placement, wood decay rates either increased or decreased from the R stage and were similar among the forested stages. The relative increase in overstorey litterfall at early stages was more rapid than the increase in live biomass, mirroring the large decline in gap fraction. Gap fraction, litterfall, and overstorey biomass all increased from M to O stages.

**Fig. 4.** Patterns of change in mesofaunal (soil nematodes, forest floor collembola, decayed stump collembola, forest floor spiders, forest floor carabid beetles, carabid *Z. matthewsii* abundance) (a) abundance and (b) species diversity in the postharvest chronosequence plots.

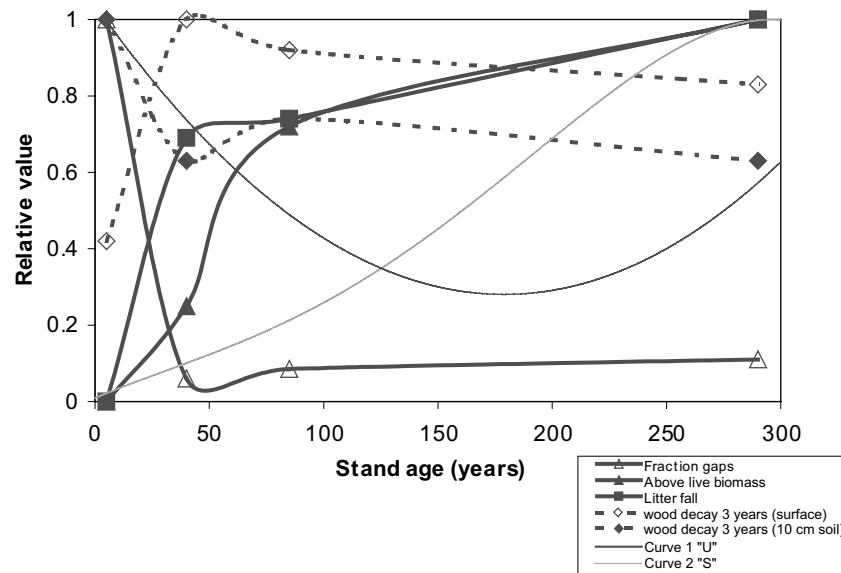


Overall the post-fire conceptual model of succession poorly described the postharvest changes in attributes as inferred by the chronosequences. Few of the attributes followed the broad U-shaped or low slope S-shaped curves suggested by Franklin and Spies (1991b), confirming that disturbance type matters. Postharvest stands will have less snags and downed wood than post-fire stands, although more slash will contribute to the forest floor. Planting will minimize time to crown closure and speed overstorey growth, causing a steeper S-shaped pattern of change early in succession. However, it is unclear if, left

**Fig. 5.** Patterns of change in arboreal lichen, plant, and fungi diversity, and achlorophyllous plant and fungus *R. xerampalina* abundance in the postharvest chronosequence plots.



**Fig. 6.** Patterns of change in gap fraction, annual litterfall, live biomass, and 3-year surface and buried wood block decay rate in the postharvest chronosequence plots.



undisturbed, these forests would follow the successional path inferred by the chronosequence or that which gave rise to the old-growth forests on each site (Wells and Trofymow 1997). Certainly relatively minor changes during stand succession can influence the stand later. Study of the old-growth forest at the VWS site showed that density-dependent effects differentially affected survival of late-successional tree species, thus influencing stand composition (He and Duncan 2000). Silvicultural treatments (thinning or

fertilization) in immature stands adjacent to the VWN site still affected understory species composition when remeasured 30 years later (He and Barclay 2000).

These results have forest management implications. After harvesting, although the absence of large woody structures in younger stands may negatively affect some species or processes, the more rapid canopy closure may be beneficial for other species or processes requiring forest interiors. Thus, forest practices that retain structure after harvesting and promote canopy closure might allow for forest interior species and processes to recover more rapidly than during post-clearcut or post-fire succession. However, this assumes that the distribution of stand ages in the landscape is such that adequate sources of dispersing organisms are available to recolonize the young forests if they were unable to survive in the remnant structures left after harvest.

## Conclusions

All old-growth plots exceeded the minimum age criteria and some but not all of the minimum structural attribute criteria for old-growth Douglas-fir forests in the US Pacific Northwest, reflecting regional or site type differences in rates of stand development. Good definitions of old growth in British Columbia are hindered by a lack of research describing structural, compositional, and functional characteristics of old growth (Hamilton and Nicholson 1991). This project provides some data on which to base definitions and is supportive of 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. This project provides 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.

Although postharvest stands, mature stands in particular, were recovering many of the attributes of old growth differences still persisted. Overstorey stand mass and basal area in mature stands were becoming similar to that in the old growth, although stand structure, species composition, snag and coarse downed wood sizes, canopy gap fraction, and forest floor mass still differed. Few differences in C and P chemistries of soils and detrital fractions occurred among seral stages. Detailed C cycling and biodiversity studies showed more differences. Diversity and abundance of salamanders, carabid beetles and spiders, soil microarthropods, soil nematodes, understory vegetation, ectomycorrhizal fungi, fungal sporocarps, and epiphytic lichens, and litter decomposition and litterfall in the regeneration and immature Douglas-fir forests all differed from those in the old-growth forests. The greatest differences in most of these attributes were between the regeneration and forested stages. Although many general biodiversity attributes (total abundance, number of species) and decomposition were similar in the mature and old-growth forests, the forest epiphytic lichen species, achlorophyllus plant abundance, litter collembolan abundance, soil nematode abundance, and litterfall in the mature stands still significantly differed from that in the old growth. Several species of fungi, carabid beetles, and cryptogam plants identified were restricted to old growth or old growth and mature stands but with greatest abundance in the old growth. Multivariate analysis was able to distinguish between the plant and collembolan communities of the old-growth and mature stands.

In these postharvest stands, the overall pattern of change with succession for most attributes, as inferred from the chronosequence, was confirmed to be very different from the conceptual models for post-fire succession in the Douglas-fir forests of the US PNW (Franklin and Spies 1991*b*). Compared with the post-fire model, the greatest changes in the postharvest stands occurred early in stand development, associated with canopy closure. Although the developmental trajectory of the postharvest stands clearly differs from that for post-fire stands, it is unclear whether, if left undisturbed, individual stands will follow the successional path inferred by the chronosequence or that giving rise to the old-growth stand at each site. Repeated measurements on the same stands in these chronosequences after 10 or 20 years could be used to generate a successional vector for each plot. This could then be compared

with the curve generated from the chronosequences to determine if the plots are on the successional pathway inferred by the chronosequence.

Although multivariate analysis of groups of organisms or abundance of certain restricted species (e.g., lichens, achlorophyllous plants, select species of fungi such as *R. xeramapalina* or invertebrates such as *Z. matthewsii*) might serve as good indicators for differentiating mature and old-growth stands, their measurement likely requires specialized taxonomic knowledge and sampling. As a result these attributes may not be those best suited for monitoring for forest management purposes. Some of the species group abundance attributes may be more suitable as they are simpler and easier to measure, although most will require greater effort to measure than the simple structure attributes. Nonetheless, measurements of more specialized attributes are needed to ensure that the forest management practices that retain more structure following harvest (e.g., Beese et al. 2003; Kreamsater et al. 2003) are actually working. As the rationale for retaining structure is to provide habitat for organisms that will not be routinely monitored, it is important to monitor and demonstrate effectiveness for at least a selection of nonstructural attributes to ensure that the forestry practices are working as envisioned.

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