

## DEVELOPMENT OF TREE SIZE DISTRIBUTIONS IN DOUGLAS-FIR FORESTS UNDER DIFFERING DISTURBANCE REGIMES

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**Abstract.** Two conceptual models describe the successional and structural development of mature and transitional stands toward old-growth *Pseudotsuga menziesii* (Mirbel) Franco forests in the Pacific Northwest. The “catastrophic/maturational” model is based on infrequent catastrophic disturbances that initiate the successional cycle, while the “chronic/partial fire” model is based on low- to moderate-severity fires which, over long periods of time, can create old-growth conditions through multiple disturbances. Although both models can produce similar structural characteristics, quantitative differences in speed and pathways of structural development with respect to these models are not well understood. To elucidate these quantitative differences, diameter distributions of live trees were investigated in a chronosequence of mature, transitional, and old-growth stands subjected to these two disturbance models. Stands characterized by the “catastrophic/maturational” model exhibited varying degrees of rotated sigmoid distributions up to 250–300 years of age because of long establishment periods and differential growth and mortality rates of the component species. They also showed a modest trend toward reverse-J distributions with increasing stand age. Stands characterized by the “chronic/partial fire” model had a stratum of distinctly older emergent trees with younger cohorts of *Pseudotsuga menziesii*, *Tsuga heterophylla* (Raf.) Sarg., and *Thuja plicata* Donn. and exhibited reverse-J distributions within about 150–200 years after disturbance. These results suggest that reconsideration of current definitions of what constitutes old-growth on *Tsuga* sites may be necessary. A conceptual model is presented, which links pathways of structural development to disturbance regimes. This model indicates that active management can hasten the development of old-growth structure, even in some older forests.

**Key words:** diameter distribution; Douglas-fir; fire, fire suppression; partial disturbance; Pacific Northwest; reverse-J; rotated sigmoid.

### INTRODUCTION

Structurally complex old-growth *Pseudotsuga menziesii* (Mirbel) Franco (Douglas-fir) forests are characterized by a high variability in tree sizes, a variety of tree species and other vegetation, many large live old trees, multilayered canopies, standing dead trees and snags, and large amounts of coarse woody debris (Franklin et al. 1981, 2002, Spies et al. 1988, 1990, Franklin and Spies 1991, Spies and Franklin 1991). Two main successional/developmental models have been identified for the transition from the single-layer canopy of mature forests to the multilayer canopy of old-growth and the maintenance of structurally complex old-growth *Pseudotsuga* forests in the western Cascades (Franklin et al. 2002, USDA Forest Service 2003). Both models recognize that the development of old-growth structure is profoundly affected by the intensity and frequency of coarse- and fine-scale canopy disturbance events and the resultant species composi-

tion of the young cohort (Spies et al. 1990, Gray 1995, USDA Forest Service 2003).

Under the “catastrophic/maturational” model, infrequent catastrophic disturbances initiate the successional cycle (e.g., Bormann and Likens 1979, Oliver 1981, Carey and Curtis 1996, Franklin et al. 2002). In even-aged *Pseudotsuga* stands, structural complexity develops during a maturation (Franklin et al. 2002) phase (also called the understory reinitiation [Oliver 1981] phase or transition [Bormann and Likens 1979] phase). This phase is characterized by fine-scale gap disturbances that break up the relatively uniform canopy and drive the transition to multi-layer old-growth forests with lower tree densities, increased tree sizes, and a gradual replacement of overstory *Pseudotsuga* by increasing amounts of regenerating/invasive shade-tolerant *Tsuga heterophylla* (western hemlock), *Thuja plicata* Donn. (western red cedar), and *Abies amabilis* (Dougl.) Forbes (Pacific silver fir) (Franklin et al. 1981, Stewart 1986a, b, Spies and Franklin 1989, 1991, Spies et al. 1990, Moer 1993). In even-aged mixed species stands of *Pseudotsuga*, *Tsuga*, and *Thuja*, structural complexity may develop faster, because different growth rates lead to stratification of these species into

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TABLE 1. Stand information, in order of maximum observed diameter. For dbh, values are means (with 1 SD in parentheses).

Characteristic	Stand				
	Cedar Creek	Fivepoint Creek	Salpeter Creek	Upper Silverstairs Creek	Upper Layng Creek
Classification	mature	transition	transition	transition	transition
dbh-age range					
<i>P. menziesii</i>	61–107	85–200	198–250	156–253+	249–285
<i>T. heterophylla</i>	94–107	150–180	98–199+	96–177	168–251
No. trees/ha	870	571	530	624	436
<i>P. menziesii</i>	340	252	189	243	131
<i>T. heterophylla</i>	171	259	324	257	242
<i>T. plicata</i>	356	59	6	16	27
No. trees > 100 cm dbh	0	0	3	3	16
Basal area (m <sup>2</sup> )	77.9	96.2	87.3	97.6	99.8
<i>P. menziesii</i>	46.8	74.2	61.2	70.8	69.8
<i>T. heterophylla</i>	17.1	16.8	24.8	22.8	26.8
<i>T. plicata</i>	13.9	4.8	0.8	2.7	2.8
dbh (cm)	30.3	40.2	38.8	37.3	44.3
	(14.8)	(23.1)	(24.3)	(24.5)	(31.0)
<i>P. menziesii</i>	40.1	59.9	62.5	59.2	80.7
	(11.8)	(12.8)	(14.6)	(14.5)	(16.9)
<i>T. heterophylla</i>	32.7	23.1	25.8	27.4	31.2
	(14.4)	(17.1)	(17.6)	(19.5)	(21.0)
<i>T. plicata</i>	19.9	30.5	35.2	40.2	30.2
	(9.9)	(10.9)	(22.0)	(24.2)	(20.1)

Notes: Species are *Pseudotsuga menziesii*, *Tsuga heterophylla*, and *Thuja plicata*. Classifications are based on watershed analyses conducted by the U.S. Forest Service (USDA Forest Service 1995, 1997). Age ranges (in years) are from a subsample of breast-height increment cores across the diameter distribution; + indicates individual trees for which the pith was not reached.

distinct size classes (Wierman and Oliver 1979), resulting in a stand with a wide range in tree sizes and a deep multilayered canopy, but a narrower range in ages.

Alternatively, the “chronic/partial disturbance” model is based on low- to moderate-severity fires (or to a lesser extent windthrow, insects, diseases, etc.) which, over long periods of time, can create old-growth forests through multiple disturbances (Morrison and Swanson 1990, Agee 1993). Under this model, the maturation phase is predicted to rarely, if ever, be achieved (Oliver and Larson 1996). Partial disturbances may destroy fire-susceptible species and initiate new cohorts of regeneration (fire) or release advance regeneration (wind) (Goslin 1997, Tappeiner et al. 1997, Zenner et al. 1998, Winter et al. 2002b), resulting in multicohort mixed stands with structures similar to those in the catastrophic/maturational model (Oliver and Larson 1996). More frequent partial stand fires create biological legacies that become key elements of the post-disturbance stand development, which has created a patchwork of stands with residual trees that have persisted through at least one fire (Stewart 1988, Morrison and Swanson 1990, Agee 1993, Huff 1995, Goslin 1997). In fact, partial fires are thought to be necessary to initiate new cohorts of *Pseudotsuga* in natural stands and to interrupt its complete replacement with more shade-tolerant species (Agee 1993, Swanson et al. 1994, Goslin 1997).

Catastrophic and chronic disturbance models both account for variable tree ages and allow the development of structurally diverse old-growth forests (Franklin and Waring 1980, Means 1982, Franklin et al. 2002). Although structural and successional pathways are known to differ between these disturbance regimes (USDA Forest Service 2003), resulting in highly variable structural characteristics of old-growth forests across the region (Spies and Franklin 1991, Spies 1998), quantitative differences in speed and pathways of structural development of mature and transitional *Pseudotsuga* stands toward old-growth with respect to disturbance regimes are not well understood.

To elucidate these differences, diameter distributions and differences in relative sizes and ages among species were investigated in this study. Diameter distributions of live trees in unmanaged coniferous forests are strongly related to forest structure, disturbance history, and time since the last stand-replacement disturbance (Spies 1998). Tree size distributions integrate individual structural features (e.g., live old-growth trees) and stand structural features (e.g., foliage distribution, multiple canopy layers) and are closely linked to the potential to produce future structural features (e.g., snags, coarse woody debris [Spies 1998]). Size distribution statistics of live overstory trees have been successfully used in distinguishing young, mature, and old-growth stands (Spies and Franklin 1991), in measuring similarity to old-growth structure (Acker et al. 1998), and

TABLE 1. Extended.

Stand				
Upper Dinner Creek	Upper Alex Creek	Upper Harvey Creek	Rose Hill	Junetta Creek
transition	transition	transition	old growth	old growth
193–289	201+–262	234–299	102–309+	259+–435+
183–212	161–232	127–287	55–158	87–129
520	404	586	378	351
153	137	145	34	49
221	250	375	300	260
113	16	35	29	3
14	25	27	31	49
103.2	105.0	106.8	85.0	108.9
58.0	74.3	81.3	44.8	76.4
21.7	27.3	17.9	33.5	30.6
14.3	2.9	5.5	4.7	0.2
42.0	47.4	35.7	40.8	44.8
(27.7)	(32.6)	(32.4)	(34.7)	(44.2)
65.8	80.8	80.1	128.7	135.8
(22.3)	(19.5)	(25.9)	(29.6)	(38.0)
29.5	29.4	19.3	32.8	31.4
(19.6)	(23.0)	(15.3)	(18.6)	(22.7)
32.6	41.9	36.6	35.1	22.0
(23.6)	(24.3)	(25.9)	(29.6)	(19.5)

in describing successional pathways and structural development (Goff and West 1975).

Despite the inherent variability of structural characteristics in old-growth forests, reverse-J diameter distributions have been ascribed as an emergent property of true old-growth *Pseudotsuga* forests (Franklin and Spies 1984, Oliver and Larson 1996). A reverse-J shape diameter distribution describes a curve of numbers of trees over diameter that is steeply and steadily declining (Leak 2002) and approximates negative exponential distributions (Goff and West 1975). Reverse-J diameter distributions can develop under the “catastrophic/maturational” model early in even-aged mixed-species stands (Oliver and Larson 1996) or later when stands are dominated by small canopy gaps (Whitmore 1989). There is evidence that stands exposed to the “chronic/partial disturbance” model may also exhibit reverse-J diameter distributions (Goslin 1997). It is unknown, however, how the diameter distributions along those pathways change, if they eventually lead to a reverse-J distribution, and in what time frame. One goal of this study was to quantify the structural development along a chronosequence of mature, transitional, and old-growth *Pseudotsuga* stands in south central Oregon, and to determine whether diameter distributions in stands exposed to the chronic/partial fire disturbance regime (prior to fire suppression) develop reverse-J distributions sooner than those exposed to the catastrophic/maturational disturbance regime. The second goal was to develop a conceptual model that links easily-measured diameter distributions to successional and structural developmental pathways. Such a model

would provide a framework for managers seeking to enhance the development of old-growth forest characteristics under varying time horizons.

## METHODS

### *Study area*

Sampling was conducted in natural mixed conifer forests in the lower and mid-elevations of the *Tsuga heterophylla* zone (Franklin and Dyrness 1973) in the Layng (nine stands) and Brice (Cedar Creek) Creek watersheds of the Umpqua National Forest on the western slope of the Cascade Range in the southern region of the Willamette Province (latitude 43°40' N, longitude 122°37' W) in Oregon (USA). Most natural stands in the Layng and Brice Creek watersheds (USDA Forest Service 1995, 1997) are multistoried, between 150 and 300+ years old, and stocked predominantly by *Pseudotsuga menziesii*, *Tsuga heterophylla*, *Thuja plicata*, and smaller components of *Libocedrus decurrens* Torr. (incense cedar) and *Taxus brevifolia* Nutt. (Pacific yew). The climate is temperate, with average precipitation ranging from around 1300 to over 1760 mm. Approximately 65% of the precipitation occurs between November and March, while less than 3% occurs in July and August. Elevations in the watershed range from 340 m to over 1400 m; stands were located between 610 m and 1160 m.

Fire played a major role in watershed structure and processes prior to the beginning of suppression efforts around 1900; very little of these watersheds was left unburned between 1600 and 1900. The results of fire

history studies conducted as part of watershed analyses (USDA Forest Service 1995, 1997) indicated a variable fire regime, ranging from infrequent, high-severity fires (more than 100 years between fires) that resulted in stand replacement to more frequent, light- to moderate-severity fires (25–100 year intervals) that resulted in partial stand replacement. This created a diverse mosaic with openings in the canopy interspersed with unburned patches in the burn areas. The mean fire return interval (i.e., the average time between fire occurrences) of these watersheds was about 22 and 26 years, with natural fire rotations (i.e., the length of time necessary for an area equal to the watershed area to burn) of 46.5 and 71.3 years, respectively.

#### *Stand classification*

The Layng and Brice Creek watershed analyses (USDA Forest Service 1995, 1997) classified stands within these watersheds as mature (stands 80–150 years old), transitional (stands over 150 years old), or old-growth (PNW-447 definition, Old Growth Definition Task Group [OGDTG] 1986). Transitional stands exceed 150 years of age, and are developing toward old-growth, but fall short in one or more of the required old-growth characteristics. Old-growth *Pseudotsuga* on *Tsuga* sites are defined as having two or more species with a wide range of ages and tree sizes, a deep multilayered canopy, large snags, and abundant large coarse woody debris (OGDTG 1986). Stand classifications for the plots are noted in Table 1. This definition sometimes classifies stands with old-growth live-tree characteristics as transitional forest because of a paucity of snags or coarse-woody debris, which included in this case Upper Layng Creek, Upper Harvey Creek, Upper Dinner Creek, Salpeter Creek, and Upper Alex Creek.

#### *Study sites*

Stands without evidence of fire scars and lacking notably larger, residual trees were taken to represent development under the catastrophic disturbance model. The presence of live trees with fire scars and Douglas-fir of predominantly large diameters indicated stands that had developed under the chronic/partial fire disturbance model. Site selection of plots of sufficient size to adequately characterize structural attributes was hampered by the paucity of unmanaged natural Douglas-fir stands in this region. The 10 1-ha plots in this study (Table 1) represented the only such stands within two entire watersheds, with the exception of a few open stands with exclusively shrub understories that were excluded, with uniform topography and aspect. Species, diameter at breast height (dbh), crown ratios, and canopy class relative to the general canopy for all live trees  $\geq 5$  cm in dbh were recorded. Snags were recorded by species and dbh and as one of three decay classes

(i.e., recent mortality [with needles], decay class 1; hard snags, decay classes 2 and 3; and soft snags, decay classes 4 and 5) after Cline et al. (1980). Defining density as numbers of trees, *Pseudotsuga* contributed between 9 and 45%, *Tsuga* between 20 and 79%, and *Thuja* between 1 and 41%. To supplement the watershed analysis, plots were aged by recording individual tree ages from a subsample of increment cores at breast height from the full range of diameters, and stump rings from adjacent areas were counted where present. For the largest diameter trees, these ages are minima (i.e., the pith could not be reached). The presence of fire scars was also noted on individual trees within each stand.

#### *Diameter distributions*

To describe the diameter distributions by species and plot, species-specific and compound diameter distributions were constructed with 5-cm class intervals. Diameter-class frequency distributions were then converted to relative frequency distributions. Graphical examination indicated that the distributions ranged from bell-shaped and skewed unimodal patterns to bimodal, rotated sigmoidal, and reverse-J shaped. Thus, the first-, second-, third-, and fourth-order semilogarithmic transformed polynomial functions were fitted with the relative frequencies of diameter class midpoints (Figs. 1 and 2) by using linear regression methodology. SAS Version 8 (SAS Institute Inc. 1999) was used to construct and test all statistical models.

## RESULTS

### *Size distribution of trees*

The observed diameter distributions shown in Figs. 1–3, in increasing order of maximum observed diameter, track the trajectory of structural development from mature to old-growth forest. Several tree size distribution patterns were found. A slightly skewed, near-normal distribution was observed for the catastrophic mature stand at Cedar Creek. The catastrophic transitional stands demonstrated various degrees of rotated sigmoidal patterns (Upper Silverstairs Creek, Salpeter Creek, Fivepoint Creek, Upper Layng Creek, Upper Dinner Creek, and Upper Alex Creek). Rotated sigmoid distributions (Figs. 1 and 2) or logarithmic rotated sigmoid distributions (Fig. 3) are characterized by curves of numbers or the log of tree numbers over diameter that exhibit a flattened plateau, near plateau, or bump in the mid-range of the diameter (Goff and West 1975, Leak 2002). A transitional pattern between rotated sigmoid and reverse-J distribution was observed in the chronic transitional stand (Upper Harvey Creek), while the chronic old-growth stands Rose Hill and Junetta Creek exhibited reverse-J distributions.

Catastrophic transitional stands seemed to mark a

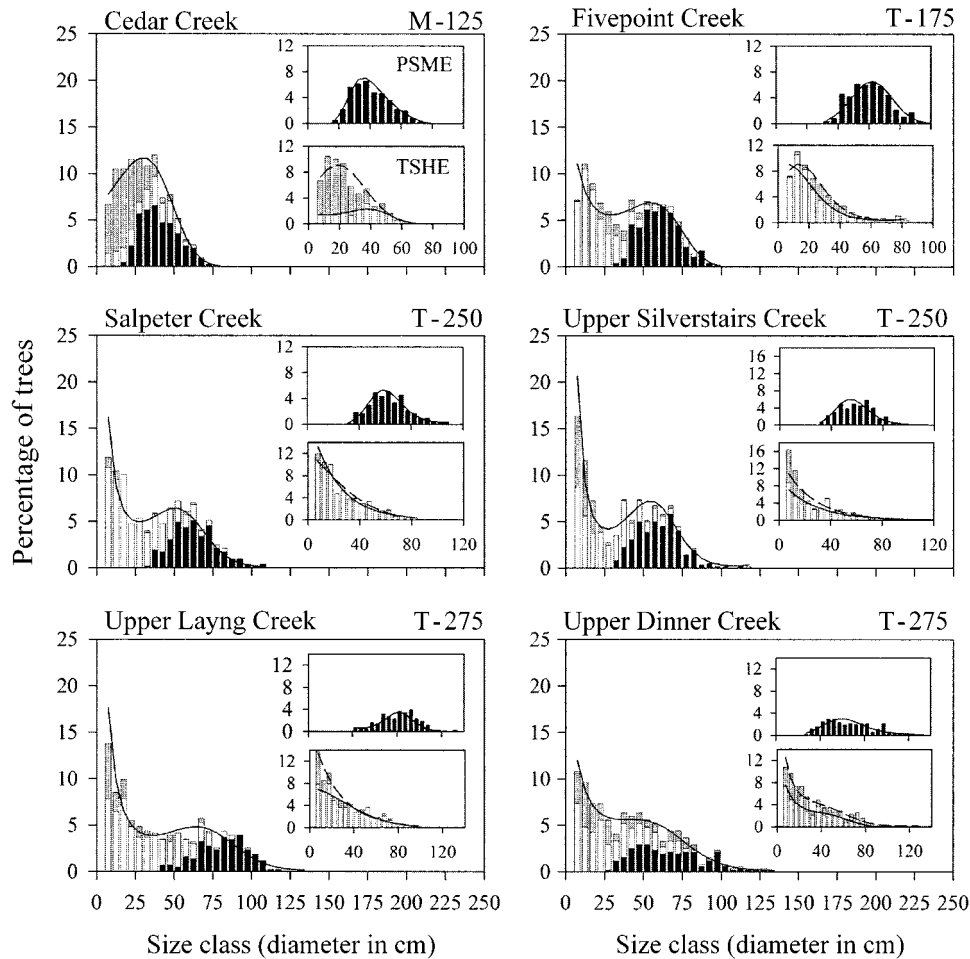


FIG. 1. Relative frequency diameter distributions for all tree species (*Pseudotsuga* [PSME], black bars); *Tsuga* [TSHE], light gray bars; and other species [OTHER], dark gray bars). Insets are for *Pseudotsuga* (PSME, black bars), *Tsuga* (TSHE, light gray bars), and a combination of TSHE plus other species except *Pseudotsuga* (non-PSME, dark gray bars). Stands are ordered by maximum observed diameter. Stand classifications are indicated after the stand's name, where M indicates a mature stand, and T indicates a transitional stand. Ages of the oldest trees cored in the stands are given after the stand classification label. Regression curves are superimposed on the diameter distribution.

gradual evolution of the rotated sigmoid toward reverse-J distributions. Chronic transition and old-growth were also distinguished from the catastrophic mature and transition as having (1) trees distributed among a greater number of size classes, contributing to overall larger means and standard deviations of the tree diameters, (2) few trees in size classes >100 cm (as opposed to extremely few or none for mature stands), and (3) generally lower tree densities per hectare.

The rotated sigmoid distributions in this study were due to the combination of two different distributions: the predominantly reverse-J distribution of the shade-tolerant species (*Tsuga*, *Thuja*, and, to a lesser extent, *Taxus*) and a bell-shaped or flat distribution of *Pseudotsuga*. *Pseudotsuga* was clearly the dominant species in all stands. Whereas the mature and catastrophic transitional stands exhibited a strong mode, *Pseudotsuga* tree size distributions in chronic transitional and old-

growth stands were characterized by "flat" diameter structures across a wide range of diameter classes, in which there were few pronounced peaks and a uniformly low number of stems. The density of *Pseudotsuga* declined markedly along the gradient from mature to old-growth.

The more shade-tolerant *Tsuga* was consistently more abundant in smaller size classes and had, with the exception of Cedar Creek, generally higher densities per hectare than *Pseudotsuga*. *Tsuga* approximated a bell-shaped distribution in the catastrophic mature Cedar Creek stand and right-skewed distributions at chronic transitional Rose Hill and old-growth Junetta Creek. Pooling all tree species present except *Pseudotsuga* generally reinforced the pattern seen with *Tsuga* alone, with the exception of Cedar Creek, where the distribution was best described by a right-skewed bell-shaped distribution.

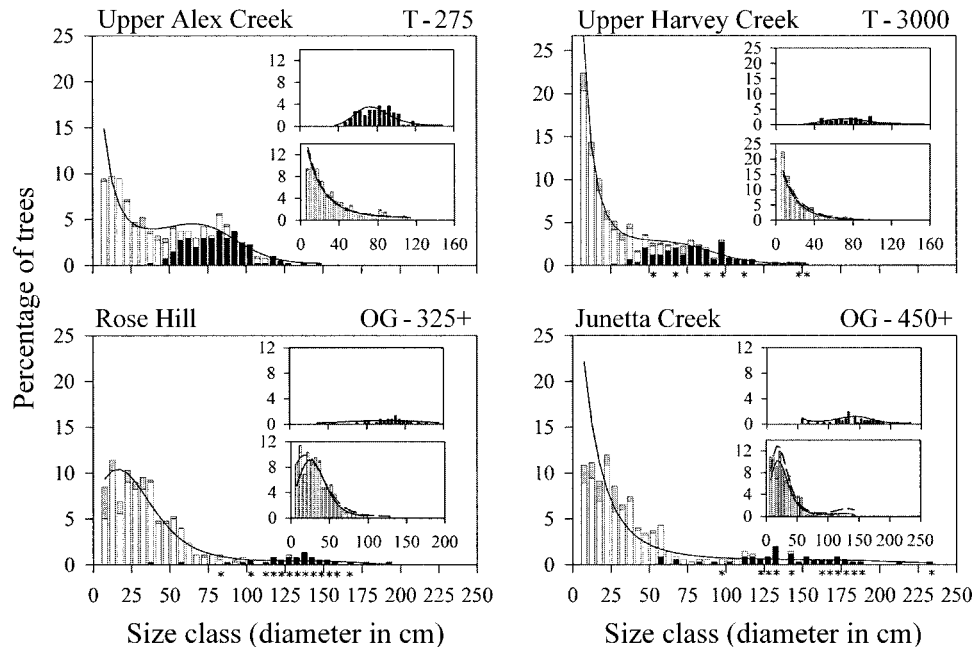


FIG. 2. Relative frequency diameter distributions for all tree species (*Pseudotsuga* [PSME], black bars); *Tsuga* [TSHE], light gray bars; and other species [OTHER], dark gray bars). Insets are for *Pseudotsuga* (PSME, black bars), *Tsuga* (TSHE, light gray bars), and a combination of TSHE plus other species except *Pseudotsuga* (non-PSME, dark gray bars). Stands are ordered by maximum observed diameter. Stand classifications are indicated after the stand's name, where T indicates a transitional stand, and OG indicates an old-growth stand. Ages of the oldest trees cored in the stands are given after the stand classification label. Asterisks in the chronically disturbed stands (i.e., Upper Harvey Creek, Rose Hill, and Junetta Creek) indicate size classes that showed evidence of past fires. Regression curves are superimposed on the diameter distribution.

#### Mortality

In all stands, both hard (decay classes 2 and 3) and soft snags (decay classes 4 and 5) integrated mortality over a longer time frame and thus had a wider range of diameter classes than recent mortality (decay class 1), especially for *Pseudotsuga* (Figs. 4 and 5). Comparing recent mortality to the live diameter distributions in Figs. 1 and 2, the greatest mortality is among the smallest diameter classes and not in the midrange of the distribution. Soft snags in both Rose Hill and Junetta Creek revealed the occurrence of fire disturbances that were probably responsible for initiating the younger cohorts observed in these stands.

#### Age structure

Arranging stands by the oldest observed ages corresponded very closely with the arrangement based on largest tree sizes and shapes of the diameter distributions (Table 1). Stand ages based on the oldest recorded tree ages varied between about 125 years in catastrophic mature Cedar Creek to over 600 years counted on cut stumps just outside the 1-ha plots in chronic old-growth Rose Hill and Junetta Creek. Transitional stands were between 200 and 300 years old.

Although the span of *Pseudotsuga* ages across 50–120+ years is attributed to a long establishment phase, the occurrence of light or patchy multiple burns can

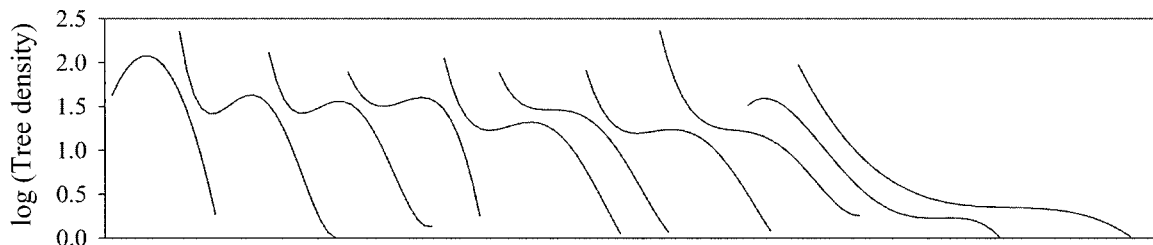


FIG. 3. Change in the shape of regression curves for all trees from mature (left) to old-growth (right) stands. Stands are ordered by maximum stand diameter.

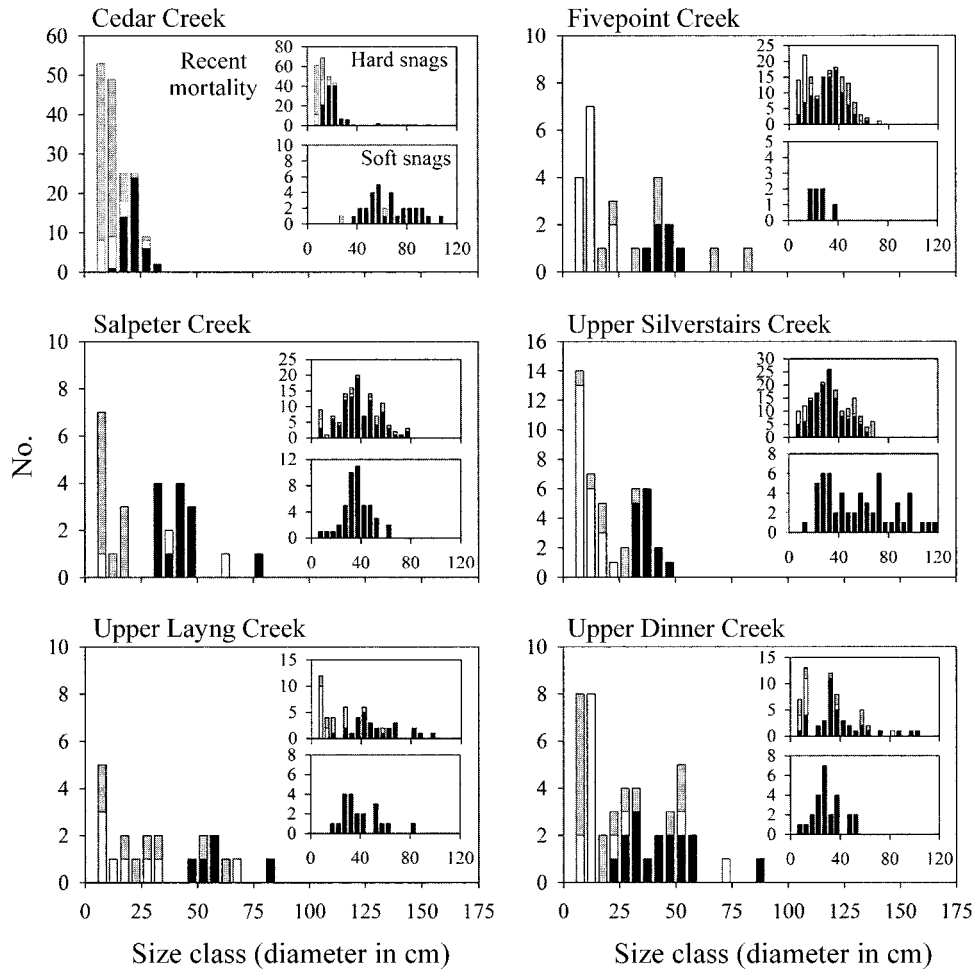


FIG. 4. Recent mortality, hard snags, and soft snags (in counts) of *Pseudotsuga* (black bars), *Tsuga* (light gray bars), and other species (dark gray bars).

not be excluded. In the three chronic stands (Upper Harvey Creek, Rose Hill, Junetta Creek) with observed fire scars on many large *Pseudotsuga* (9, 21, and 20, respectively), which were at least a century older than most shade-tolerant species, partial disturbance was followed by an extended period of regeneration of primarily shade-tolerant species, and of *Pseudotsuga* in Upper Harvey Creek and Junetta Creek.

DISCUSSION

*A conceptual model of structural development pathways in transitional Pseudotsuga forests*

Structural development of natural transitional stands can be hypothesized to vary between (1) a gradual, smooth transition to old-growth characterized by the reverse-J diameter distribution, (2) a transition that is interrupted by low to moderate intensity fires that retains a substantial number of large, old *Pseudotsuga* and leads to a quick re-establishment of the reverse-J diameter distribution due to the regeneration of shade-tolerant species, and (3) moderate to severe partial

stand replacement disturbances that keep diameter distributions in a shorter loop consisting of skewed normal and rotated sigmoid diameter distributions by also regenerating some shade-intolerant species (Fig. 6).

*The catastrophic/maturation model*

There are two pathways under the catastrophic/maturation model that would lead to the development of old-growth structures over long periods of time. A successional pathway is initiated in even-aged *Pseudotsuga* stands during the maturation phase (Fig. 6A). The process of overstory tree mortality, which can create canopy gaps, is purported to begin as early as at age 80–100 and is inaugurated when mortality shifts from density-dependent to density-independent agents (e.g., insects, disease, wind, storms) and development of decadence in overstory trees begins (Franklin et al. 2002). However, the speed of (successional) old-growth development, which depends in part on the successful establishment of young cohorts of shade-tolerant species such as *Tsuga* and *Abies*, can be slow in

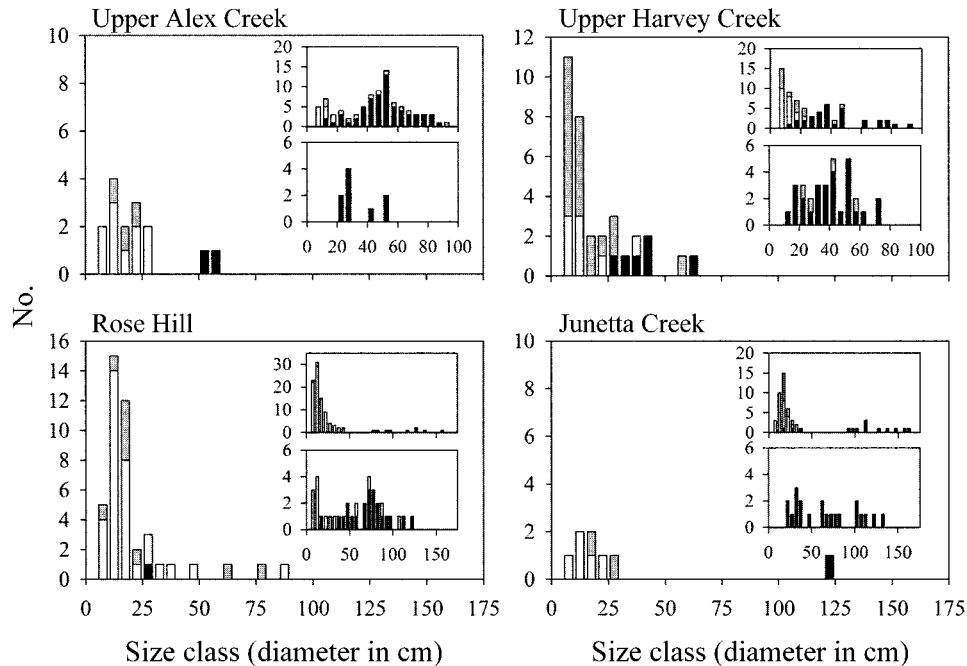


FIG. 5. Recent mortality, hard snags, and soft snags (in counts) of *Pseudotsuga* (black bars), *Tsuga* (light gray bars), and other species (dark gray bars).

tall *Pseudotsuga/Tsuga* forests because of narrow crowns and slow gap formation and filling rates that often exceed 50–100 years and up to 300–400 years without development of tree seedlings (Stewart 1986a, Spies and Franklin 1989, Van Pelt 1995).

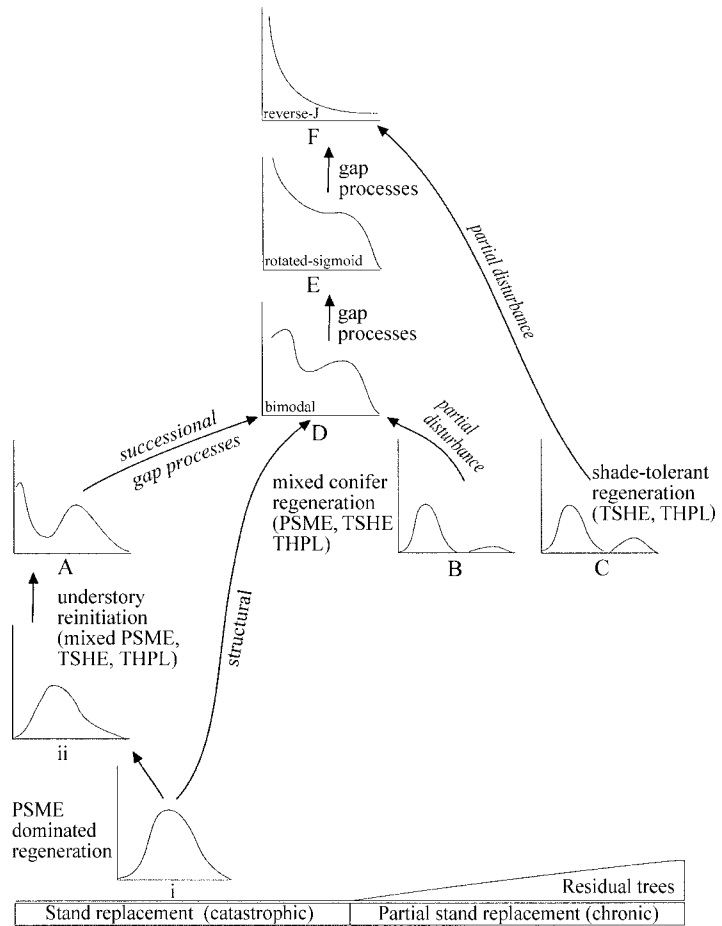
No evidence of successional replacement was found in this study. Transitional stands of 200–300 years of age were not characterized by overstory decadence and a recent reinitiation of shade-tolerant tree species (i.e., few trees were less than 100 years old and no regeneration was observed), which make gap processes an unlikely cause for the observed changes in diameter distributions. Age structures, diameter distributions, and recent mortality from this study rather suggest that the mixed *Pseudotsuga-Tsuga* stands that established following stand replacement fires followed a structural rather than successional pathway. A structural pathway develops in even-aged stands of mixed species with differential growth rates (Smith 1986, Hedman and Van Lear 1995, Oliver and Larson 1996) (Fig. 6i). In this study, this pathway resulted from long establishment periods, differential growth rates of regenerated species, and differential mortality among species and size classes.

The observed rotated sigmoid distributions, although ultimately transient, are long-lived in mixed *Pseudotsuga* stands, being similarly a result of long periods of stand establishment and species-specific growth dynamics. Stratification of species into distinct size classes due to different growth rates is a common structural feature in even-aged mixed stands and has been doc-

umented for *Pseudotsuga* and *Tsuga* in the Pacific Northwest (Wierman and Oliver 1979), where the former generally out-competes the latter after severe disturbances (Zenner et al. 1998). Stratification would soon result in a skewed normal diameter distribution (Cedar Creek) and would explain its further change to the rotated sigmoid pattern observed in younger transitional stands (Upper Silverstairs Creek). A similar sequence was reported by Goff and West (1975) for northern hardwood forests, where the plateau in the rotated sigmoid distribution was attributed to inter-specific size differentiation.

In the absence of partial disturbances, the development towards conglomerate reverse-J diameter distributions is a slow process that can take several (two to three) centuries and develops after stands exhibit various degrees of rotated sigmoid distributions for an extended period. This process is largely driven by the changes in distributions of the component species, i.e., by differential growth and differential mortality between *Pseudotsuga* and *Tsuga*. The mid-tolerant *Pseudotsuga* was characterized by a lack of stems in smaller size classes and a more or less normal diameter distribution (Figs. 1 and 2). *Pseudotsuga*'s diameter distributions exhibited varying degrees of skewness, but essentially followed a gradually widening and flattening normal distribution as stands moved towards increasing old-growthness (Figs. 1, 2, 6D–F). Higher growth rates of *Pseudotsuga* essentially stretch the distribution to the right, while higher mortality rates of the smaller overstory *Pseudotsuga* gradually erode the

FIG. 6. A conceptual model for the development of diameter distributions after complete (left) and partial (right) stand replacement disturbances in mature and old-growth *Pseudotsuga/Tsuga* stands. The speed of development toward a reverse-J distribution depends on species composition of the regeneration and the number of residual trees surviving the disturbance event. In a complete stand replacement disturbance (i), transient bimodal diameter distributions (D) would develop if the regeneration consists of a mixture of shade-intolerant and tolerant species. The pathway is of the structural type (i.e., differential growth rates). A regeneration dominated by shade-intolerant species such as *Pseudotsuga* (i) would develop first through a skewed normal distribution phase (ii) and would arrive at a bimodal distribution (D) after more shade-tolerant species such as *Tsuga* and *Thuja* establish during the understory reinitiation phase (A). This pathway is of the successional type (i.e., different age cohorts). In a partial stand replacement disturbance, the composition of the regeneration is related to the number of residual trees that survived the event. If few residual trees survive and the regeneration is mixed (B), stands would develop through a bimodal stage toward a rotated-sigmoid distribution (E). Further absence of disturbance would eventually lead to a reverse-J distribution due to increasing mortality in the upper diameter classes. Partial stand disturbances at that stage, however, may route the development through B or C. If many residual trees survive and the regeneration is dominated by shade-tolerant species (C), the development would proceed swiftly toward a reverse-J distribution (F).



saddle of the rotated sigmoid distribution. Size-class distributions of recent mortality and hard snags indicate that most of the mortality in these stands occurs in the smallest size classes occupied by *Tsuga* and *Thuja* either due to low resources or competition, followed by trees in intermediate to large size classes of mostly smaller overstory *Pseudotsuga*. Over time, the diameter distribution would be increasingly dominated by more shade-tolerant species such as *Tsuga* and *Thuja*, which had already approached a reverse-J distribution in younger transitional stands, although quite often with under-representation in the smallest size classes. Ultimately, the replacement of *Pseudotsuga* would require the successful establishment of young cohorts of *Tsuga*, because of *Tsuga*'s shorter life span than *Pseudotsuga*'s. This development sequence is consistent with previous findings that diameter distributions of tree species in uneven-aged forests are a function of their successional status and shade-tolerance (West et al. 1981, Muller 1982, Cho and Boerner 1991), which typically range from unimodal with varying degrees of skewness to reverse-J (Lorimer and Krug 1983).

*The chronic/partial fire model*

The presumption of the chronic/partial fire conceptual model that hypothesizes that low to moderate se-

verity fires may be responsible for the creation and maintenance of extensive areas of old-growth forests through multiple disturbances over many centuries in the western hemlock zone (Morrison and Swanson 1990, Agee 1993, Swanson et al. 1994) finds support in this study. Stands that have experienced at least one partial fire in this study exhibited a rotated sigmoid with a gently declining saddle and reverse-J diameter distributions. In this case, partial stand replacement fires most likely killed trees of the lower stratum, eroded the saddle of a rotated sigmoid distribution by killing smaller more vulnerable mid- and upper stratum *Pseudotsuga*, and created sufficiently large openings allowing a newer cohort including some shade intolerants (e.g., Rose Hill) to become established.

Partial stand replacement disturbances may thus either erode the saddle of a rotated sigmoid if the disturbance is light (Fig. 6C), or possibly initiate a new cohort with fewer residual trees left on site in the case of moderate partial-stand replacement disturbances (Fig. 6B). Moderate partial stand-replacement fires may be the key to regenerating *Pseudotsuga* while maintaining some overstory component through multiple disturbances (Morrison and Swanson 1990, Goslin 1997), which would explain the wide range in ages of

*Pseudotsuga* in the old-growth stands. Similarly, Means (1982) concluded that the broad range of tree ages (80–460 years) found in two dry-site *Pseudotsuga* stands was the result of periodic fires that killed lower strata and some of the older, larger trees and enabled the prolonged establishment of *Pseudotsuga* and *Libocedrus* among the large residual trees. In the absence of partial fires, *Pseudotsuga* is not replacing itself in these stands as evidenced by the absence of *Pseudotsuga* in small size classes and decreases in abundance with increasing old-growthness. Not all partial disturbances, however, may lead to the regeneration of *Pseudotsuga*. Whereas *Pseudotsuga* can establish on mesic sites in canopy openings >0.075 ha (Spies and Franklin 1989, Spies et al. 1990), canopy disturbances that thin rather than clear the canopy over the affected areas (e.g., insects, wind, disease) may not promote *Pseudotsuga* regeneration (Winter et al. 2002a, b). Such a disturbance would more likely lead to a pulse of *Tsuga* regeneration and growth increases in released older *Tsuga* (Winter et al. 2002a, b).

It further appears that under the chronic/partial fire model the development toward a reverse-J diameter distribution may be accelerated over that following the catastrophic/maturation model. Although chronic old-growth stands were older than the catastrophic stands, it does not appear that the reverse-J diameter distribution is a mere consequence of the age difference, but is rather due to the developmental pathway. Apart from very old and very large residual trees that survived at least one partial disturbance, mid- to lower-stratum *Tsuga* and *Thuja* in Rose Hill and Junetta Creek that were mostly younger than 200 years of age were primarily responsible for achieving a reverse-J distribution in these stands in less than 150–200 years. In contrast, stands following the catastrophic/maturation model still exhibited rotated-sigmoid distributions at ages between 200–300 years (Figs. 1–3). The reason for this difference is the species composition of stands following either a partial or complete stand replacement disturbance. For example, Rose Hill and Junetta Creek had low proportions (by density) of *Pseudotsuga* (9% and 13%, respectively) that were between one-half and one-third those of younger transitional stands (29–44%). Consequently, a higher proportion of shade-tolerant species that more strongly tend towards reverse-J diameter distributions would explain the expedient restoration of the reverse-J structure after partial disturbances. Differences in partial disturbances between Upper Harvey Creek and Rose Hill/Junetta Creek, where densities of *Pseudotsuga* were 3–4 times higher at the former site, would explain why Upper Harvey Creek occupies an intermediate position between rotated sigmoid and reverse-J distributions.

Results from this study further support the conclusion that in the case of partial fires, structural and successional pathways as well as speed of development depend heavily on the nature of the disturbance (e.g.,

size, intensity, and frequency) and the legacies created by the disturbance (e.g., density and spatial pattern of residual trees) (Hansen et al. 1995, Goslin 1997, Zenner et al. 1998, Franklin et al. 2002). A cohort may be dominated by shade-tolerant trees if it grows beneath a dense overstory (Marquis 1992) or by shade-intolerant species if it grows beneath a light residual overstory (Minckler and Woerheide 1965, Oliver and Stephens 1977, Runkle 1982). For example, the proportion of *Pseudotsuga* in the young cohort is generally reduced and that of *Tsuga* is generally increased if more residual trees survive a partial stand replacement fire (Goslin 1997, Zenner et al. 1998). Thus, resulting diameter distributions can be quite variable and the pathway and speed with which stands develop toward reverse-J distributions may vary. For example, diameter distributions from a study of mixed, dual-aged *Pseudotsuga/Tsuga* stands with variable densities of surviving residual trees following partial stand replacement fires in the western central Cascades of Oregon (see Zenner et al. [1998] for stand descriptions) revealed several developmental pathways (Fig. 7). When many residual trees survived the fire, the young cohorts were dominated by *Tsuga* and arrived at a reverse-J diameter distribution within 110–120 years. With fewer surviving residual trees, *Pseudotsuga* dominated the young cohorts and exhibited mostly skewed normal diameter distributions. When the young cohort was a mixture of *Pseudotsuga* and *Tsuga*, rotated sigmoid distributions were observed before age 90. Similarly to some transitional stands in this study, the *Tsuga*-dominated and mixed *Pseudotsuga-Tsuga* stands exhibited many old-growth live-tree characteristics, but did not meet the PNW-447 definition of old-growth because of a paucity of snags or coarse-woody debris.

#### Fire suppression

Results of this study have to be interpreted with respect to potential effects of the policy of fire exclusion and suppression on the observed structural development of these stands. Significant evidence exists of frequent historic fire disturbances in the *Tsuga* zone of the Pacific Northwest (Agee 1993) as well as of these specific watersheds. Natural fire rotations of 95–145 years over the last five centuries in the Cascades (Morrison and Swanson 1990) are somewhat longer than the 45–71 years estimated for these watersheds (USDA Forest Service 1995, 1997). It is therefore very likely that most stands in this study would have experienced some partial fire. Thus, the apparently gradual change of diameter distributions in mixed *Pseudotsuga-Tsuga-Thuja* transitional stands (Fig. 3) is most likely an artifact of the policy of strict fire suppression rather than a prominent natural development pattern. More importantly, however, the process of old-growth development may have been retarded by fire suppression, because one of the more important mortality agents that move successional and structural developments along

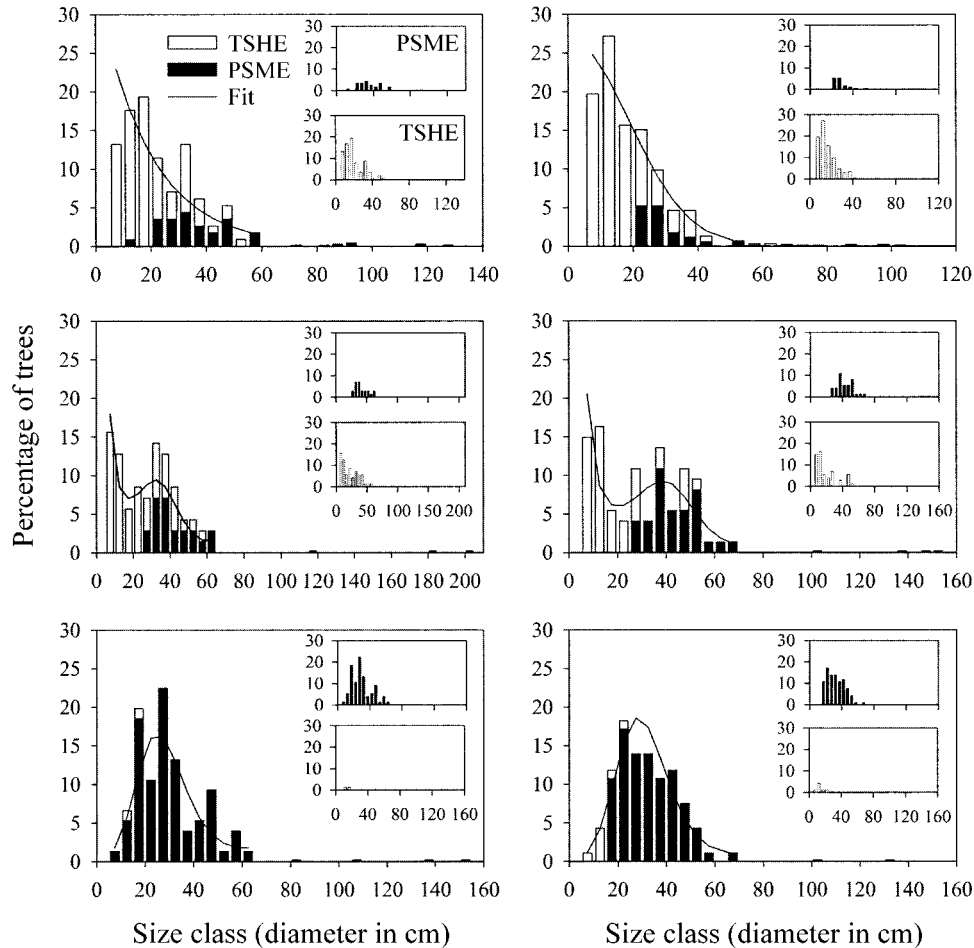


FIG. 7. Representative relative frequency diameter distributions for *Pseudotsuga* (PSME, black bars) and *Tsuga* (TSHE, light gray bars) based on stands described in Zenner et al. (1998). The different diameter distributions are closely related to the amount of *Pseudotsuga* in the regeneration.

has been eliminated. As a corollary, an increased recognition of the pervasive influence of fire in structuring forests would also call for a re-evaluation of the role of small gaps resulting from mortality of single or small groups of overstory trees in forest dynamics. Regeneration in gaps, if it exists at all, would be most vulnerable to partial fire disturbances and may thus play only a minor role in the development of old-growth structure in areas subject to the chronic/partial fire regime. Thus, the conclusion that small gaps may be relatively unimportant in forest dynamics in regions where large disturbances are frequent (Spies et al. 1990) may have to be extended to include regions where partial disturbances are frequent relative to the life span of the dominant tree species.

#### Scale issues

Although the plot sizes of 1 ha used in this study were large enough to capture the effects of partial disturbances (Goslin 1997, Zenner et al. 1998), the scale at which both disturbances and management take place

are usually much larger. Consequently, it is very likely that moderate partial disturbances may create openings with very few biological legacies interspersed with areas that are entirely skipped by the direct effects of the disturbance. Within the context of these larger scales, the concepts of catastrophic/maturation and chronic/partial are an artificial distinction given that partial disturbances most likely create a gradient of conditions encompassing both concepts at smaller scales (i.e., areas with none to many residual trees). Therefore, all of the structural developments alluded to in Fig. 7 are relevant at the landscape scale and may also be important at the scale of a partial disturbance. Not all of these structures would meet the PNW-447 definition of old-growth, however. For example, repeated chronic/partial fires may result in a pure *Pseudotsuga* stand of a wide range of sizes (and some of them large sizes), but without the fire-susceptible *Tsuga* and *Thuja*. Although these forests would be old, they would not meet the PNW-447 definition of old-growth. Therefore, old-growth definitions based on structures (sensu Oliver

and Larson 1996) would have to be expanded to encompass all outcomes of the structural development pathways. While Fig. 6 represents the set of possibilities that can be expected for structural development, further research is needed to allow better predictions of these pathways under different overstory retention regimes.

#### *Management implications*

Several important policy and management implications can be found in the results of this study. First, although similar forest structures can arise from different stand histories, developmental pathways, and processes (Spies 1998), it appears that a variety of disturbance patterns (or lack thereof) can lead to old growth with subtly different structural characteristics. For example, a catastrophic/maturational stand of only *Pseudotsuga* would take a long time to reach the PNW-447 definition for old-growth. Because shade-tolerant species would have come in several decades to centuries later, they would always be smaller than *Pseudotsuga*. In contrast, a mixed catastrophic/maturational stand would reach the PNW-447 definition much faster and *Tsuga* and *Thuja* that would be almost as large as *Pseudotsuga*. A chronic/partial stand resulting from a disturbance such as wind would also reach the PNW-447 definition faster, but may have large *Tsuga* and *Thuja* in the overstory as well as considerably smaller *Tsuga* and *Thuja* in the younger cohort. Repeated chronic/partial fires may result in a pure *Pseudotsuga* that would not meet the PNW-447 definition for an old-growth. It thus appears that the PNW-447 structures are just one of several structures that can result from *Pseudotsuga* forest development over long times without stand-replacing disturbance. Thus, the PNW-447 definition of old-growth may be too restrictive and may need to be broadened to include more of the potential structural variation in old-growth forests.

Second, a better understanding of the relationship between disturbances and structural pathways may help forest managers design better silvicultural and restoration practices intended to emulate natural disturbance processes in these forests, where current forest management policies place an increased emphasis on creating new and maintaining existing old-growth forests. For example, the Northwest Forest Plan requires application of silvicultural systems in Late-Successional Reserves (LSR's) that enhance the development of old-growth forest characteristics from currently young and mature stands and prevent large-scale disturbances that would destroy existing late-successional forests (Forest Ecosystem Management Assessment Team 1993, USDA and USDI 1994a, b). In matrix forests, the management objective is a combination of timber production and creation of structures similar to old-growth (USDA and USDI 1994a, b).

Based on the conceptual model presented in this study, managers operating under the catastrophic/mat-

urational model might choose transitional stands exhibiting eroded rotated sigmoid distributions as candidates for old-growth designation in LSR's. These stands can develop with little or no management, but it may take as long as 250 to 450 years to fully achieve late-successional forest conditions (Franklin and Spies 1991). In the long run, absence of management, however, can only lead to three possible outcomes. First, if stands remain undisturbed for hundreds of years, they will transition to *Tsuga*. Second, even with fire suppression, the odds are good that these stands will eventually burn and, if so, due to huge fuel loads and layered canopies, will be completely destroyed. Third, some stands may not develop to old-growth if they are too densely stocked and do not differentiate enough. For example, Tappeiner et al. (1997) found that densities of old-growth stands were far lower than those observed in mature stands in this study. In that case, they suggest that thinning may be needed in dense stands to speed the development of old-growth characteristics. Furthermore, Wilson and Oliver (2000) suggest that high-density stands have a limited stand-height window during which stand stability can be improved. Trees with higher height to diameter ratios that are more unstable (Wilson and Oliver 2000) combined with simulation results that indicate that young trees with as few as 250 trees/ha will develop along different developmental pathways than old-growth stands (Tappeiner et al. 1997), may preclude the development of old-growth structures in some mature forests.

Alternatively, the chronic/partial fire model might offer alternatives to hands-off management in matrix forests. Managers might choose to silviculturally emulate the effects of partial fires through partial cuttings (e.g., thinning and underplanting or green-tree retention), or reintroducing partial fires to create snags and coarse woody debris (Cissel et al. 1999) to speed up the creation of old-growth structures. Such active management would require a deliberate choice of fire intensity and the amount and pattern of residual trees, i.e., retaining enough large old overstory *Pseudotsuga* to garner their life-boating effects, but not too many to preclude the regeneration of shade-intolerants such as *Pseudotsuga* itself. For stands that are also expected to produce timber, the successful regeneration of *Pseudotsuga* in the presence of large residual trees will be a cornerstone of management that retains some commodity production while perpetuating old-growth conditions. In this case, retention levels of large old overstory trees will need to be low enough to facilitate *Pseudotsuga* regeneration (Fig. 6B rather than C); perhaps as low as 40 trees/ha (Zenner et al. 1998). Such stands that regenerate new cohorts with a sizeable amount of *Pseudotsuga* would be expected to again exhibit various degrees of rotated sigmoid distributions, depending on the species composition. In contrast, if few overstory trees are harvested, a reverse-J distribution is likely to quickly arise through the re-

generation of mostly shade-tolerant species. Thus the trademark diameter distribution indicative of management that mimics a moderate partial fire regime may in fact be the rotated sigmoid distribution.

Despite their historic importance in uneven-aged management, diameter distributions are, however, just one of many features managers consider when managing for development of old-growth structure. Just as old-growth cannot be reduced to large trees, it cannot be reduced to a single diameter distribution. However, retention of enough big trees is essential in any management alternative that seeks to follow natural precedents. Big old *Pseudotsuga* are the prerequisite that not only take the longest to develop, but that provide the future material needed for the large snags and logs, slowly decomposing coarse woody debris, and multiple canopy layers that are the hallmark of structurally complex old-growth forests in this part of the world.

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