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Fire-mediated pathways of stand development in Douglas-fir/western hemlock forests of the Pacific Northwest, USA

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Abstract. Forests dominated by Douglas-fir and western hemlock in the Pacific Northwest of the United States have strongly influenced concepts and policy concerning old-growth forest conservation. Despite the attention to their old-growth characteristics, a tendency remains to view their disturbance ecology in relatively simple terms, emphasizing infrequent, stand-replacing (SR) fire and an associated linear pathway toward development of those old-growth characteristics. This study uses forest stand- and age-structure data from 124 stands in the central western Cascades of Oregon to construct a conceptual model of stand development under the mixed-severity fire regime that has operated extensively in this region. Hierarchical clustering of variables describing the age distributions of shade-intolerant and shade-tolerant species identified six groups, representing different influences of fire frequency and severity on stand development. Douglas-fir trees >400 years old were found in 84% of stands, yet only 18% of these stands (15% overall) lack evidence of fire since the establishment of these old trees, whereas 73% of all stands show evidence of at least one non-stand-replacing (NSR) fire. Differences in fire frequency and severity have contributed to multiple development pathways and associated variation in contemporary stand structure and the successional roles of the major tree species. Shade-intolerant species form a single cohort following SR fire, or up to four cohorts per stand in response to recurring NSR fires that left living trees at densities up to 45 trees/ha. Where the surviving trees persist at densities of 60–65 trees/ha, the postfire cohort is composed only of shade-tolerant species. This study reveals that fire history and the development of old-growth forests in this region are more complex than characterized in current stand-development models, with important implications for maintaining existing old-growth forests and restoring stands subject to timber management.

Key words: developmental pathways; Douglas-fir; forest age structure; mixed-severity fire regime; Pacific Northwest, USA; Pseudotsuga menziesii; Tsuga heterophylla; *western hemlock.*

INTRODUCTION

Forests dominated by Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) in the Pacific Northwest (PNW) of the United States have profoundly influenced concepts and policy concerning old-growth forest conservation, yet their disturbance ecology is not well understood and has been highly simplified in public and policy debates (Spies 2009). Development of old-growth structure along a linear trajectory initiated by stand-replacing (SR) fire with no subsequent disturbances other than gap-forming processes (e.g., wind, insects, or pathogens) at the scale of individual to small groups of trees has been emphasized since some of the earliest studies in the region (Munger 1930). Recently, this pathway was elaborated to illustrate variation in the abundance, size, and vertical and horizontal distributions of live vegetation and coarse woody debris over long intervals since the stand-initiating disturbance (Franklin et al. 2002).

Although the traditional view of Douglas-fir/western hemlock forest development has emphasized SR fire, several fire-history studies over the last three decades suggest an important role of non-stand-replacing (NSR) fire (i.e., fire that kills <70% of the overstory trees; Agee 1993) in drier parts of the region, including much of the western Cascade Range in Oregon (Means 1982, Stewart 1986, Morrison and Swanson 1990, Weisberg 2004) and the east sides of the coastal mountain ranges in Washington and Oregon (Impara 1997, Wetzel and Fonda 2000). Within the central western Cascades of Oregon, for instance, NSR fire accounts for 74% of the area burned across two, 2000-ha study areas in the 19th century (Morrison and Swanson 1990) and 70% of the area burned by the 1991 Warner Creek Fire (Kushla and Ripple 1997).

Despite our knowledge of large areas of NSR fire in part of the Douglas-fir/western hemlock region (Fig. 1), we lack conceptual models that address the complexity of disturbance regimes and successional pathways.

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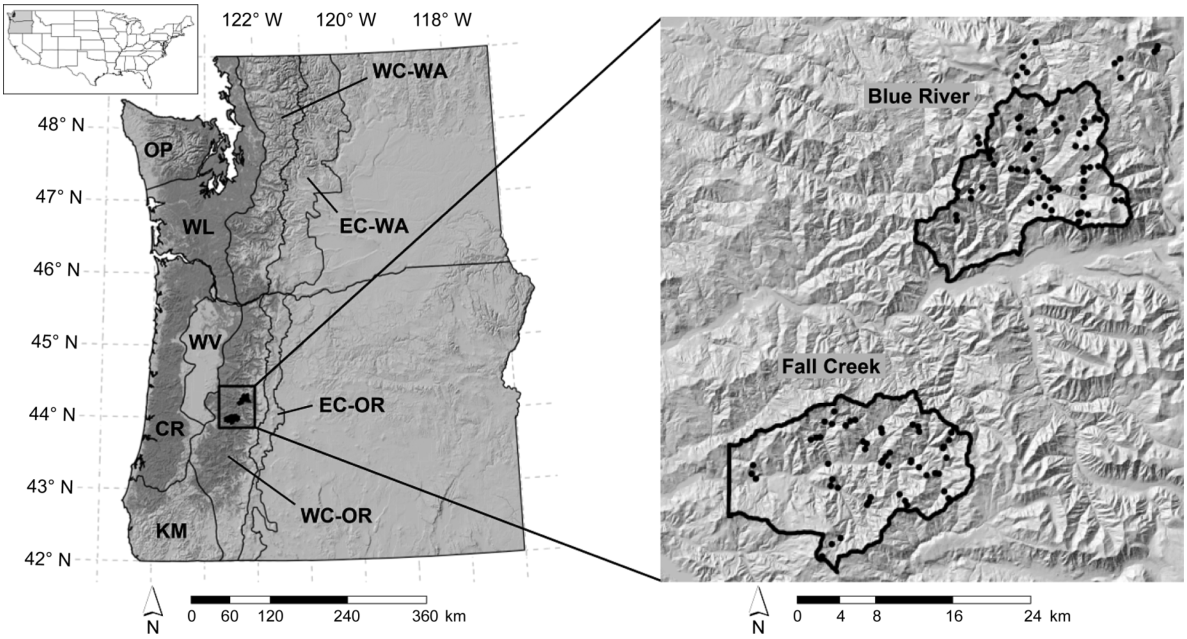


FIG. 1. Study areas and sampled transects in relation to the extent of Douglas-fir/western hemlock forests (dark shading, based on GIS data available at www.landfire.gov) and physiographic provinces of western Oregon and Washington, USA (WC-OR, Western Cascades of Oregon; EC-OR, Eastern Cascades of Oregon; WV, Willamette Valley; CR, Coast Range; KM, Klamath Mountains; WC-WA, Western Cascades of Washington; EC-WA, Eastern Cascades of Washington; WL, Western Lowlands; OP, Olympic Peninsula).

Highly simplified models of disturbance-driven forest dynamics could limit our understanding of the effects of climate change and forest management on forest development. For example, the widely accepted Douglas-fir development model based on SR disturbance (Franklin et al. 2002) acknowledges that the "disturbance and legacy creation" stage can contain trees that survive a fire, but it does not elaborate on development patterns and processes where substantial densities of trees survive fire and remain a major, if not dominant, component of forest structure throughout the development of one or more younger cohorts. Thus, using the SR fire model as the sole basis for restoration could greatly underrepresent the diversity of old-growth forest structures and development processes in portions of the region. Current restoration guidelines for moist forests west of the crest of the Cascade Range emphasize diversifying dense, young plantations and creating patches of diverse early-seral vegetation (Franklin and Johnson 2012). While these are critical restoration strategies for the SR component of these fire regimes and in the limited set of options available in plantations, it is important to also consider the roles of the NSR component in maintaining the diversity of vegetation and successional pathways where it has been historically important.

Effort thus far to develop conceptual models of this particular mixed-severity fire regime has been limited. Zenner (2005) used tree size distributions to propose two models of stand development (one influenced by infrequent, "catastrophic" fire and the other by chronic, partial disturbances) but this was based on data from only 10 stands, only three of which were interpreted as having experienced NSR fire. Other studies have characterized fire frequency and the occurrence of NSR fire by sampling fire scars and ages of Douglas-fir trees in recently harvested stands under the assumption that Douglas-fir is the species most likely to regenerate in response to fire (Weisberg 2004, Poage et al. 2009). However, the focus on ages of Douglas-fir provides limited insight into fire effects on compositional and structural development of entire stands. The few studies that examine ages of all species in stands with a history of NSR fire suggest strong potential for age-structure data to elucidate these effects (Means 1982, Stewart 1986, Goslin 1997), but these studies were conducted in a very small number of stands without a broader sampling framework conducive to gaining insight into the relative importance of SR and NSR fire beyond those stands.

The objectives of this study are to characterize the different pathways of stand development mediated by fire of varying frequency and severity in the central western Cascades of Oregon and evaluate the contribution of each pathway to variation in contemporary stand structures across a broad landscape. To address these objectives we pose the following questions: (1) What are the patterns in forest age structure (e.g., continuous establishment vs. discrete pulses of establishment) in stands across two large (240–300 km^2) watersheds? (2)

What do the patterns of forest age structure imply about the relative importance of SR and NSR fire? (3) To what extent do different histories of SR and NSR fire account for variation in contemporary forest structure?

This study focuses on the influences of fire on forest development pathways at the scale of local forest stands, where stand is defined as an area (10s of ha to ~100 ha) of relatively uniform forest structure and tree-age distribution at a particular slope position and aspect on a given slope facet. Thus, fire effects are evaluated at this fine scale even though the fires that most strongly affect broad patterns of forest structure in this region typically are large events (1000s to 100 000s of ha) that burn across numerous slope facets and produce complex mosaics of burn severity (Agee 1993). Sampling across the range of physiographic settings in two large watersheds enables inferences regarding the relative importance of SR and NSR fire across the broader landscape. The influences of topography on spatial variation in fire occurrence and severity will be evaluated in ongoing work based on the findings of Tepley (2010) to permit a stronger focus on fire-mediated stand development patterns in the present study.

METHODS

Study area

Sampling was conducted in two study areas, each centered on a large watershed in the central western Cascades of Oregon, USA (Fig. 1). The Blue River study area has deeply dissected terrain characteristic of the eastern part of the western Cascade Range. It includes the 240-km^2 Blue River watershed plus 33 km^2 to the north. Elevation ranges from 316 to 1753 m, and most major ridges reach elevations above 1200 m. The Fall Creek study area is the eastern 300 km^2 of the Fall Creek watershed (Fig. 1). It has lower topographic relief, representative of the western part of the western Cascades. Elevation ranges from 254 to 1519 m, but only the highest ridges along the southern perimeter of the study area are higher than 1200 m.

The climate of the central western Cascade Range in Oregon is characterized by mild, wet winters and warm, dry summers. Annual precipitation averages 233 cm in the Blue River study area and 182 cm at Fall Creek (Daly et al. 2008). Most precipitation falls in the winter, and a seasonal snowpack accumulates above ~900 m.

Two of the Vegetation Zones described by Franklin and Dyrness (1988) comprise almost the entire forested area of both study areas. The Western Hemlock zone accounts for nearly all of Fall Creek and the majority of Blue River, excluding ridges higher than ~1200 m. Forests of this zone are dominated by Douglas-fir, and the major shade-tolerant associates are western hemlock and western redcedar (*Thuja plicata* Donn ex D. Don). The Pacific Silver Fir zone is represented on ridges higher than ~1200 m, including most major ridges of the Blue River study area and a few ridges in the southern part of Fall Creek. Abundant shade-intolerant species of this zone are Douglas-fir and noble fir (*Abies procera* Rehd.), and the major shade-tolerant species are Pacific silver fir (*Abies amabilis* (Dougl. ex Loud.) Dougl. ex Forbes), western hemlock, and mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.). The Mountain Hemlock zone is found on the highest ridges in the Blue River study area, and the Douglas-fir climax type occurs locally at the driest sites in both study areas.

Field methods

Sampling was conducted in 124 stands: 71 in the Blue River study area and 53 at Fall Creek. Stands were located using a stratified random method that distributes sampling intensity throughout each study area while capturing most of the physiographic variation (Appendix A). Sample sites were identified by randomly selecting slope facets (areas of common aspect extending from ridgetop to valley bottom) across each study area and delineating the forested area at upper, mid, and lower slope positions of each facet. The forested area at each slope position was considered a stand, and a point was generated randomly within each stand to serve as the midpoint of a 120-m-long transect for sampling forest stand and age structure. Each transect consists of five, 0.02-ha circular plots at 30-m intervals. The entire transect is treated as a sample unit, providing one transect per stand and three stands per slope facet in most cases (see Appendix A). Sampling was conducted in five plots along a 120-m transect rather than a single plot of equivalent area to increase the likelihood that age classes are spread over broad areas, and thus, are likely to represent effects of widespread disturbance rather than local tree-fall gaps.

Stand-structure data include the diameter at breast height (dbh) of all live and standing dead trees >15 cm dbh throughout each 0.02-ha plot and the number of saplings and shrubs 1.5–15.0 cm dbh by species in a 0.01-ha subplot within each plot. Evidence of fire, including charred bark and open catfaces (wounds usually extending to a height of 1–2 m from the base of the tree and commonly formed due to damage to the cambium by fire), was recorded for each tree.

Age-structure data were collected by coring a subset of the live trees >15 cm dbh (>10 cm dbh for Pacific yew [*Taxus brevifolia* Nutt.]). The subset was determined by dividing each 0.02-ha plot into four quadrants and coring the largest tree of each species in each quadrant. These criteria ensured that each species was sampled nearly proportional to its frequency in the transect. Selecting the largest tree increased the likelihood of sampling the oldest individuals of each species, but sampling one tree per species per quadrant ensured that smaller trees also were sampled. In all, 3277 trees were cored, representing an average of 27 trees per transect, or 76% of the live trees >15 cm dbh. Eighty-five percent of the cores were cross-dated. Establishment dates were estimated for 3038 trees, limited to cores that intersected the pith or where the inner ring formed a complete arc.

Methods for processing tree cores are presented in Appendix B.

Age-structure data set

A set of four variables was selected to describe the distribution of establishment dates for shade-intolerant and four variables for shade-tolerant species. Species were grouped by shade tolerance to make use of the strong inverse relationship between shade tolerance and resistance to fire-caused mortality for the species in this study area, while avoiding influences of factors other than fire that affect the presence or relative abundance of individual species at the scale of the sample sites. Some of the variables characterizing the age distribution of shade-intolerant species differ from those used for shade-tolerant species to account for the potentially multimodal age distributions for shade-intolerant trees that are more likely to survive fire (e.g., due to thick bark, self-pruning of shaded lower branches, and higher resistance to rot if injured by fire), but whose regeneration tends to occur in pulses initiated by disturbances and continuing until the development of canopy closure in the post-disturbance cohort. By contrast, shade-tolerant species of the study area may exhibit nearly continuous regeneration in the absence of large disturbances, but their thin bark, shallow rooting, and low crown base height render them highly susceptible to fire-caused mortality.

Variables were selected to characterize the overall form of the age distribution without emphasizing establishment in particular time periods to facilitate identification of stands that followed similar development trajectories regardless of whether they burned in the same events. However, a threshold year of 1780 was used to identify trees that predate the more recent of two periods of widespread fire suggested by a regional synthesis of fire-history studies (the late 1400s to ca. 1650 and ca. 1800 to ca. 1925; Weisberg and Swanson 2003).

The variables for shade-intolerant species are (1) the proportion of trees that established before 1780, (2) the overall range of ages, (3) the age range of trees that established after 1780, and (4) the proportion of trees with charred bark. The proportion of shade-intolerant trees that established before 1780 may distinguish stands that remained unburned during the recent period of widespread fire from those that were burned. The overall range of ages may distinguish single- from multi-cohort stands, whereas the range of ages for trees that established after 1780 is likely to increase with the number of cohorts initiated after 1780. The oldest and youngest shade-intolerant tree in each stand was excluded from the overall age range. This trimming of the range had minimal influence on all but a very small number (i.e., <5) of transects where it avoids placing undue influence on a single tree that predates a younger cohort or an individual tree that established after a small-scale or low-intensity disturbance that otherwise did not promote widespread regeneration by shade-intolerant species. The proportion of trees with charred bark, while not an age-structure variable per se, provides an approximate ratio of trees that survived at least one fire to those that established following the most recent fire.

The variables for shade-tolerant species are (1) the proportion of trees that established before 1780 and the (2) range, (3) mean, and (4) standard deviation (SD) of shade-tolerant tree ages. A large proportion of shade-tolerant trees with establishment prior to 1780 would suggest the stand remained unburned during the recent period of widespread fire, and the range, mean, and SD of shade-tolerant tree age are likely to increase with time since fire. The last three variables were calculated after excluding the oldest shade-tolerant tree in each stand to reduce the influence of a single shade-tolerant tree that may have survived fire.

Analyses

Prior to statistical analyses, the values of each age-structure variable were converted to the number of SDs from the mean in order to equalize variance among variables measured on different scales and in different units. Transects were grouped by age-structure variables using hierarchical agglomerative cluster analysis, conducted in PC-ORD version 5.04 (McCune and Mefford 2006), with Euclidean distance and Ward's linkage method (Ward 1963). Dendrograms were scaled by Wishard's objective function (the sum of the error sum of squares from each group centroid to the group members; McCune and Grace 2002).

For the groups of stands identified by clustering of age-structure variables, differences in stand structure were evaluated using one-way ANOVA, followed by multiple comparisons using Tukey's HSD test (Venables and Ripley 1997). Assumptions of normality and homogeneity of variance were evaluated with normal probability plots and Levene's test (Fox 1997). If these assumptions were not met, the Kruskal-Wallis test was used, followed by multiple comparisons using the Behrens-Fisher test (Munzel and Hothorn 2001). The above analyses were conducted in R (R Development Core Team 2008).

Because this study seeks to interpret the different fire-mediated pathways of forest development with a focus at the scale of local forest stands, each transect is treated as an independent sample unit in the hierarchical clustering and ANOVAs. However, given that the study was conducted in two study areas with sampling at upper, mid, and lower slope positions along randomly selected slope facets, further analyses were conducted to evaluate whether the associations of stand structure with age-structure type found in the ANOVAs represent real differences rather than artifacts of the study design. In Appendix C, a measure of variable importance for age-structure type in the ANOVAs that treat each transect as an independent sample unit is compared to that of study

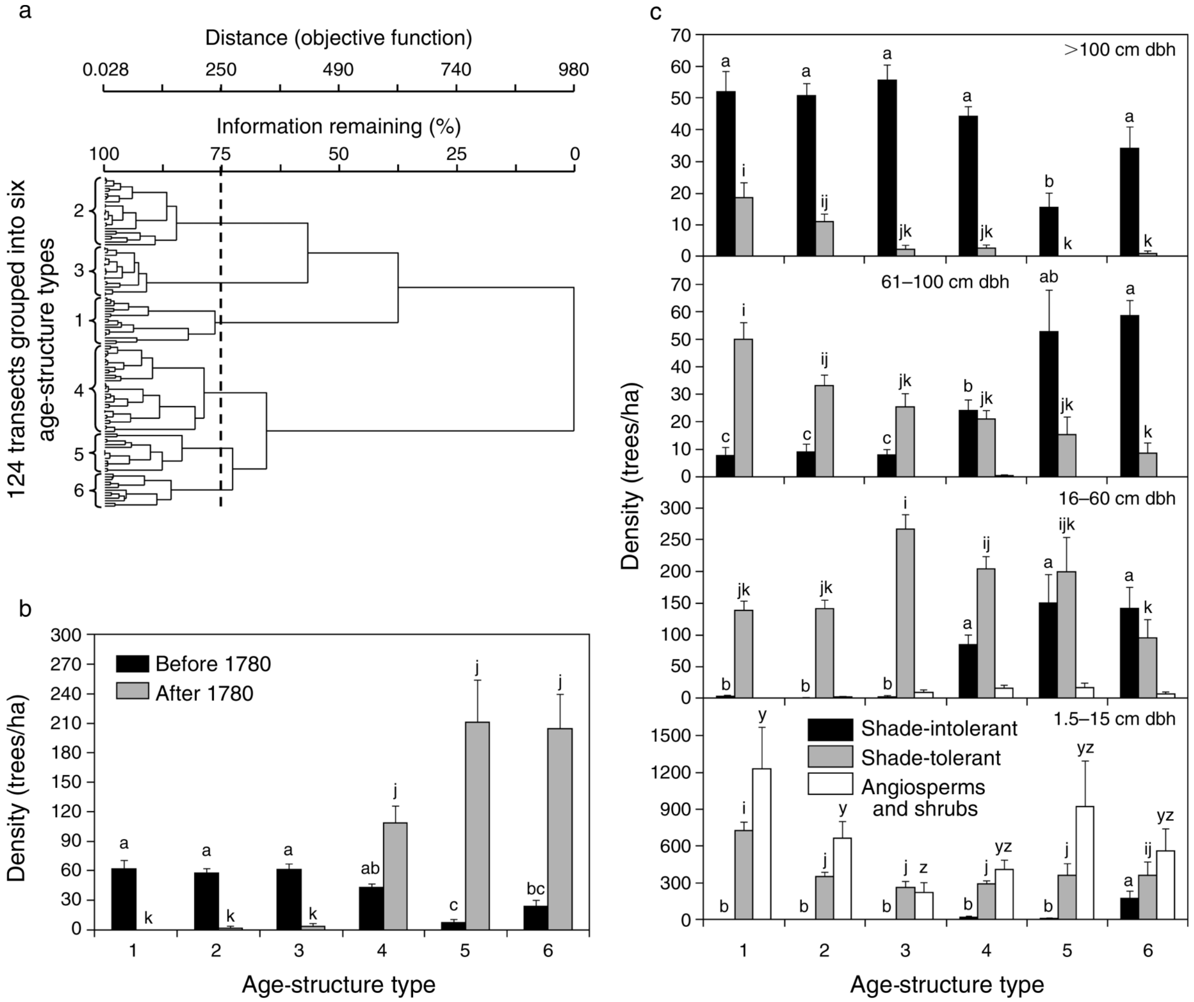


FIG. 2. (a) Hierarchical clustering of 124 stands by eight age-structure variables (four variables for shade-intolerant trees and four for shade-tolerant trees as described in the *Methods: Age-structure data set*), and comparisons of the (b) density (mean + SE) of shade-intolerant trees that established before and after 1780, and (c) density (mean + SE) of shade-intolerant trees, shade-tolerant trees, and angiosperm and shrubs species in four dbh classes among the six age-structure types. The dendrogram was scaled by Wishard's objective function (sum of the error sum of squares from each group centroid to the group members). Lowercase letters indicate statistically significant differences ($P < 0.05$) based on Tukey's HSD test or the Behrens-Fisher test.

area and slope position under a mixed-effects analysis that fully represents the study design of three slope positions nested within the two study areas.

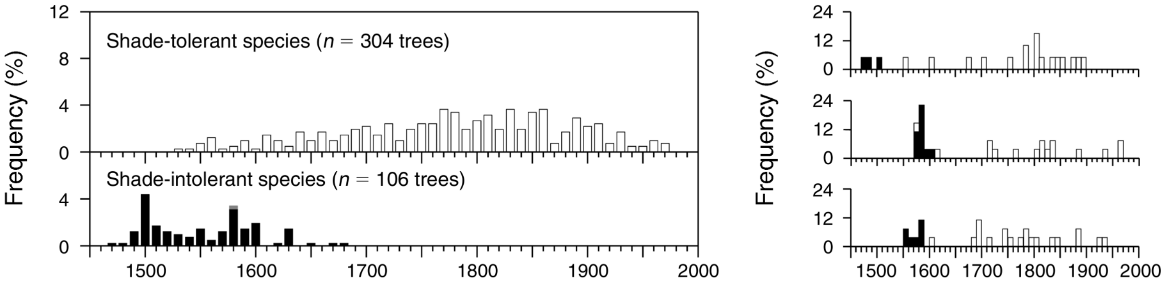
RESULTS

Age structure and developmental pathways

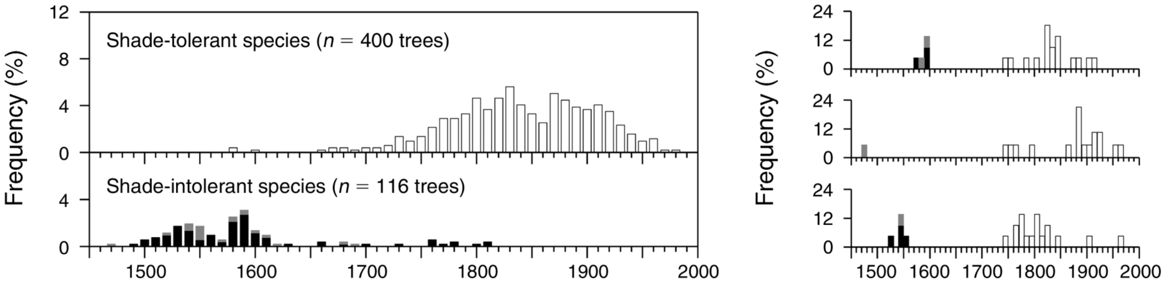
Almost all (96%) shade-intolerant trees in the age structure data set are Douglas-fir. The other shade-intolerant species are noble fir, incense cedar (*Calocedrus decurrens* (Torr.) Florin), western white pine (*Pinus monticola* Dougl. ex D. Don), and sugar pine (*Pinus lambertiana* Dougl.). The most abundant shade-tolerant species are western hemlock (69%), western redcedar (14%), and Pacific silver fir (11%). Pacific yew, mountain hemlock, grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.), and Alaska yellow cedar (*Callitropsis nootkatensis* (D. Don) D.P. Little) comprise the remaining 6%.

Hierarchical clustering of the eight age-structure variables produced six distinct groups (Fig. 2a), hereafter referred to as age-structure types. Within- and between-group variability of the age-structure types is further evaluated in Appendix D. The primary division of the dendrogram reflects differences in the age distribution of shade-intolerant species. In most stands, establishment dates for shade-intolerant trees fall within ~40-year-long pulses, and multiple pulses per stand are separated by an interval at least 80 years long with no recorded establishment of any species. Age-structure types 1–3 all have a single pulse of establishment, or cohort, of shade-intolerant trees initiated before 1780. All stands of types

a) Age-structure type 1 (*N* = 18 transects)



b) Age-structure type 2 (*N* = 26 transects)



c) Age-structure type 3 (*N* = 19 transects)

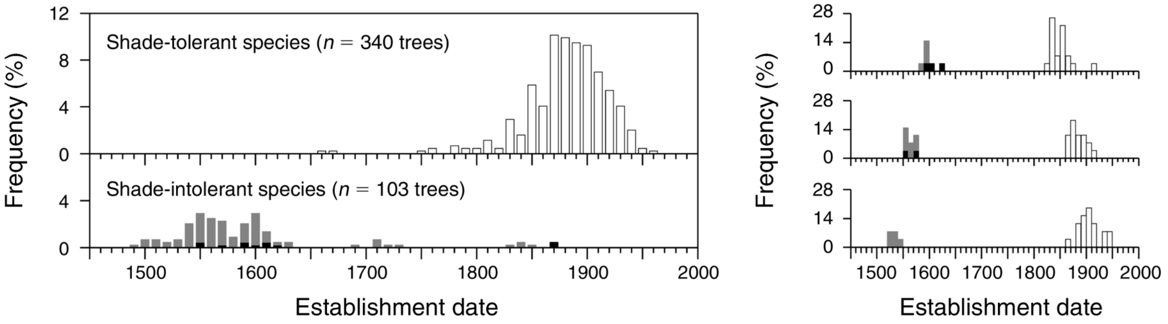


FIG. 3. Comparison of age distributions for shade-intolerant and shade-tolerant species among six age-structure types in the central western Cascades of Oregon. For each type, the composite histogram for all stands is shown on the left. Histograms for three representative stands are shown on the right to better illustrate the distinctiveness of establishment pulses in individual stands. Establishment dates for shade-intolerant species are shown in gray if the trees have charred bark and in black otherwise. White shading represents shade-tolerant species. Establishment dates prior to 1450 are not shown.

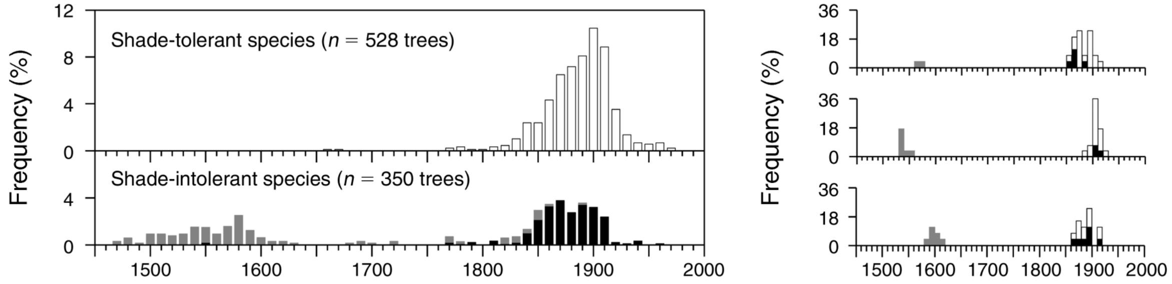
4–6 have at least one cohort initiated after 1780, usually in addition to one or more older cohorts (Fig. 2b).

Stands of age-structure type 1 each have a single cohort of shade-intolerant trees, which was initiated between 1470 and 1610 in all but two older stands that were initiated in the late 12th and early 13th centuries. A lack of fire since the initiation of this cohort is suggested by the absence of charred bark on living trees. Also, the stands show no recruitment of shade-intolerant trees since the establishment of the initial cohort, whereas shade-tolerant trees show nearly continuous establishment to the time of sampling (Fig. 3a).

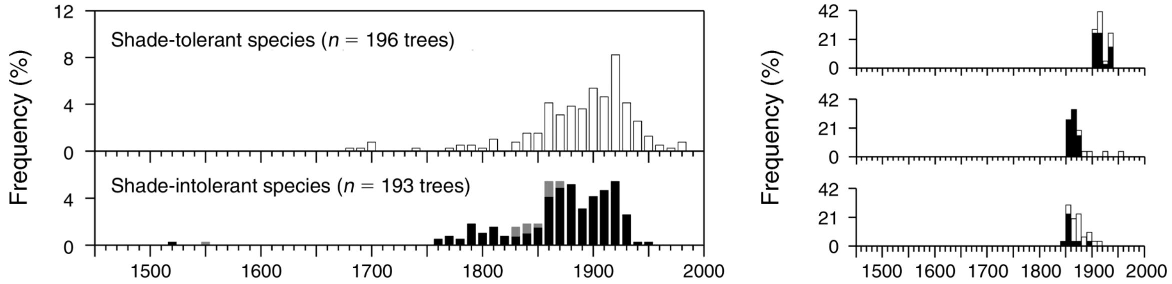
Age-structure types 2 and 3 resemble type 1 in the density and ages of shade-intolerant trees, but they differ from type 1 by the presence of charred bark on these trees and by younger ages of shade-tolerant species (Fig. 3a–c). Charred bark was recorded in each stand of age-structure type 3 and most stands (58%) of type 2. The fires that produced this charcoal probably caused little mortality of shade-intolerant trees, as indicated by the mean density of shade-intolerant trees in age-structure types 2 and 3 (60 and 65 trees/ha, respectively), which is nearly identical to that in type 1 (62 trees/ha), where stands are of similar age and lack evidence of fire since stand initiation (Table 1, Fig. 2b).

In age-structure type 3, prolific regeneration of shade-tolerant species, presumably after the latest of at least one NSR fire since stand initiation, produced a distinct cohort beneath the older cohort of shade-intolerant trees (Fig. 3c). On average, 85% of the establishment dates for shade-tolerant trees at each stand fall within a 40-year window beginning in the 19th to early 20th century.

d) Age-structure type 4 ($N = 33$ transects)



e) Age-structure type 5 ($N = 15$ transects)



f) Age-structure type 6 ($N = 13$ transects)

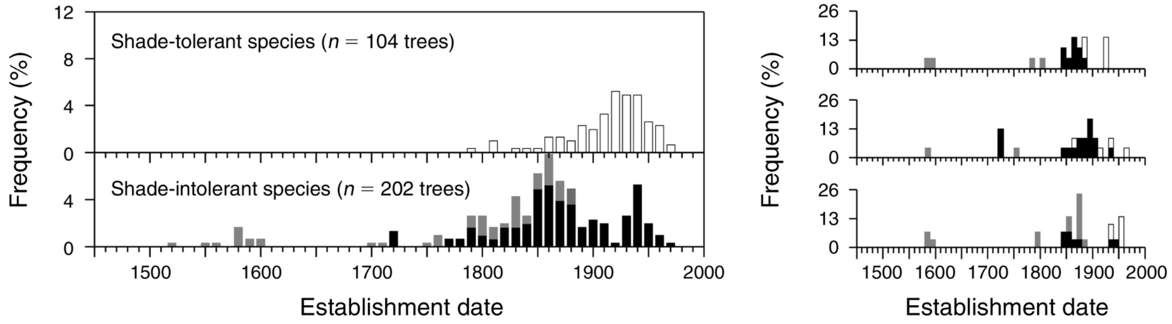


FIG. 3. Continued.

Compared across stands, the initiation of these establishment pulses is staggered, suggesting that similar age distributions developed in stands that burned in different events. Minimal survival of fire by shade-tolerant species is illustrated by the almost complete absence of shade-tolerant trees that predate these establishment pulses (Fig. 3c).

In age-structure type 2, at least two development pathways could have contributed to a shade-tolerant tree age distribution intermediate between types 1 and 3 (Fig. 3). Under one pathway, stands could have experienced at least one NSR fire that killed most shade-tolerant trees and enabled development of a new cohort similar to age-structure type 3, but the most recent fire probably was up to 100 years earlier than in type 3. Under another pathway, stands may have experienced 19th-century NSR fire patchy enough or of intensity low enough that several shade-tolerant trees survived, resulting in an abrupt pulse of shade-tolerant tree establishment in the 19th century and shade-tolerant trees at a density ≥20 trees/ha that predate this pulse, beneath the older cohort of shade-intolerant trees. The role of fire in the initiation of the 19th-century establishment pulse is supported by the correspondence of the initiation of this pulse with the initiation of a cohort including shade-intolerant species at the other stands sampled along the same slope facet and charred bark on the trees that predate these cohorts.

Stands of age-structure type 4 are characterized by two cohorts of shade-intolerant trees: one initiated between 1470 and 1610 and the other between 1780 and 1940 (Fig. 3d). The older cohort is of similar age to the cohort of shade-intolerant trees in age-structure types 1–3. However, trees of this cohort have charred bark in every stand, and their average density (45 trees/ha) is only about two-thirds that in types 1–3 (60–65 trees/ha; Table 1, Fig. 2b). Thus, a portion of the shade-intolerant trees most likely was killed either in a single

TABLE 1. Comparison of stand-structure variables among six age-structure types in the central western Cascades of Oregon, USA.

	Age-structure type											
	1 (n = 18)		2 (n = 26)		3 (n = 19)		4 (n = 33)		5 (n = 15)		6 (n = 13)	
Variable†	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Density (trees/ha)												
All species	274^{bc}	62	250^{c}	62	368^{ab}	112	397^{a}	132	452^{a}	157	351^{b}	109
Shade-intolerant	62^{b}	34	60^{b}	26	65^{b}	26	152^{a}	94	234^{a}	158	236^{a}	111
Large shade-intol.‡	52^{a}	27	50^{a}	20	55^{a}	21	44^{a}	17	15^{b}	17	34^{a}	24
Shade-tolerant	212^{b}	62	189^{bc}	57	294^{a}	95	230^{ab}	112	234^{abc}	213	115^{c}	103
Large shade-tolerant§	39^{a}	21	19^{b}	15	12^{bc}	16	6^{c}	11	7^{c}	14	3^{c}	8
Sapling and shrub¶	1947^{a}	1457	1007^{ab}	716	482^{c}	522	705^{bc}	462	1285^{ab}	1413	1089^{ab}	585
Basal area (m^2/ha)												
All species	133.2^{a}	36.2	129.7^{a}	24.2	129.5^{ab}	35.0	118.9^{ab}	28.7	89.5^{c}	26.0	99.7^{bc}	25.8
Shade-intolerant	76.3	36.8	88.9	24.6	92.7	32.6	88.3	31.4	69.4	33.0	88.4	28.5
Shade-tolerant	56.9^{a}	22.3	40.7^{b}	15.3	36.2^{bc}	14.5	29.6^{bc}	16.0	25.2^{cd}	25.8	11.8^{d}	12.3
dbh (cm)												
All species mean	66.8^{a}	11.0	68.0^{a}	12.4	53.7^{b}	10.7	51.8^{b}	9.7	46.8^{b}	11.7	51.7^{b}	10.4
All species SD	42.4^{ab}	7.5	48.4^{a}	7.6	42.3^{ab}	7.9	36.9^{bc}	8.0	23.6^{d}	9.3	33.5^{c}	8.6
Shade-intolerant mean	123.5^{a}	30.0	142.5^{a}	26.0	134.8^{a}	22.3	82.9^{b}	24.4	62.8^{b}	19.6	64.6^{b}	17.7
Shade-intolerant SD	21.9^{d}	9.5	23.8^{bcd}	10.2	25.2^{bcd}	11.2	43.9^{a}	17.5	15.3^{cd}	17.3	33.8^{bc}	24.3
Shade-tolerant mean	50.2^{a}	9.0	46.1^{a}	10.0	36.2^{b}	7.5	36.4^{b}	8.0	30.9^{b}	8.6	31.3^{b}	11.8
Shade-tolerant SD	30.6^{a}	8.0	27.2^{a}	8.8	17.0^{b}	6.6	16.9^{b}	6.3	12.5^{b}	7.6	12.1^{b}	8.6

Notes: The six age-structure types were determined by hierarchical clustering of eight age-structure variables as shown in Fig. 2a. Different lowercase superscript letters indicate statistically significant differences ($P < 0.05$) between groups based on the Tukey HSD test or the Behrens-Fisher test.

† Data are for trees >15.0 cm dbh unless otherwise noted.

‡ Large shade-intolerant trees are >100.0 cm dbh.

§ Large shade-tolerant trees are >80.0 cm dbh.

¶ Sapling and shrub refers to trees and shrubs 1.5–15.0 cm dbh.

fire or by two or more NSR fires, thereby enabling development of a mixed cohort of shade-intolerant and shade-tolerant species, as opposed to a cohort of only shade-tolerant trees in type 3 where the fire probably killed fewer shade-intolerant trees of the upper canopy (Fig. 3c, d).

Age-structure type 5 includes stands initiated following high-severity fire after 1780, and most stands lack evidence of additional fire to the present (Fig. 3e). All stands have a cohort of shade-intolerant trees initiated after 1780. Trees that established before 1780 are present at a lower density (9 trees/ha) than in any other age-structure type (Fig. 2b).

Age-structure type 6 is characterized by three or more cohorts of shade-intolerant trees in most stands, suggesting the occurrence of several NSR fires that enabled establishment of shade-intolerant species. Stands contain an average of 24 trees/ha that established before 1780, usually along with at least two younger cohorts of shade-intolerant trees (Figs. 2b and 3f). Shade-intolerant trees that established after 1780 have establishment dates spanning an average of 112 years per stand, compared to 35 and 37 years in age-structure types 4 and 5, respectively. The 112-year range includes a period averaging 44 years long with no recorded establishment. This gap in the age distribution most likely separates cohorts initiated after different fires, as suggested by charred bark on only the older trees and by healed-over fire scars found in increment cores with dates that coincide with the initiation of the younger cohort (Fig. 3f).

Fire effects on stand structure

The different age-structure types account for a much larger portion of the variation in stand-structure variables among stands than differences between the two study areas or among slope positions (Appendix C). All but one of the stand-structure variables show statistically significant ($P < 0.05$) differences among the age-structure types (Table 1). Age-structure type accounts for up to 65% of the variance in the stand-structure variables, including >20% of the variance in 11 variables (Appendix C). Only six variables differ significantly between the two study areas and eight variables differ by slope position. Study area and slope position respectively account for only 2.1–8.5% and 4.2–14.6% of the variance in these variables (Appendix C). Thus, the analysis by age-structure type is robust to artifacts of the study design.

Age-structure type 1 provides a baseline for the structure of old-growth stands with no NSR fire since stand initiation >400 years ago. Shade-intolerant trees are limited to the largest size classes (Fig. 2c) and the density of large shade-tolerant trees (39 trees/ha) and the basal area of shade-tolerant trees (56.9 m^2/ha) are the greatest of all age-structure types (Table 1). A patchy stand structure consistent with response to local canopy gaps rather than extensive disturbances is evident in the shrub/sapling layer (trees 1.5–15.0 cm dbh), which is dense overall (1947 stems/ha) and highly variable along each transect and among stands (SD = 1457 stems/ha; Fig. 2c).

The long-term effects of the NSR fires that charred the bark of the shade-intolerant trees of age-structure types 2 and 3 (Fig. 3) are most evident in the density and sizes of shade-tolerant trees that form the mid- and lower canopy. These age-structure types show little difference from type 1 in the density or sizes of shade-intolerant trees, but types 2 and 3 both have fewer large shade-tolerant trees (Table 1, Fig. 2c). In type 3, the postfire cohort of shade-tolerant trees forms such a uniformly dense mid-canopy that the density of saplings and shrubs (1.5–15.0 cm dbh) beneath this layer (482 stems/ha) is the lowest of all age-structure types (Table 1).

Age-structure type 5 provides baseline structure for stands of mature age (~80–200 years old) that initiated following SR fire, whereas types 4 and 6 illustrate the structure of stands with a mature cohort of shade-intolerant trees initiated following NSR fire. Type 5 has the lowest density of large (>100 cm dbh) shade-intolerant trees (15 trees/ha), but the density of large shade-intolerant trees in types 4 and 6 (44 and 34 trees/ha, respectively) is not significantly different from that in type 1 (52 trees/ha; Table 1). In age structure type 6, the presence of up to four cohorts of shade-intolerant trees per stand (Fig. 3f) contributes to a higher proportion of shade-intolerant trees (67%) than found in any other age-structure type (Table 1) and the distribution of shade-intolerant trees across the broadest range of dbh classes (Fig. 2c).

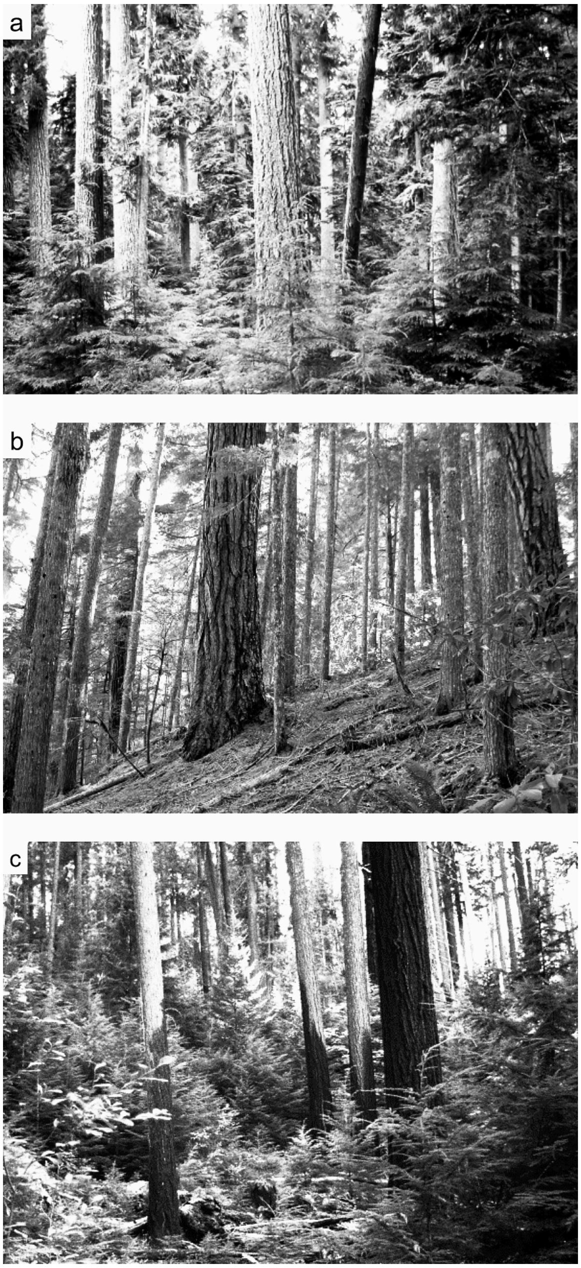


Plate 1. Comparison of stand structure of (a) age-structure type 1, illustrating the dense mid and lower layers of shade-tolerant trees of a wide range of ages, to (b) age-structure type 3, illustrating large Douglas-fir trees and a post-fire cohort of uniformly sized western hemlock trees with a sparse understory. In panel (c), a stand is shown 15 years after NSR fire, depicting large trees of an approximately 500-year-old cohort, widespread smaller trees of an approximately 150-year-old cohort, and abundant seedlings and saplings of a new cohort. Note the charred bark on the trees that survived the fire. Photo credits: A. J. Tepley.

Discussion

Conceptual model of fire-mediated stand development

The sampling of forest stand and age structure in 124 stands clarifies the relative importance of SR vs. NSR fire in the development of forest structure across a large swath of the central western Cascades of Oregon. It also provides a basis to improve our understanding of geographic variation in the fire regime in the Douglas-fir/western hemlock region of the PNW (Fig. 1). Stand development along a linear pathway following SR fire with no subsequent burning, consistent with the pathway of Franklin et al. (2002), is clearly evident (27% of stands; Fig. 4), but not the dominant pathway for the existing old-growth forests in our study area. Douglas-fir trees >400 years old are present in 84% of the sampled stands. However, age-structure type 1, which is the only old-growth type lacking evidence of NSR fire, accounts for only 18% of these stands (15% overall). The other stands supporting these old trees have charred bark and age-cohort evidence of at least one NSR fire since stand initiation (Fig. 3). Also, whereas 77% of all stands have either charred bark or a cohort of shade-intolerant trees providing evidence of fire between 1780 and 1940, only 16% of these stands (12% overall) experienced SR fire during this period (age-structure type 5; Fig. 3). It was far more common for NSR fire to leave large numbers of surviving trees (≥30 trees/ha) and set the stand along an alternative development trajectory rather than resetting the linear sequence.

We used several data sources (e.g., age structure, stand structure, and the presence or absence of charred bark) and multiple lines of reasoning to support the development of a conceptual model of fire-mediated pathways of stand development and forest dynamics in order to elucidate the various stand-development pathways influenced by SR and NSR fire (Fig. 4). We propose that this model structure applies throughout the Douglas-fir/western hemlock region (Fig. 1), or with further detail suggested by subdivision of some of the pathways (Appendix E). However, the proportion of the landscape that followed the different pathways will vary geographically along climatic and topographic gradients.

The model is hierarchical, with the multiple development pathways organized in three groups, each accounting for at least one of the age-structure types and representing the different development patterns possible within a mixed-severity fire regime, where fire intervals and severities may vary over time at a given stand and more broadly across the landscape. Because some stands may remain unburned for centuries between SR fires, whereas others may experience several NSR fires between SR events, we label these groups as development pathways characteristic of (1) infrequent (>200 years) SR fire, (2) episodic NSR fire (intervals generally 100–200 years long), and (3) chronic NSR fire (intervals rarely >100 years long). These fire intervals are drawn from fire-history studies overlapping the present study area (Means 1982, Morrison and Swanson 1990, Weisberg 2004).

The model includes four levels of fire severity (underburn, low, moderate, and high; Fig. 4), where severity is defined in terms of fire-caused mortality of overstory trees (Agee 1993). We consider underburn and low-severity fire as fire that kills primarily subcanopy trees and leaves the upper canopy largely intact, with the distinction that a greater number of shade-tolerant trees survive an underburn. Moderate-severity fire is defined as fire that partially opens the upper canopy (i.e., kills 30–70% of overstory trees; Agee 1993), whereas high-severity fire is assumed to kill the majority (>70%) of trees in a stand. Similar to Schoennagel et al. (2011), inferences about fire severity were based on the abundance of trees that predate the most recent fire, but we compare tree density of the older cohort to that in unburned stands of similar age (Fig. 2b), and thereby gain further insight into how fire affected the stands.

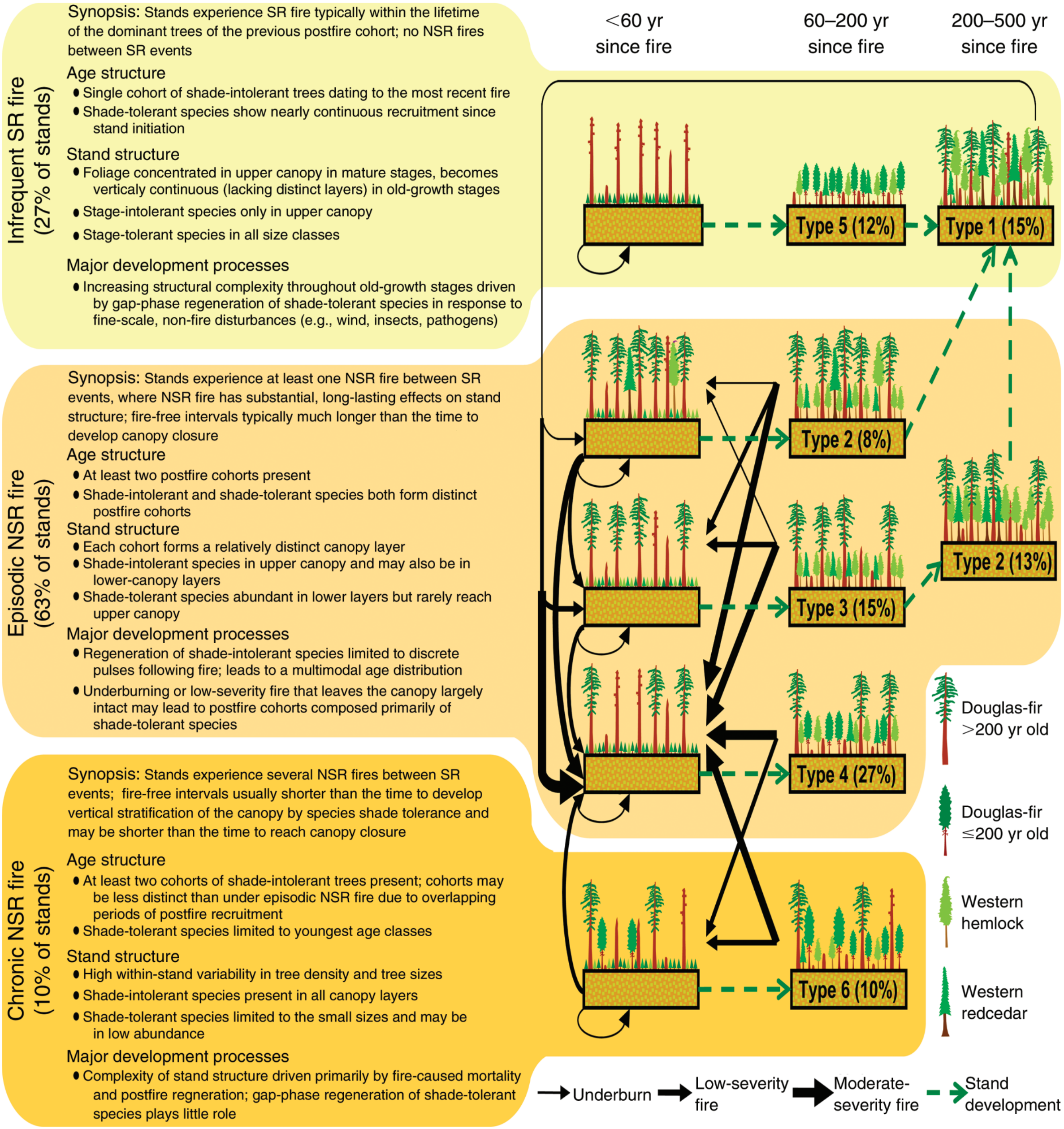
The model includes several pathways that could lead to the present stand and age structure of each of the age-structure types (Fig. 4) to account for our incomplete knowledge of the number of times a stand has burned. Trees with charred bark were found in the majority of stands (68% overall and 72% of stands supporting trees >400 years old), but fire scars were essentially unavailable for sampling. For Douglas-fir trees in this region, fire-caused wounds affecting more than ~10% of bole circumference tend to rot. Only small scars that form in bark fissures and heal within ~15 years are likely to be preserved, but these scars are not visible on live trees (Morrison and Swanson 1990, Skinner and Taylor 2006). In all, 29% of the 1463 live Douglas-fir trees recorded in the transects had charred bark, but only eight of them had an open wound likely caused by fire. Each of these trees had heartrot. Previous fire-history work was conducted in recently harvested stands, where healed-over fire scars could be viewed on cut stumps (Weisberg 2004), but most of these stumps now are too decayed for sampling.

The sampling of stand and age structure in five plots along 120-m-long transects and the use of multiple lines of evidence (tree ages, stand structure, and charred bark) makes it unlikely that non-fire disturbances complicate our interpretations. Disturbances by wind, insects, and pathogens are pervasive in the PNW, but they tend to affect individual or small groups of trees in Douglas-fir/western hemlock forests (Holah et al. 1997, Powers et al. 1999, Sinton et al. 2000), unlike forests dominated by pine (*Pinus*) or spruce (*Picea*), where bark beetles can cause extensive mortality. Furthermore, previous evaluation of tree ages and growth rates shows the strongest effect of non-fire disturbances is to elicit growth increases in shade-tolerant trees already present in the understory rather than promote new establishment (Winter et al. 2002*a*). This contrasts our finding of abrupt establishment pulses for shade-intolerant and shade-tolerant species in stands with direct evidence of NSR fire, such as charred bark on living trees (Fig. 3).

Pathways characteristic of infrequent SR fire

Age-structure types 1 and 5 represent mature and old-growth stages, respectively, along a development sequence following SR fire with no subsequent burning until the next SR fire resets the sequence (Fig. 4). In the absence of NSR fire, stands typically support a single cohort of shade-intolerant trees dating to the last SR fire (Franklin et al. 2002). This cohort developed relatively quickly across the study area. In individual stands, 84% of the establishment dates for shade-intolerant trees in age-structure type 1 and 93% in type 5 fall within 40 years of the earliest establishment date of the cohort.

In the absence of NSR fire, shade-tolerant species tend to exhibit nearly continuous regeneration, initiating either along with the shade-intolerant trees (Winter et al. 2002*b*) or lagged several decades behind the establishment of shade-intolerant species, possibly reflecting removal of seed sources by repeated burning (Wimberly and Spies 2001). The time since stand initiation in age-structure type 1 approaches the maximum ages reported for the shade-tolerant species of this region, which makes it difficult to determine the initial establishment patterns for shade-tolerant species. In the younger stands of type 5, shade-tolerant species were found to establish both along with and lagged behind the



Infrequent SR fire (27% of stands)

Synopsis: Stands experience SR fire typically within the lifetime of the dominant trees of the previous postfire cohort; no NSR fires between SR events

Age structure
- Single cohort of shade-intolerant trees dating to the most recent fire
- Shade-tolerant species show nearly continuous recruitment since stand initiation

Stand structure
- Foliage concentrated in upper canopy in mature stages, becomes verticaly continuous (lacking distinct layers) in old-growth stages
- Stage-intolerant species only in upper canopy
- Stage-tolerant species in all size classes

Major development processes
- Increasing structural complexity throughout old-growth stages driven by gap-phase regeneration of shade-tolerant species in response to fine-scale, non-fire disturbances (e.g., wind, insects, pathogens)

Episodic NSR fire (63% of stands)

Synopsis: Stands experience at least one NSR fire between SR events, where NSR fire has substantial, long-lasting effects on stand structure; fire-free intervals typically much longer than the time to develop canopy closure

Age structure
- At least two postfire cohorts present
- Shade-intolerant and shade-tolerant species both form distinct postfire cohorts

Stand structure
- Each cohort forms a relatively distinct canopy layer
- Shade-intolerant species in upper canopy and may also be in lower-canopy layers
- Shade-tolerant species abundant in lower layers but rarely reach upper canopy

Major development processes
- Regeneration of shade-intolerant species limited to discrete pulses following fire; leads to a multimodal age distribution
- Underburning or low-severity fire that leaves the canopy largely intact may lead to postfire cohorts composed primarily of shade-tolerant species

Chronic NSR fire (10% of stands)

Synopsis: Stands experience several NSR fires between SR events; fire-free intervals usually shorter than the time to develop vertical stratification of the canopy by species shade tolerance and may be shorter than the time to reach canopy closure

Age structure
- At least two cohorts of shade-intolerant trees present; cohorts may be less distinct than under episodic NSR fire due to overlapping periods of postfire recruitment
- Shade-tolerant species limited to youngest age classes

Stand structure
- High within-stand variability in tree density and tree sizes
- Shade-intolerant species present in all canopy layers
- Shade-tolerant species limited to the small sizes and may be in low abundance

Major development processes
- Complexity of stand structure driven primarily by fire-caused mortality and postfire regneration; gap-phase regeneration of shade-tolerant species plays little role

FIG. 4. Conceptual model of stand development pathways in Douglas-fir/western hemlock forests of the central western Cascades of Oregon, with an overview of the age structure, stand structure, and development processes characterizing the three main groups of development patterns. Dashed arrows represent stand development in the absence of fire, and solid arrows represent NSR (non-stand-replacing) fire. High-severity fire at any stage is assumed to lead to stand conditions in the upper left corner of the diagram (arrows not shown). The three columns from left to right represent developmental stages when the youngest cohort is of young, mature, and old-growth age. SR means stand-replacing.

establishment of shade-intolerant trees, with concurrent establishment more common (see Appendix E).

Structural complexity typically is high following SR fire due to abundant snags and logs and a small number of live trees (e.g., 9 trees/ha that predate the most recent fire in age-structure type 5; Fig. 2b) carried over from the previous stand. The complexity of forest structure typically reaches a minimum in mature stands, corresponding to the biomass accumulation/competitive exclusion stage of Franklin et al. (2002), and represented by age-structure type 5, which has the lowest density of large (>100 cm dbh) shade-intolerant trees (15 trees/ha) and the least variation in tree size (SD of dbh = 23.6 cm) of all age-structure types (Table 1).

In the continued absence of fire, the growth, maturation, and thinning of the initial cohort of shade-intolerant trees along with gap-phase regeneration of shade-tolerant trees in response to fine-scale disturbances by wind, insects, and pathogens contributes to increasing structural complexity throughout the old-growth stages (Fig. 4). The effects of such gap-phase regeneration are evident in age-structure type 1, where shade-tolerant trees span a broad range of ages (Fig. 3a) and are abundant in all size classes (Fig. 2c), producing a heterogeneous mid- and lower canopy, consistent with the horizontal diversification stage of Franklin et al. (2002).

Pathways characteristic of episodic NSR fire

Stand initiation following SR fire with NSR fire occurring periodically throughout stand development is the most widespread development pattern across the two watersheds sampled in the central western Cascades of Oregon. It accounts for age-structure types 2, 3, and 4 (63% of the sampled stands; Fig. 4). Across these age-structure types, charred bark was found on living trees in 86% of the stands, and the average density of shade-intolerant trees that predate the most recent fire (55 trees/ha) approaches that in the unburned stands of type 1 (62 trees/ha; Fig. 2b). Unlike the small number of remnant trees that predate an otherwise SR event in age-structure type 5 (average 9 trees/ha; Fig. 2b), the abundant surviving trees in types 2, 3, and 4 remain a dominant component of the stand and influence the species composition, tree density, and growth rates in the postfire cohort long after the fire (Goslin 1997, Zenner 2005).

When NSR fire occurs episodically between SR events, it fosters development of multi-cohort stands where shade-intolerant and shade-tolerant species both form distinct age cohorts (Fig. 4). Although the age distribution of living trees does not provide a complete record of fire, the rarity of cohorts initiated in the 17th and 18th centuries (Fig. 3) suggests many stands experienced a 100–300 year fire-free interval during their development. Such fire-free intervals are important in the development of tree- and stand-level attributes that enable development of distinct age cohorts in response to subsequent NSR fire. For example, under fire-free intervals longer than the time required for disturbed stands to develop canopy closure, regeneration of shade-intolerant species is limited to relatively discrete pulses following fires that open the canopy (Fig. 3d), and the development of thick bark and the pruning of shaded lower branches of shade-intolerant trees render them relatively resistant to fire-caused mortality. By contrast, regeneration only of shade-tolerant trees following canopy closure limits the most fire-sensitive species to the lower canopy. As a result, subsequent low-intensity fire may kill most fire-sensitive, shade-tolerant trees of the lower canopy while leaving the upper canopy largely intact.

At the stand level, NSR fire may either reduce structural complexity relative to unburned stands or sustain complex structure throughout the development of younger cohorts (see Plate 1). Simplification of forest structure is most likely after stands have reached canopy closure and the fire kills lower-strata vegetation while causing little mortality to upper-canopy trees. Persistence of complex structure is likely when the fire generates canopy openings of sufficient size to permit establishment of shade-intolerant trees, but numerous trees survive (e.g., an average of 45 trees/ha that predate the most recent fire in age-structure type 4; Fig. 2b).

The simplification of stand structure by NSR fire is exemplified by age-structure type 3, where each stand has a 400–550-year-old cohort of shade-intolerant species and a younger postfire cohort of shade-tolerant trees (Fig. 3c). Unlike stands that develop in the absence of NSR fire and have vertically continuous foliage (Franklin et al. 2002), each of the two cohorts in age-structure type 3 forms a relatively distinct canopy layer. Although vertical aspects of stand structure were not measured in this study, Van Pelt and Franklin (2000) characterize the vertical structure of an old-growth stand within the Blue River study area, where a mid-1800s postfire cohort of shade-tolerant trees formed a dense foliage layer 15–25 m high beneath the 60–70 m tall Douglas-fir trees. Shading by such a postfire cohort may hinder understory development more than a century after the fire (Stewart 1986), as illustrated by the low abundance of saplings and shrubs (1.5–15.0 cm dbh) in age-structure type 3 (Table 1).

Age-structure type 4 illustrates the potential for NSR fire to sustain complex forest structure through the development of younger cohorts. Each stand has an old-growth cohort of shade-intolerant species over a younger (initiated after 1780), mixed cohort of shade-intolerant and shade-tolerant species (Fig. 3d). Retention of numerous old-growth trees (average of 45 trees/ha; Fig. 2b) enabled stands to forgo the otherwise low structural complexity characteristic of mature stands initiated after SR fire (Franklin et al. 2002). Abundant trees in the older cohort promote a lower tree density in the postfire cohort (Fig. 2b) with greater horizontal patchiness in tree density than typical of single-cohort stands initiated after SR fire (Goslin 1997).

Pathways characteristic of chronic NSR fire

Age-structure type 6 (10% of sampled stands) is the only age-structure type where NSR fire was a relatively frequent occurrence throughout stand development. A relatively high frequency of NSR fire fosters development of multi-cohort stands, where shade-intolerant species span a broad range of ages and are abundant in all canopy layers (Fig. 2c). The occurrence of up to four cohorts of shade-intolerant trees per stand, with the oldest cohort initiated in the 16th century (Fig. 3f), suggests these stands are unlikely to have experienced fire-free intervals much longer than 100 years during their development. At this relatively high frequency of NSR fire, fine-scale patchiness in fire-caused mortality and postfire regeneration of shade-intolerant species replaces gap-phase regeneration of shade-tolerant species as the dominant process contributing to complexity in forest structure (Means 1982; Fig. 4).

NSR fire is likely to be a chronic occurrence at only particularly dry sites in the central part of the western Cascade Range (Means 1982). At sites too dry to support high canopy cover, Douglas-fir may function as a climax species capable of regenerating and forming a broad age distribution in the absence of fire (e.g., the *Pseudotsuga*/*Holodiscus discolor* plant association of Franklin and Dyrness [1988]), making it difficult to distinguish influences of fire on stand development from effects of the harsh environment. However, charred bark was found in all stands of age-structure type 6, and in most stands of this type (62%), shade-tolerant trees were abundant (average density of 150 trees/ha, or 42% of the live trees >15 cm dbh) and the understory species composition was characteristic of more mesic plant associations where western hemlock typically replaces Douglas-fir in the absence of fire.

CONCLUSIONS

This work builds on previous research that used Douglas-fir ages and fire-scar data counted in the field in recently harvested stands to characterize the history of fire events (Morrison and Swanson 1990, Weisberg 2004) by adding elements that were lacking or received little emphasis in previous studies (e.g., high-resolution dating of establishment dates for all species, stand-structure data, and the presence of charred bark on living trees). The combination of these data sources across a broad study area enables us to better understand the long-term effects of fires of varying frequency and severity on the diverse pathways of stand development in our study area and more broadly in the Douglas-fir/western hemlock region of the PNW.

Our objective to characterize the multiple pathways of stand development mediated by fire of varying frequency and severity was guided by three questions: (1) What are the patterns in forest age structure in stands across two large watersheds? (2) What do these patterns imply about the relative importance of SR and NSR fire? (3) To what extent do these differences account for variation in contemporary forest structure? The first two questions were addressed by hierarchical clustering of the age-structure variables (Fig. 2a) and the use of multiple lines of evidence (e.g., presence/absence of charred bark and comparisons of the species composition and tree density across cohorts of burned and unburned stands) to understand the relative influences of SR and NSR fire (Figs. 2b and 3). Although forest structural development along a linear sequence initiated by SR fire with no subsequent disturbances other than fine-scale tree-fall gaps has become the reference model in the PNW (Franklin et al. 2002), we found that only 27% of stands followed this pathway (age-structure types 1 and 5; Fig. 4). Douglas-fir trees >400 years old are present in 84% of the sampled stands and present at a density $\geq$30 trees/ha in 89% of these stands (75% overall). However, charred bark and age-cohort evidence of NSR fire was found in 73% of the stands supporting these old Douglas-fir trees (Fig. 4; Appendix E).

The third question regarding the long-term effects of differences in the histories of SR and NSR fire on contemporary forest structures was addressed by comparing forest structure among the different age-structure types (Table 1). The age-structure types account for 13.2–65.0% of the variance in the stand-structure variables, compared to only 2.1–14.6% explained by the different study areas and slope positions (Appendix C). Among the most pronounced effects are a shift toward higher densities but smaller sizes of shade-tolerant trees following low-severity fire that does not reduce the density of large shade-intolerant trees relative to unburned stands (age-structure type 3) or shift to a broader size distribution of shade-intolerant trees with the initiation of a new postfire cohort following moderate-severity fire that partially opens the canopy (age-structure type 4; Fig. 2c, Table 1; see also Plate 1). Multiple, recurring NSR fires could lead to three or more cohorts of shade-intolerant trees per stand, with shade-intolerant trees dominant in all size classes and shade-tolerant species limited to the smallest sizes (age-structure type 6).

The conceptual model of fire-mediated development pathways (Fig. 4; Appendix E) provides a framework for interpreting variation in stand structure in relation to regional and local variation in the fire regime. For example, in comparison to the null hypothesis of no difference in the abundance of the different age-structure types between the two study areas, the age-structure types affected by NSR fire (types 2, 3, 4, and 6) are slightly more abundant than expected at Fall Creek and those unaffected by NSR fire (types 1 and 5) are slightly more abundant than expected at Blue River (Appendix F). These differences are too small to reject the null hypothesis. Yet, when viewed in relation to other studies in western Oregon, they are consistent with a broader trend of increasing representation of stands containing two or more cohorts of Douglas-fir trees, suggesting increasing importance of NSR fire, with decreasing annual precipitation (Appendix F). In ongoing work based on the findings of Tepley (2010), we will evaluate the hypothesis that the three major groups of stand development patterns (Fig. 4) are associated with different topographic settings, creating local, topographically constrained variation nested within the broader climatically controlled gradients.

The complexity of developmental pathways revealed in this study has implications for ecosystem dynamics and ecologically based management. At the stand level, NSR fire may either simplify forest structure (age-structure type 3) or sustain complex structure through the development of younger cohorts under a residual overstory (age-structure type 4). However, fine-scale variation in fire severity within individual fires and over successive events undoubtedly has produced greater heterogeneity in forest structure across the landscape than if forest dynamics were controlled only by infrequent SR fire. The fact that SR and NSR fire control the diversity of old-growth forest structures across these landscapes should stimulate research aimed at understanding the implications of these different structures for wildlife species, ecosystem function, restoration, and fire management.

Our findings do not speak to the question of whether the diversity of developmental pathways and associated spatial mosaics of stand structures and densities need to be maintained or restored to maintain certain elements of biodiversity or lower the risk of large high-severity fires. They do suggest, however, that these landscapes have been shaped by a great diversity of fire histories and stand development patterns. Effort to keep fire out of these systems, which occurs when managers suppress the numerous small lightning-caused fires that start across in the western Cascades every year, could lead to greater homogeneity in stand conditions across the landscape than has occurred over the last several centuries. The broader ecological implications (e.g., to species and ecological processes) of reducing the role of fire in these systems are not clear and warrant further work. However, as a general principle, allowing fire to diversify mature and old-growth stands and their patterns across the landscape is consistent with their ecological history and our general knowledge of the importance of ecological heterogeneity in the maintenance of biodiversity and in promoting resilience in the face of prospective climatically induced changes in disturbance regimes or management systems.

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SUPPLEMENTAL MATERIAL

Appendix A

Methods for selecting sample sites (*Ecological Archives* E094-157-A1).

Appendix B

Methods for the collection and processing of tree cores (*Ecological Archives* E094-157-A2).

Appendix C

Mixed-effects analysis comparing the proportion of variance in stand-structure variables explained by the age-structure types to that explained by study area and slope position (*Ecological Archives* E094-157-A3).

Appendix D

Summary statistics for the age-structure variables and a comparison of within- and between-group variability of the age-structure types (*Ecological Archives* E094-157-A4).

Appendix E

Expanded conceptual model of fire-mediated stand development pathways for Douglas-fir/western hemlock forests of the Pacific Northwest (*Ecological Archives* E094-157-A5).

Appendix F

Spatial variation in the representation of age-structure types between the two study areas and along broader climatic gradients (*Ecological Archives* E094-157-A6).