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Stand development, fire and growth of old-growth and young forests in southwestern Oregon, USA

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ABSTRACT

We studied stand development in three distinct forest types in southwestern Oregon using six stands each in uncut and clear-felled old-growth stands and nearby young stands (18 total). Old-growth stands showed a wide range of tree ages (>300 years) and low tree densities for several centuries; rapid early growth produced trees with large crowns and diameters, as well as low height-to-diameter ratios. In contrast, young stands established much quicker and at higher tree densities; beyond their initial 20 years, trees had smaller diameters at equivalent ages, slower growth rates, smaller crowns and higher H:D than trees in old-growth stands. Low-intensity disturbance, likely dominated by fire, was common in old-growth stands during their early development. Fire scars showed these stands burned frequently from 1700 to 1900, and low levels of tree recruitment occurred in a complex relationship with fire during this 200 years. There was no evidence of fire, however, in either old-growth or young stands after 1909, and their densities were well above that of 1900; in old-growth stands, 15–25% of the basal growth occurred from 1950 to 1990, and it appears that they are on a development pathway different from what they experienced from 1700 to 1900. Furthermore, tree recruitment has been limited in both old-growth and young stands since 1950 while biomass and fuels continue to accumulate rapidly. Past stand dynamics can be emulated by prescribed fire and light thinning to reduce risk of loss from severe fire or insects, as well as to partially restore stand conditions that existed prior to fire exclusion. Our results suggest that young stands can be grown to produce high levels of biomass/wood, or their development can be altered to more closely follow that of old-growth stands depending on management objectives.

1. Introduction

Sustainable forest management in drier forest types like those in southwestern Oregon requires an understanding of long-term forest development and disturbance regimes, primarily fire, which differs from that of more northern forests on more mesic sites. These drier forests have lost many older, dominant trees that are >1 m diameter at breast height (DBH; 1.37 m) to stand-replacing fire. Also, the mortality of large trees in unburned stands has been high, likely due to increasingly high stand densities (Latham and Tappeiner, 2002) and drought stress from 1987 to 1992 and 2000 (Sensenig et al., 1994). In addition to drought stress and high stand density, pathogens and insects contributed to mortality. Recent old-tree mortality rates exceed replacement by younger trees and, if this trend continues, presage a pronounced reduction in old-growth dry forest ecosystems (Lehmkuhl et al., 1991).

Beginning around 1900, land management and fire suppression policy led to major changes on forest lands throughout western North America. Suppression policy was initiated following severe fires, often reburns, which covered millions of hectares of forests, destroyed towns and burned entire watersheds. The relative absence of regular surface fire has facilitated establishment of an overabundance of small fire-sensitive trees (Agee, 1993, Taylor and Skinner, 2003). Generally overstocked conditions in forest stands, accumulations of surface and aerial fuels, and increased susceptibility to fire create a dilemma for forest managers. These dense old stands, while susceptible to drought-related mortality and to fire, are also the habitat for late-successional species (FEMAT, 1993). Maintaining this habitat in old-growth stands, and growing it in younger stands, are major objectives of federal forest management in western Oregon (FEMAT, 1993).

The Northwest Forest Plan specifically calls for managing over 7.5 million acres of federal forests for late successional/old-growth habitat and another 2 million acres of riparian reserves; however, currently about 80% of these forests are composed of dense stands of relatively small trees (20–24 cm dbh) that are <40–120 years of

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age (FEMAT, 1993). These are classic even-aged stands that regenerated following timber harvest, wildfire, mining or other disturbance; they lack diversity in overstory tree size, age, and species as well as understory species and abundance (Spies and Franklin, 1991). Forest managers are concerned that such stands are particularly susceptible to drought-related mortality and stand-replacing wildfire. Thus, current policy calls for stand management to reduce mortality and fire hazard, and promote habitat characteristics associated with old-growth stands. Understanding tree growth, establishment of regeneration, and fire occurrence in both young and old stand types will help managers meet objectives for both stand types.

Studies on moist sites in northwestern Oregon have shown that large trees in old-growth stands grew much more rapidly at young ages than trees in young stands on similar sites (Tappeiner et al., 1997). Rapid early growth was an important characteristic of large old-growth trees (Poage and Tappeiner, 2002). Also, tree ages in old-growth stands were much more variable than those in young stands, suggesting a much different development in the two stand types. In a study throughout much of northwestern Oregon, Bailey and Tappeiner (1998) found that trees in old-growth stands had larger crowns, and stems were much larger in diameter relative to their height than trees in young trees (low height to diameter ratios-H:D). The crowns and stems of old trees are important components of stand structure and habitat in old-growth stands and the low H:D is indicative of resistance to damage from wind, ice, and snow (Wilson and Oliver, 2000). Knowledge of tree architecture (live crown length and H:D ratios) in old and young stands would provide goals for managing trees in young stand to achieve the characteristics of those in old stands. The objectives of this study were to provide forest ecologists and managers an understanding of old-growth and young forest development in three major forest types in southwestern Oregon, ranging from the mixed-conifer forests in the eastern Cascade through the Siskiyou mountains and into the mixed-evergreen forests of the coast ranges (Table 1). The old-growth stands we studied corresponded to Spies and Franklin's (1991) definition of old-growth forests for southwestern Oregon. We evaluated fire occurrence along with tree ages, growth rates and architecture with the methods used in more northerly forests (Tappeiner et al., 1997; Bailey and Tappeiner, 1998; Poage and Tappeiner, 2002), including:

(1) tree recruitment from 1700 to 1990;
(2) tree age distributions (1340–1990);
(3) stand density (trees and basal area/ha) from 1800 to 1990;
(4) stand-level fire occurrence from 1700 to 1990 by aging fire scars; and
(5) tree growth/architecture obtained by comparing radial growth rates of trees at the same ages in old-growth and young stands;
(6) tree architecture from measured tree height and crown length, and calculated live-crown ratios, and height-to-diameter ratio (Wilson and Oliver, 2000; Tappeiner et al., 2007).

1.1. Study area

This study was conducted in forests of three common and distinct ecological regions in southwestern Oregon: the Cascades (the eastern extent of the mixed conifer type in southern Oregon); the Siskiyous (the drier mixed conifer forests); and the mixed evergreen forests mid-Coast Range mountains. Douglas-fir is common in all these forests, and density of other conifers varies considerably among sites (Atzet et al., 1996; Franklin and Dyrness, 1973; Table 1).

Table 1
Locations and average stand characteristics (in 1990) of 18 old-growth and 18 young stands studied in three forest types as defined by.

Forest type	Elevation (m)	Latitude	Longitude	Stand type	Trees (ha)	Basal area (m^2/ha)	Diameter (cm)	Tree ages (years)	Douglas-fir (%)	White fir (%)	Ponderosa Pine (%)
Cascades	1050–1739	N42-10–N42-20	W122-00–W122-30	Old-growth	98 (40–150)	47 (25–50)	66 (18–208)	(20–630)	(50–100)	(16–50)	(0–3)
				Young	780 (350–800)	43 (30–58)	25 (5–63)	(20–90	(14–93)	(0–82)	(0–6)
Siskiyous	1360–1800	N42-10–N42-25	W122-50–W123-10	Old-growth	101 (90–160)	49 (24–70)	70 (12–172)	(50–580)	(54–78)	(5–23)	(11–25)
				Young	895 (750–1100)	44 (30–53)	25 (5–66)	(20–90)	(50–89)	(12–56)	(0–2)
mid-Coast	530–1380	N42-30–N42-40	W123-30–W123-50	Old-growth	98 (70–160)	59 (50–90)	82 (11–170)	(120–500)	(50–81)	(2–20)	(4–25
				Young	740 (600–1060)	38 (28–72)	23 (6–78)	(20–90)	(66–100)	(0–38)	(0–2)

Franklin and Dyrness (1973). Values in parenthesis are ranges.

Annual precipitation across our study sites ranges from approximately 97–142 cm in the Cascades, 90–107 cm in the Siskiyous, and 91–138 cm in the mid-Coast Range, and mostly falls from October through May (Graumlich, 1987; Redmond, 1992). The growing seasons ranges from as early as March in the mid-Coast to May and June for the Siskiyou and Cascade sites, respectively. It generally abruptly ends with snowfall in October in both the Cascades and Siskiyou sites but usually continues beyond November in the mid-Coast sites. Productivity therefore spans site classes II and III (Hann and Scrivani, 1987) across all sites in the three forest types. Because of these differences in climate, growing season, productivity, and species composition, we expected that tree growth and fire occurrence would differ among these forest types.

1.1.1. Cascades forest type

Major tree species in the mid-elevation Cascades forests, included Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco], ponderosa pine (*Pinus ponderosa* Dougl. Ex Laws.), white-fir [*Abies concolor* (Gord. & Glend.) (Lindl. Ex Hildebr.], and incense-cedar (*Calocedrus decurrens* Torr.). Primary hardwoods are California black oak (*Quercus kelloggii* Newb.) and Pacific madrone (*Arbutus menziesii* Pursh). Green-leaf manzanita (*Arctostaphylos patula* Green) and golden chinkapin [*Castanopsis chrysophylla* (Dougl. A.DC.] are the major shrub species.

1.1.2. Siskiyous forest type

Again, Douglas-fir, ponderosa pine, white-fir and incense-cedar are the major conifer species; canyon live oak (*Quercus chrysolepis* Liebm.), Oregon white oak (*Quercus garryana* Douglas. Ex Hook.), California black oak, and Pacific madrone are the major hardwoods in these forests. Shrubs include buckbrush [*Ceanothus cuneatus* (Hock) Nutt.] in addition to green-leaf manzanita and golden chinkapin.

1.1.3. Mid-Coast Range forest type

The major coniferous tree species of the mid-Coast Range forests are Douglas-fir, ponderosa pine and incense-cedar. Tanoak [*Lithocarpus densiflorus* (Hook. & Arn. Rehd] is an evergreen hardwood that frequently dominates the understory. Pacific madrone is very common on drier sites. Pacific rhododendron (*Rhododendron macrophyllum* D. Don), salal (*Gaultheria shallon* Pursh) and golden chinkapin are common in the understory.

2. Methods

We studied tree age and radial growth rates, and determined the approximate years of fire, on large-tree stumps in 18 areas (six in each forest type), where old-growth stands had been clear-felled. Each area was matched with a nearby uncut old-growth stand, to examine tree architecture (heights, diameter, and live crown length), as well as an uncut young stand (60–100 years) for a total of 54 stands. We tested the hypothesis that there was no difference in stand development, tree growth and architecture, and fire occurrence between old-growth and young stands in these forest types. Tree ages, density, basal area, and diameters in old-growth stands all fell within the ranges of these parameters describing such stands on dry and moderate sites in southwestern Oregon (Spies and Franklin, 1991, Table 1). The young stands had regenerated naturally beginning about 1900, following logging, severe fire, and/or other disturbance that left only scattered remnants of the previous stand (<1 tree/ha).

2.1. Tree measurements

We measured surface radial growth and fire occurrence on stumps in each ~8-ha clear-felled stand, a size consistent with many old-growth stands in southwestern Oregon (BLM, 1994; Spies and Franklin, 1991). Each area was harvested 5–10 years prior to our study, presenting a full view of annual xylem rings and fire scars on stump surfaces and allowing a good estimate of tree age/growth as well as year of fire. Unlike less productive forest types, 10-years radial increment was rarely <1.0 cm and usually >2.0 cm, so counting rings on stump surfaces (and increment cores) was not difficult. If xylem rings were not clear, a new surface was cut and cleaned with a wire brush; a magnifying glass was used to identify smaller rings. Radial growth from pith to bark (in 10-years increments) was marked with pins along an average radius of each surface. Since we were particularly interested in the age and growth rates of large trees, all tree stumps >0.7 m in diameter in each 8-ha area were measured. We then randomly located three 0.1-ha plots within each stand to count and age stumps regardless of size. We calculated 10-year radial growth over the lifetime of each tree, and basal area growth rates for each tree on a 50-years basis from 1700 to 1950, with a 40-years basis for 1950–1990.

We compared these growth rates (measured on stumps of old-growth trees) with that of young stands growing on comparable slopes, aspects and elevations within 1 km of each harvested old-growth stand. We installed three randomly located 0.04-ha plots in each young stand and measured diameter, bark thickness, and 10-year radial growth from increment cores. This was the same methodology used to compare ages and growth rates of old-growth and young trees in similar studies (Poage and Tappeiner, 2002; Tappeiner et al., 1997). We measured a total of 419 old trees and 1766 young trees: 149, 136 and 134 old trees and 571, 652, and 543 young trees, respectively, in the Cascades, Siskiyous, mid-Coast Range forests.

We also measured total tree height and live crown length of the first 50 trees along randomly-located belt transects in both young stands (3 m wide belts) and unharvested old-growth stands (10 m wide) for each of six sites in the three forest types (1800 total trees). We then calculated live crown ratio (LCR) and height-to-diameter ratio (H:D, total tree height/diameter both measured in the same units).

2.2. Fire occurrence and fire scar dating

We documented stand-level fire occurrence within our 18 harvested old-growth stands (post 1700), as well as within each of our 18 young stands. Our purpose was not to determine a precise fire history, which would require additional sample collection, preparation and cross-dating (Douglass, 1941). These are time-consuming steps for simply comparing basic patterns of tree growth and fire occurrence during known time periods (Stokes and Smiley, 1968). Weisberg and Swanson (2001), working in similar Douglas-fir forests, found that cross-dating required over 20-times more time than field counting xylem rings, and they estimated that field counting provides estimates of fire scar dates ±10 years of cross-dating 87% of the time. Fire scars are more easily identified on complete stump surfaces relative to uncut trees, and we were confident in our ability to estimate the year of fires on such well-prepared stump surfaces with wide growth rings.

We tabulated fire occurrence and calculated both fire return interval and length of fire-free periods for all stands (Agee, 1993; Dieterich, 1980; Means, 1989). Where more than one scar occurred on a single stump, each fire was individually dated and those fire intervals were recorded; on such trees, we measured the diameter when it was first scarred. Grouping fire scars enabled us to estimate the number of fires at each site; dates were grouped at three levels of precision: ±3, ±6, and ±10 years per Weisberg and Swanson's (2001) conclusions. For example, two fire scars separated by 5 years would be considered two fires when grouping ±3 years, but only one fire in the latter two precision groupings. Using the ±6- and ±10-year groupings only, we estimated the mean fire return interval and the three longest fire free periods from 1700 to 1900 at each site.

Finally, in young stands only, we examined the exterior of all trees within our plots, and along 10-m transects among plots, for potential fire scars and/or charred bark. We also looked for potential fire scars or other anomalies on all increment cores from young trees.

2.3. Data analysis

2.3.1. Tree establishment and stand density

For all sites, we calculated the proportion of total trees (all species combined) on our plots in 1990 that established during each preceding decade beginning 1700, a period of 290 years during which >80% of the trees were established. Trees that died at young ages could not be detected in this study. Ages of trees from each of the three 0.1 ha plots in each clear-felled old-growth stand in the three forest types were plotted using box and whisker plots. Since tree ages among the young stands were so similar, we include only one modal stand per forest type for comparison. Trees/ha and stand basal areas were calculated for each plot (using stumps in old-growth stands) and summarized for each 50-year period from 1800 to 1950, with 40 years from 1950 to 1990. Trees were likely too few and/or too small prior to 1800 to enable reliable reconstruction of basal area. We used t-tests ($p \leqslant 0.05$) and ANOVA to compare differences in basal area and trees/ha between the old-growth stands in each forest type.

2.3.2. Radial growth rates and tree architecture

We compared 10-year periodic radial growth (cm/decade) of trees at equivalent ages in young and old-growth stands in each forest type using 95% confidence intervals of plot means at 10-year intervals when trees were 10–80 years old (10–60 years for mid-Coast Range sites). This is the methodology used by Tappeiner et al. (1977) and Poage and Tappeiner (2002). For trees in young stands, we took increment cores at dbh and stump height on two trees/plot in each 5-cm diameter class, and then adjusted radial growth at dbh for each species and site to compare to radial growth at stump height for in old-growth trees (Sensenig, 2002). Only the largest 50% of the trees in young stands were used for this analysis, since they were deemed most likely to survive competition-based mortality to remain in a future old-growth stand (Franklin et al., 2002; Oliver and Larson, 1990); all trees in the old-growth stands were included in this analysis.

We analyzed diameter growth rates using 95% confidence intervals of all species combined in old-growth and young stands. Douglas-fir was the principle species in these mixed conifer forests (Table 1). Other conifers occurred too irregularly among stands on a site and among plots in the stands to enable reliable species comparisons. We provide an example of radial growth of old-growth Douglas-fir compared to that of ponderosa pine and white fir from the Siskiyous where those species were best represented: 117 Douglas-fir; 27 ponderosa pine and 24 white fir trees across all six sites.

We used linear regression to test the null hypothesis that the size of older trees all species combined at 150 and 200 years of age was not related to their growth rate and size when young. The strength of the relationship between tree periodic radial increments (cm 10 years^{-1}) at 50 years and tree diameter at these later ages was examined by regression. And we compared differences in live crown ratios and height-to-diameter ratios between old and young trees using percentage of trees within crown ratio and H:D classes using t-tests ($p \leqslant 0.05$).

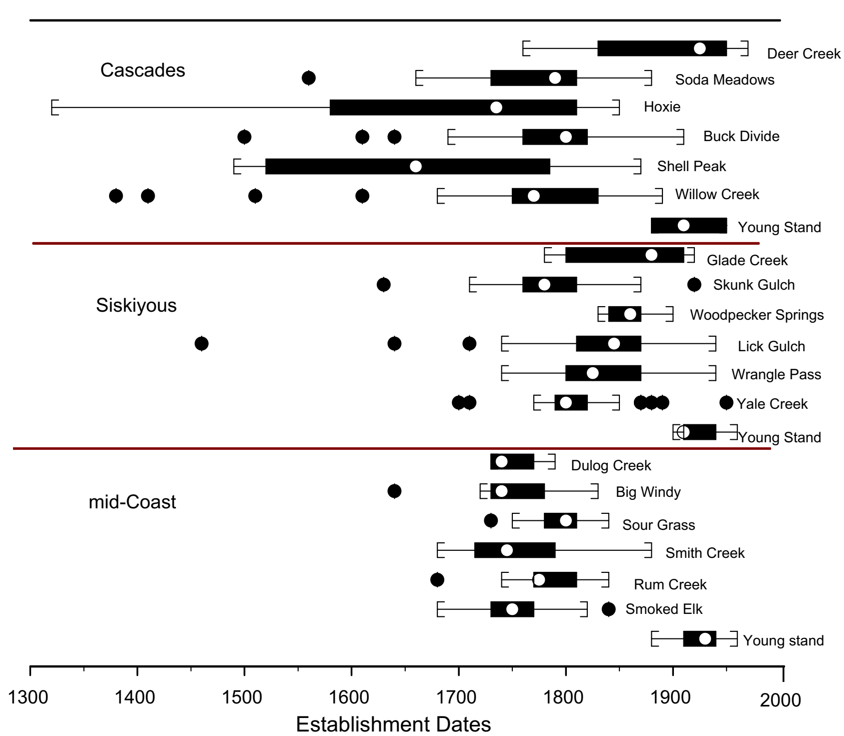

Fig. 1. Estimated establishment dates of trees in 18 old-growth stands and three modal young stands for comparison. Triangles are medians; black bars are the interquartile ranges (middle 50% of the observations); horizontal lines include values 1.5 times the quartile range; and black circles indicate individual trees outside this range.

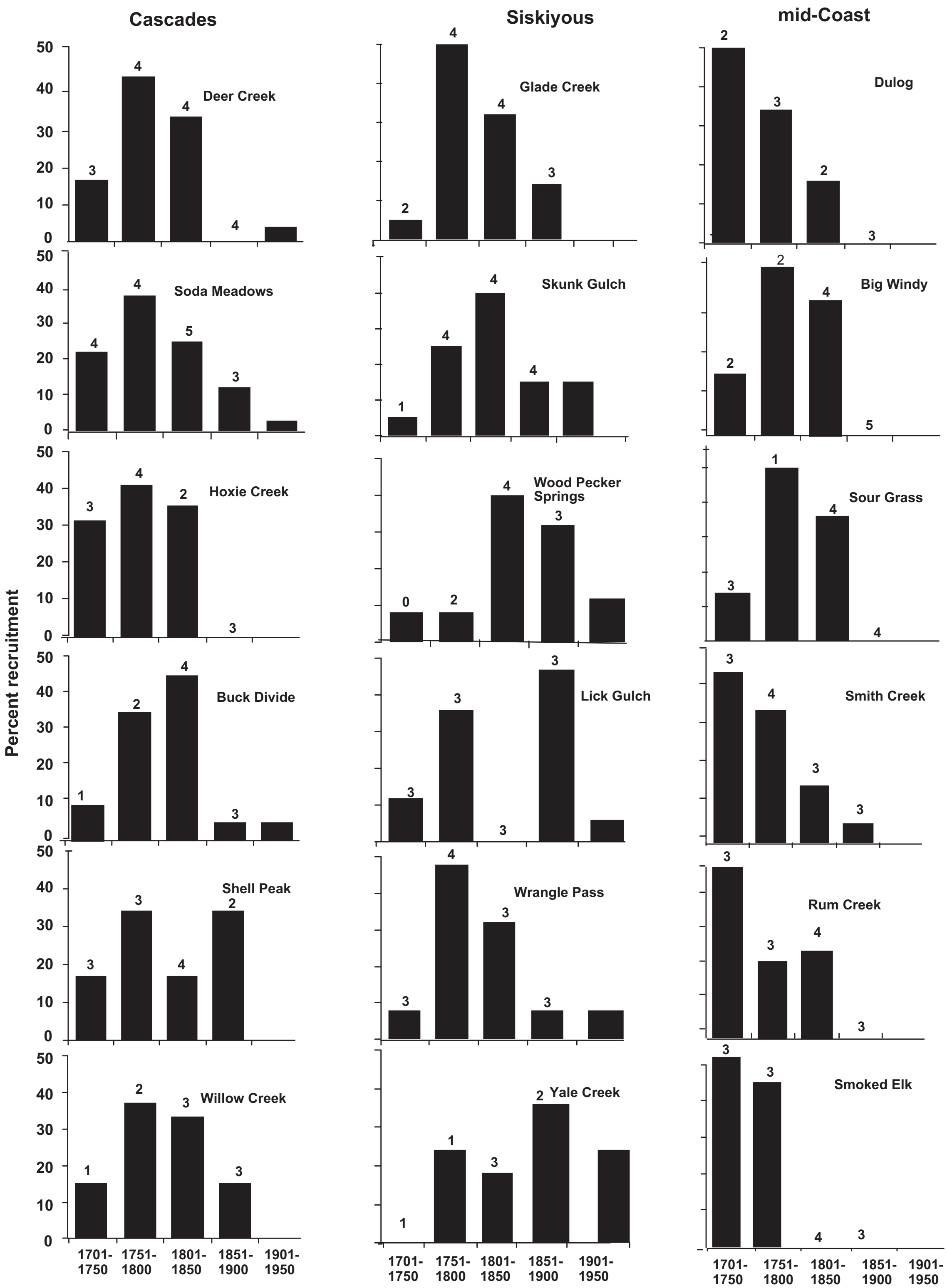

Fig. 2. Percent tree establishment and fire occurrence in old-growth stands by 50-years periods from 1700 to 1950. Numbers above bars indicate numbers of fires within that 50-years period. Beneath each forest type, the sites are listed in the same order as in Table 2. Note the variability in both fire occurrence and tree establishment.

2.3.3. Fire occurrence and tree establishment

We tested the null hypothesis that there was no difference in stand-level fire occurrence (with ±3-, ±6-, and ±10-year groupings of fire scars) among the three forest types using one-way analysis of variance ($p \leqslant 0.05$). We grouped percent tree establishment and numbers of fires by 50-year periods from 1700 to 1900 for the three forest types and used a Chi-square test ($p \leqslant 0.05$) to determine if there was a relationship between fire occurrence and conifer establishment from 1700 to 1900. We did this analysis for each forest type and for the three types combined.

3. Results

3.1. Tree ages and establishment

Tree establishment in old-growth stands on our sites began as early as 1340; however, establishment mostly fell between 1700 and 1900 across all three forest types (Fig. 1). The exceptions were at Shell Peak and Hoxie in the Cascades where 56% and 22% of the trees were established before 1700. Overall, though, we found relatively low percentages of trees that established before 1700: only 13%, 5%, and 7% in the Cascades, Siskiyous, and mid-Coast Range, respectively, with even less establishment after 1900 in these old-growth stands: 4%, 5%, and 0%, respectively. No trees established after 1950. The broadest interquartile ranges (Fig. 1), spanning the middle 50% of the observations, occurred in the Cascades and ages ranged from 60 to >200 years; this interquartile range was only 25–100 years in the Siskiyous and 30–80 years in the mid-Coast Range types, respectively. However, the upper and lower 25% of the observations indicated ranges of 200–400, 75–200 and 50–200 years in the Cascades, Siskiyous and mid-Coast Range, respectively.

Tree establishment patterns from 1700 to 1990 were quite variable among sites and forest types, even when classified broadly by 50-year intervals (Fig. 2). Overall, about one-third of the sites had heavy (>80%) recruitment in only two 50-years periods; about one-third had relatively balanced recruitment over four or five 50-years periods; about a third were irregular. For example at Yale Creek we estimated that two trees were established before 1700, and then none until 1750; 18–35% of the recruitment then occurred in each of the following three 50-years periods to 1900. In contrast, about 33% of the trees at Hoxie were established in each of the first three periods from 1700 to 1850, with none after 1850.

Natural establishment of the young stands occurred in much shorter time periods than old-growth stands. Only 5%, 2%, and 2% of the trees in the Cascades, Siskiyous and mid-Coast Range stands, respectively, were present in 1900; then, essentially all trees established within 50 years (Fig. 1), with the lower interquartile age $\leqslant$20 years. Only 8%, 7%, and 13% of young trees established after 1950.

3.2. Stand density and basal area

The timing and amount of increase in both density and basal area were quite different between old-growth and young stands (Fig. 3). Average tree density in old-growth stands was consistently lower than young stands across the three forest types and all 18 study sites (Table 1). Although basal area was more similar between old-growth and young stands, old-growth stands averaged more (47–59 m^2/ha; range 25–90 m^2/ha) and was more variable than young stands (38–44 m^2/ha; range 25–72 m^2/ha). Our reconstructed tree densities for old-growth stands in 1800 were 57, 55 and 79 trees/ha, respectively across forest types, followed by a 10–30% increase to 98, 101 and 98, respectively, by 1990 (Fig. 3). Tree densities in young stands increased from near zero in 1900 to 740–895 trees/ha by 1990. In contrast to this difference in the pattern for tree density, both old-growth and young stands showed large and consistent increases in basal area from 1950 to 1990.

Our estimates of average basal area for old-growth stands in 1700 were negligible. Estimated basal area increased from 2 to 8 m^2/ha in 1800 to 20–35 m^2/ha in 1900 across the three forest types (Fig. 3), then approximately doubled to 43–59 m^2/ha from 1900 to1990; 15–21% of this increase in old-growth basal area occurred from 1950 to 1990, the last 40 years of record, and exclusively as growth on standing trees. Basal area in the young

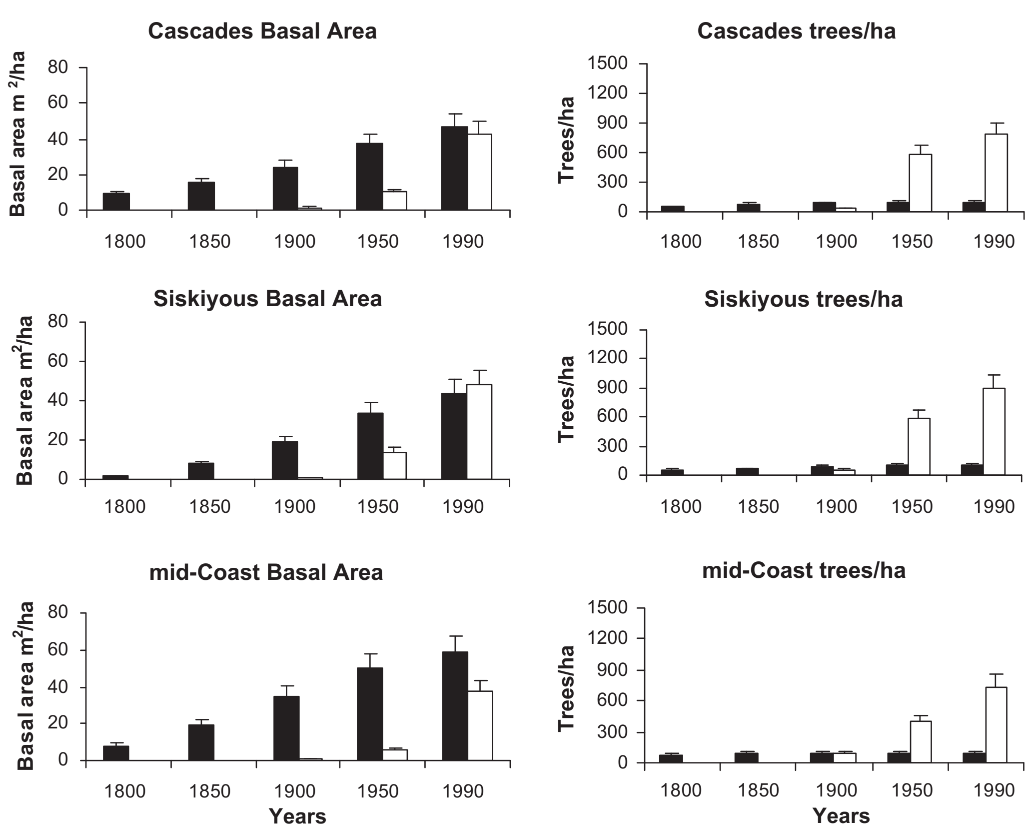

Fig. 3. Average basal area and trees/ha in six old-growth (solid) and six young stands (open) each in three forest types in southwest Oregon: Cascades, Siskiyous and mid-Coast Range mountains. We did not estimate tree density and basal area prior to 1800 due to uncertainty about tree survival following fire. One standard error across three plots is shown.

stands increased from near zero in 1900 to 43 and 48 m^2/ha by 1990 in the Cascades and Siskiyous, comparable basal area to that in old-growth stands. Basal area was less in the mid-Coast Range (significantly different at $p \leqslant 0.001$ from the old-growth stands: 38 vs. 59 m^2/ha); however, these stands were 20 years younger than in the other two forest types. Basal area growth in the young stands was based on growth of established trees as well as minor recruitment of trees from 1950 to 1990; 70–86% of growth occurred from 1950 to 1990, much more than for the same period in old-growth stands.

3.3. Radial growth and old-tree diameters

Compared at the same age, old-growth trees consistently sustained greater radial growth rates for longer periods than young stand trees after the initial growth period (Fig. 4). Trees in young stands grew more rapidly than similarly-aged trees in old-growth stands for only their first decade or two ($p \leqslant 0.05$), but growth rates in young stands rapidly and steadily decreased thereafter. In contrast, trees in old-growth stands consistently increased radial growth over five decades or more (to surpass radial growth of trees in young stands) and then sustained higher growth rates ($p \leqslant 0.05$). The 10-year radial growth rate at age 50 ranged from about 2.3–3.3 cm/decade in old-growth stands compared to 1.5–2.0 cm/decade in young stands. Moreover, the growth rate of trees in old-growth stands remained high at 80 years (Fig. 4). Data from the Siskiyous indicated that these radial growth rates vary by species. Douglas-fir and ponderosa pine grew rapidly the first three decades and then maintained relatively constant growth, significantly ($p \leqslant 0.05$) greater than that of white fir for the next five decades or more (Fig. 4). Radial growth of white fir was consistently lower ($p \leqslant 0.05$) than that of Douglas-fir and ponderosa pine for 80 years.

Tree diameters at 150 and 200 years were significantly ($p \leqslant 0.001$) and strongly related to their radial growth rates at 50 years (Fig. 5). Equations using log-transformed (to improve the regression fit) 50-years radial growth rates explained 58–71% of the variation from mean tree diameter at age 150 years across forest types. The relationships were not as strong for diameter at age 200, but still accounted for 43–61% of the variation from mean tree diameter. Simple linear relationships (not shown) of 50-years radial growth to 150- and 200-years diameter similarly accounted for 59–68% and 44–61% of the variation from mean diameter at 150 and 200 years, respectively.

3.4. Tree architecture

We found fundamentally different tree crown and stem characteristics in old-growth vs. young stands consistent with the patterns in stand density and growth rate (Fig. 6). Across the three forest types, almost 90% of the trees in the old-growth stands had high live crown ratios, ranging from 50% to over 70%. Only 30% to 50% of the trees in young stands had ratios >50%. Similarly, trees in old-growth stands were larger in diameter relative to their height than trees in young stands, with >50% of them having H:D ratios of $\leqslant$50. Only about 10% of the trees in young stands had such low H:D ratios (Fig. 6).

3.5. Fire occurrence and frequency

Fire was very common from 1700 to 1900 in all our old-growth stands in all three forest types (Fig. 7; Table 2). We identified a total of 1203 fire scars across all sites: 441 scars in Cascades mixed-conifer, 443 in Siskiyous mixed-conifer, and 319 in mid-Coast Range mixed-evergreen. This represents from 16 to 170 fire scars per 8-ha stand with no significant difference ($p = 0.61$) in the

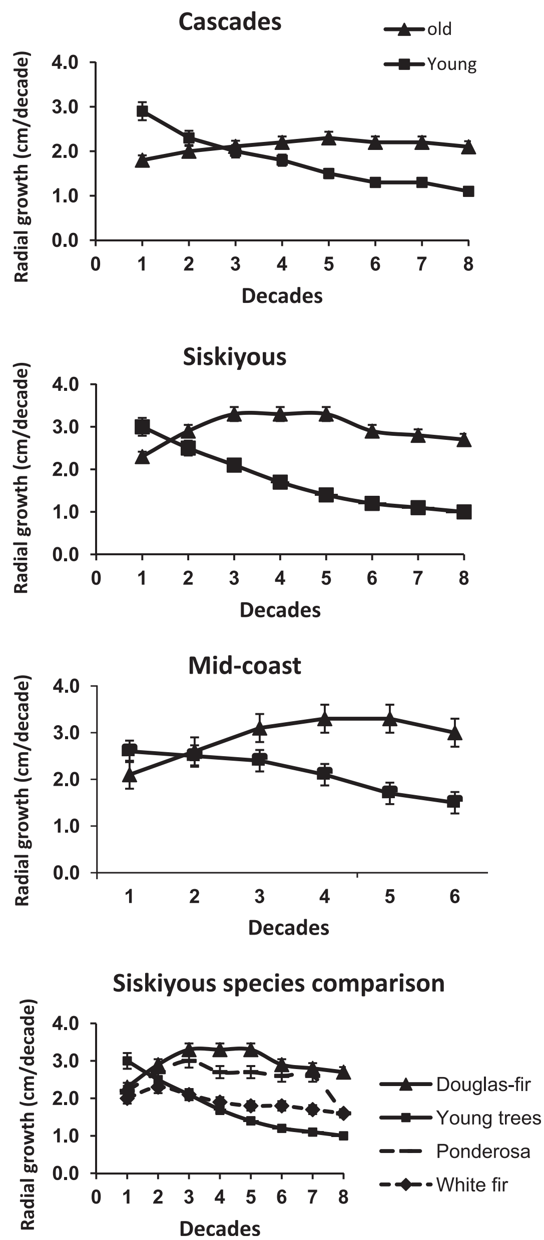

Fig. 4. Radial growth rate (cm/decade) of naturally-regenerated old-growth and young trees in 18 stands each in southwestern Oregon during their early decades. There were consistent differences in growth rate pattern over time, with old-growth trees increasing for many decades when they are young, and sustaining greater rates than their counterparts in dense young stands after the first 20–30 years. Error bars are one standard error across all trees.

average number of fire scars detected per 8-ha stands among forest types. The earliest fires detected in this study area occurred about 1430, 1620 and 1600 AD across the three forest types. We found only three 20th-century fire scars in old-growth stands (dated to 1901, 1903, and 1909), one in each forest type. We found no fire scars on 60- to 100-years-old trees in nearby young stands, though the few scattered old trees in these stands often had evidence of fire scars and/or charred bark dating to unknown events.

When we grouped fire scars nominally ±6 years, we estimated that there was an average of 11–13 separate fires per 8-ha site during the 200 years between 1700 and 1900; these estimates were reduced only slightly to 9–10 fires per site when grouped most conservatively at ±10 years and, conversely, increased to 15–16 when group by ±3 years (Table 2). Twelve fires in 200 years

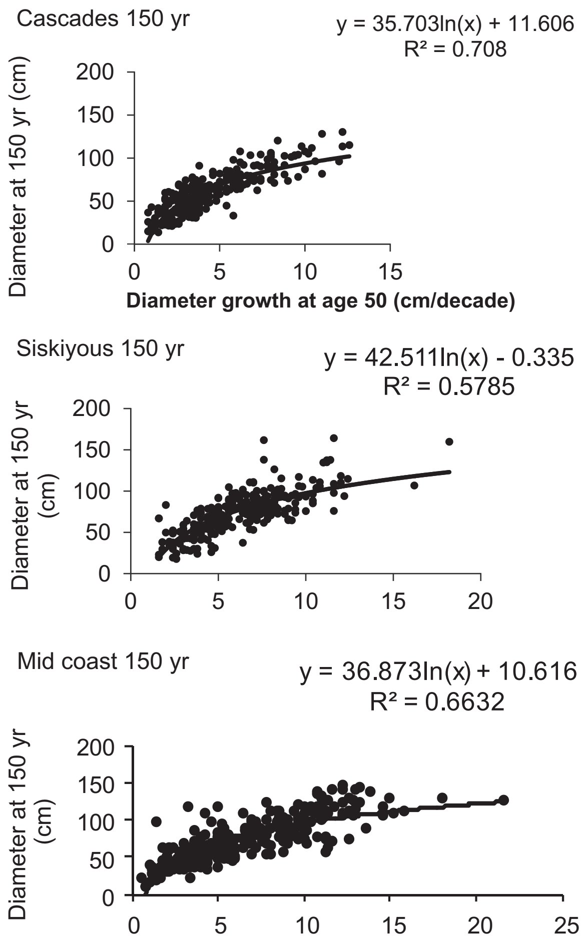

Fig. 5. Diameter at age 150 as predicted from radial growth at age 50 for naturally-regenerated old trees in 18 sampled stands in southwestern Oregon. Trees that grew rapidly at age 50 were consistently the largest trees at age 150 years regardless of their decade of establishment.

equates to a mean fire return interval of 17 years at an 8-ha scale, or one fire about every other decade (Fig. 7). Overall, most 50-year periods had two or more fires across all sites, and nearly two-thirds of all decades from 1700 to 1900 had at least one fire across forest types. Viewed differently, from 1700 to 1900, the longest fire-free periods across sites based on grouping scars ±6 years were ⩽50 years with only one exception (76 years in the Siskiyous; Table 2). Fire-free periods were typically two to four decades whether fire scars were grouped ±6 or ±10 years. Even based on an aggressive ±3-year grouping, all sites still had at least one 15-year fire free period, and 15 of the 18 sites had at least one period ⩾20 years. Only one site each in the Cascades and Siskiyous and three sites in the mid-Coast had fire-free periods ⩾30 years.

3.6. Fire and tree establishment

We found no consistent relationship between fire and tree establishment across all sites ($p = 0.145$) when fires were grouped ±6 years; Chi-square tests were significant at 0.745, 0.017, and 0.59 for the Cascade, Siskiyous, and mid-Coast sites, respectively. Using ±10-year grouping of fire occurrence, these values were: 0.056, 0.409, and 0.573 for these sites and 0.111 with all types combined. We found that tree recruitment from 1700 to 1900 occurred during periods both with and without fire at all sites in all three forest types, and that establishment was highly variable (Figs. 2 and 7). In the Cascades, 37–94% of establishment occurred in decades with fire. In the Siskiyous these percentages were 26–78% and, in the mid-Coast Range, 41–84%. Conversely, in the three longest fire-free periods (Table 2), 3–44%, 7–52%, and 14–44% of the trees were established. Data from 0.1-ha plots indicated that many small trees (<10 cm diameter) were present when fire occurred. From 42–67% of 119 trees across forest types that had multiple fire scars were <10 cm diameter when their first scar occurred. Also, for 50–56% of the trees on our plots, we estimated that there was a fire within 10 years following their establishment date, and 80–89% within 20 years of establishment.

4. Discussion

4.1. Tree and stand growth

Old-growth stands clearly developed differently than younger stands in these three southwestern Oregon forest types. The broad range of tree ages, overall low tree densities, and rapid early individual tree diameter growth in old-growth stands are in strong contrast to a narrower age range, higher stand density and slower diameter growth in young stands throughout the region. This difference is quite similar to that seen in more northerly forests (Tappeiner et al., 1997; Poage and Tappeiner, 2002; Poage et al., 2009). Rapid diameter growth throughout the first century, low H:D ratios, and large crowns in old-growth stands likely result from: (a) overall lower rates of tree establishment, (b) variable tree density with very low density in parts of a stand, and/or (c) slow recruitment over longer time periods that gave trees established earlier a competitive advantage over those established later. Fire undoubtedly contributed to all three (Agee, 1993; Bailey and Covington, 2002).

There were likely more trees and therefore more basal area in our old-growth stands in the 1700's than we could detect in 1990, given the effects of fire and/or decomposition over 290 years; however, we believe that our estimates of density and basal area/ha from 1800 to 1990 are representative of the basic differences in stand development in these two stand types. Large trees that were dead at the time of harvesting would likely be left standing and thus still present. We saw little or no evidence of any large-tree mortality on our plots, which would have been evidenced by large snags and pieces of wood on the forest floor. Small saplings (<10 cm diameter) might have been obliterated during logging and site preparation, or killed/consumed by frequent fires, but trees this size account for very little basal area. Nevertheless, there was a large increase in net biomass production in the last century as indicated by basal area growth, linked primarily to diameter increases of dominant trees with large crowns and greater access to belowground resources. Continued increases in total stand-level biomass will probably make these old-growth stands increasingly susceptible to climate- and drought-related stresses (McDowell et al., 2003) and uncharacteristic stand-replacing fire (Agee, 1993).

Young stands initiated and developed immediately following stand-replacing disturbance with much higher densities than their neighboring old-growth stands, and as a single cohort of relatively even-sized, comparatively small trees (Table 1). Their developmental pathway closely resembles the classic stand initiation and stem (or competitive) exclusion stages of Oliver and Larson (1990) and Franklin et al. (2002). Trees in these young stands were growing slowly by age 30 (Fig. 4) because of density-induced competition for resources. High stand density is frequently associated with slow rates of individual tree growth even on productive sites (Drew and Flewelling, 1979; Marshall and Curtis, 2002; Tappeiner et al., 2007). Establishment of a large number of trees over a relatively short period and the absence of thinning (e.g., by fire or mechanical treatment) resulted in young stands that were quite

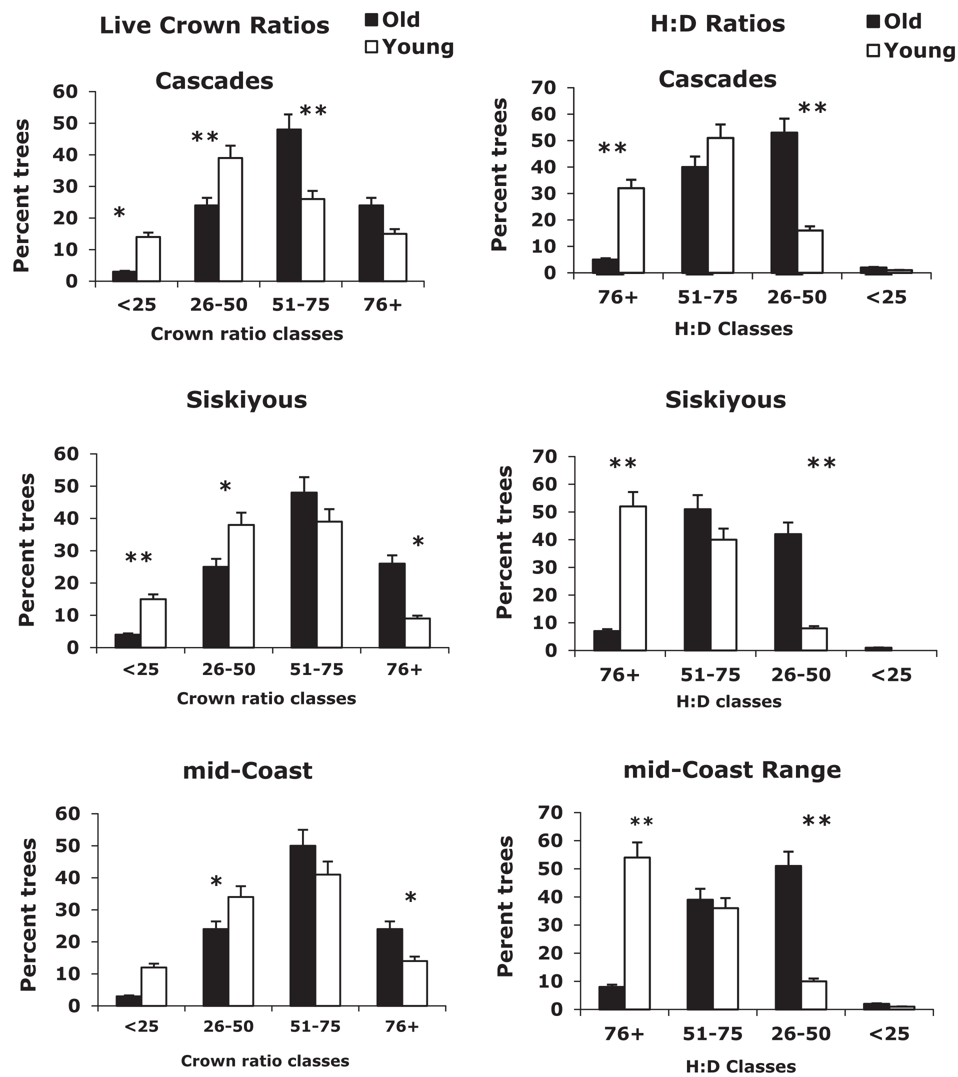

Fig. 6. Live crown ratios and height:diameter ratios for young and old trees (six sites each in each forest type). Bars marked with ** denote difference at $p \leqslant 0.05$; * denotes $p = 0.10–0.05$). Axis are arranged to show ratios of smaller trees on the left, ranging to larger trees on the right. Trees in old-growth stands had significantly more trees with larger crowns and lower H:D ratios than trees in young stands. Error bars are one standard error across plots.

productive, in sum, but restricted in terms of individual tree growth. During the last 40 years, their rates of stand-level basal area growth were greater that those of old-growth stands, and thus they accumulated more biomass and cubic volume of wood since 1900 than old-growth stands. The relative density of young stands in 1990 averaged 42–55% of stand maximum; thus, they are at or close to the zone of imminent competition-based mortality (Drew and Flewelling, 1979; Long et al., 1988). Without substantial increase in growing space, these stands will not likely develop the tree sizes, structures, and understory characteristics of old growth for many years, if at all (Bailey and Tappeiner, 1998; Bailey et al., 1998; Muir et al., 2002).

The relationship of tree size at 150 and 200 years with diameter growth rate at 50 years confirms the importance of low density and early rapid diameter growth rate in the development of old-tree characteristics. Poage and Tappeiner (2002) report that the basal growth rates of the largest 25% of trees in old-growth remained relatively constant after about 50 years. Thus, thinning in young stands would likely enable trees to maintain diameter growth- and reach large sizes. The rapid growth of trees is commonly associated with larger crowns and limbs (Tappeiner et al., 2007). In contrast, trees in dense stands grow slower and have smaller crowns. Trees in the old-growth stands generally maintained their crowns and associated diameter growth rates. The rapid, continued growth rate of old-growth trees also enabled these trees to develop large stems in relation to their heights, that is to develop low H:D ratios, that are associated with resistance to wind throw and ice damage (Wilson and Oliver, 2000, Tappeiner et al. (2007). Old, large trees with large crowns (Fig. 6) can be important components of a stand. These large old trees were found to respond in additional growth after stand density reduction by thinning (Latham and Tappeiner, 2002; McDowell et al., 2003). Because of their large crowns, they are an important structural component of old-growth stands providing habitat for a variety of taxa (Franklin et al., 2002).

4.2. Fire occurrence

Most previous studies of fire occurrence have been conducted at larger scales with the expressed purpose of characterizing fire regimes for a particular forest or watershed, typically >1000 ha. In this study, we characterized the regime at the stand level in order to help understand its relationship to stand dynamics and development in old-growth forests. Fire was clearly common at the stand level on all our sites before 1900 (Fig. 7). Surprisingly, there was no

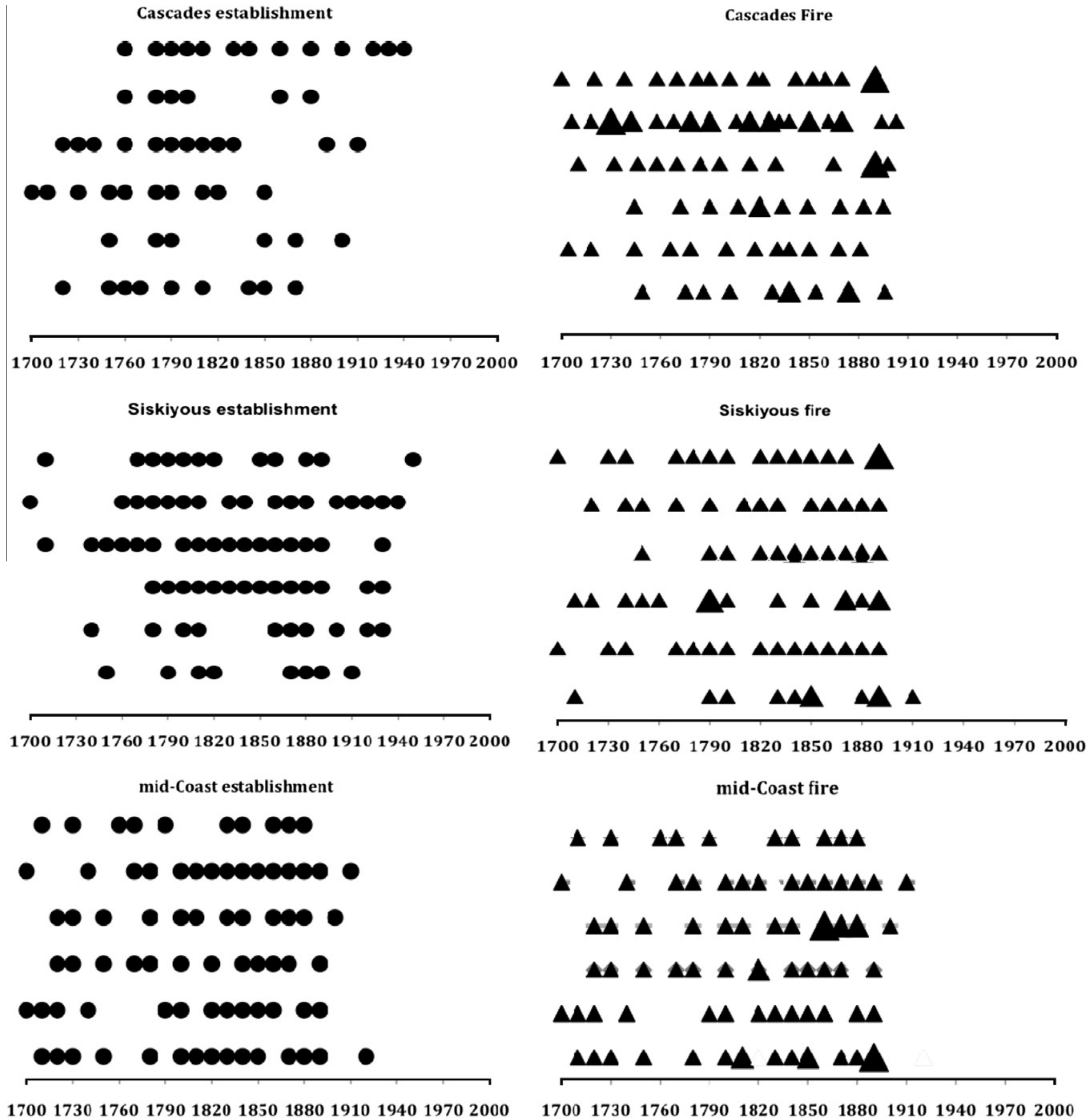

Fig. 7. Decade of tree establishment and fire occurrence for the 18 old-growth stands; fire decade estimated by grouping fire scars ±6 years. Size of fire symbol indicates fire occurrence based on ⩽4 fire scars (smallest), 5–9 scars (mid-sized) symbols, or ⩾10 scars (large). Sites are listed in the same order (1–18) as in Table 2. There is no clear relationship between fire occurrence and tree establishment prior to 1900.

apparent difference in fire occurrence among the three forest types even though the mid-Coast Range has greater annual precipitation that occurs over a longer period of the year than the other sites. Fire cessation on our sites after about 1900 is in agreement with other studies in neighboring regions (Agee, 1990; Atzet and Martin, 1994; Atzet and Wheeler, 1982; Taylor and Skinner, 2003). Native Americans likely initiated many of the fires we observed (Zybach, 1993; Barrett and Arno, 1982); for example, Soda Creek and Deer Meadows in the Cascades (Fig. 7) were sites frequented by Native Americans (LaLande and Winthrop, 1997).

These approximated fire frequencies are remarkably similar to those of Agee (1991a,b) for similar forest types: 15 years between 1746 and 1916 in a single 2-ha stand in the Siskiyous, and 20 fires reported between 1740 and 1987 (a 12-years mean fire return interval) in Douglas-fir and hardwood stands in northern California (return intervals of 11–17 years). Taylor and Skinner (2003) reported comparable fire return intervals for this region (15–30 years from 1600–1900; north slopes averaged 16.5 years compared to 11.3–12.5 years on drier aspects). They also report no fires after 1900. There has been considerable variation in estimated fire occurrence throughout the region, though with other studies in similar forest types reporting mean fire frequencies at the upper range of our estimates (Table 2). Atzet and Martin (1994) estimated that the historical fire frequency averaged 42 years, and the time since last fire was approximately 68 years (~1920) in the Klamath Province of southwestern Oregon and northern

Table 2
Numbers of fire scars in old-growth stands in southwestern Oregon; fire occurrence at three levels of dating precision; fire return interval and three longest fire free periods at ±6- and ±10 years grouping of fire scars. Numbers and sites correspond to those in Figs. 1, 2 and 7. *p*-values test the null hypothesis that there is no difference among the means for the three forest types ($p \leqslant 0.05$).

Forest types: Sites	Total fire scars	Number of trees with multiple scars	Fires ±3 years	Fires ±6 years	Fires ±10 years	200-Years fire return interval at ±6 years Mean (range)	Three longest fire free periods ±6 years	200-Years fire return interval at ±10 years Mean (range)	Three longest fire free periods ±10 years	MFRI at individual trees Mean (range)
Cascades										
1. Deer Creek	92	13	17	15	10	13 (8–20)	20, 20, 20	17 (11–29)	29, 26, 24	43 (19–155)
2. Soda Meadows	170	19	27	16	9	12 (6–18)	18, 16, 12	18 (5–26)	26, 24, 18	79 (33–203)
3. Hoxie Creek	70	8	12	12	10	17 (12–35)	35, 20, 18	16 (5–28)	28, 24, 23	44 (40–47)
4. Buck Divide	26	2	13	10	11	20 (13–44)	44, 28, 20	19 (5–39)	39, 27, 19	54 (20–103)
5. Shell Peak	54	6	15	12	10	15 (7–26)	26, 22, 18	19 (11–32)	32, 21, 19	146 (106–180)
6. Willow Creek	29	3	9	9	9	21 (12–50)	50, 26, 25	25 (8–50)	50, 30, 28	69 (19–180)
Mean (range)	73	8	16	13	10	17 (6–50)		19 (5–50)		73 (19–203)
Siskiyou										
7. Glade Creek	134	17	22	13	10	13 (8–28)	29, 20, 14	19 (12–28)	28, 25, 20	45 (12–309)
8. Skunk Gulch	79	6	16	13	9	13 (3–25)	25, 18, 17	20 (13–27)	27, 20, 20	46 (17–98)
9. Wood P. Springs	42	4	13	9	6	21 (7–50)	50,40, 28	29 (14–52)	52, 48, 26	25 (14–53)
10. Lick Gulch	107	9	16	12	10	16 (8–27)	27, 22, 20	20 (14–28)	28, 20, 20	34 (15–82)
11. Wrangle Pass	50	3	14	13	10	16 (8–31)	31, 22, 28	21 (10–30)	30, 30, 28	39 (25–47)
12. Yale Creek	31	4	10	7	7	21 (6–76)	76, 39, 13	28 (13–76)	76, 28, 17	43 (22–72)
Mean (range)	73	9	15	11	9	23 (3–76)		23 (10–76)		39 (12–309)
mid-Coast Range										
13. Dulog Creek	16	2	10	10	8	20 (8–42)	42, 31, 25	23 (10–43)	43, 31, 25	30 (20–39)
14. Big Windy Creek	51	7	14	13	11	14 (7–38)	38, 29, 22	19 (5–36)	36, 26, 21	56 (17–161)
15. Sour Grass Creek	56	3	12	12	8	16 (8–49)	49, 29, 16	24 (11–58)	58, 23, 22	80 (5–152)
16. Smith Creek	85	7	12	12	8	15 (10–24)	24, 22, 20	16 (11–30)	30, 25, 20	31 (17–49)
17. Rum Creek	48	14	13	13	8	23 (18–44)	44, 20, 20	23 (10–42)	42, 28, 20	45 (11–140)
18. Smoked Elk	83	12	14	13	9	18 (7–28)	28, 20, 19	23 (12–28)	28, 25, 25	63 (15–145)
Mean (range)	53	7	15	12	9	18 (7–49)		21 (5–58)		51 (11–161)
p-values	0.71		0.99	0.99	1.00	0.36		0.22		0.156

California. Similarly, Agee (1990) found that recurrent fire was common for more than 500 years, with 19th century fires averaging a 34-year fire frequency. On his study sites, no fire had occurred since 1921, the longest fire-free period in more than 300 years.

Fires were likely of low- and mixed-severity, in general, with some intense crown fire undoubtedly occurring on some parts of our study sites at certain periods. Agee (1991b) reports fire occurrence as a "patchy mosaic" in the Siskiyous near our study sites. Our findings suggest that this mosaic was dominated by moderate- and low-intensity fire because many small trees ($\leqslant$10 cm diameter) survived these fires, and we estimate that fire occurred 10–20 years after establishment for over 80% of the trees on our sites. Such a complex relationship between fire occurrence and regeneration could not be maintained by widespread high-severity fire (Baker and Ehle, 2001). With frequent low-severity fires on these sites, surface and ladder fuels were kept at relatively low levels and thus reduced the potential area for and probability of severe fire.

4.3. Fire and stand development

Old-growth stand characteristics (Spies and Franklin, 1991) observed on today's southwestern Oregon landscape developed during a period of frequent fire from 1700 to 1900, followed by a modern period with little to no fire. Fire likely played a major role in maintaining overall lower stand densities and conditions for old-growth characteristics to develop, in combination with other factors such as wind, drought or insect "outbreaks" (Agee, 1993). Survival and growth of regeneration further varied in interaction with weather and topography at multiple scales. Deal et al. (1991) reported similar stand dynamics and tree establishment patterns on sites in southeast Alaska based primarily on chronic, severe wind disturbances.

The complex relationship between fire occurrence and natural seedling establishment is not surprising given the dual role of low-intensity surface fire in both facilitating and hampering tree regeneration. Fire favors regeneration of shade intolerant conifer species like ponderosa pine and Douglas-fir when it prepares a seed bed and reduces competition from herbs, shrubs and overstory trees. However, natural regeneration from seed is a relatively complicated process (Tappeiner et al., 2007) that begins with cone/seed production and includes germination, early survival (1–3 years) and growth into saplings. Stand establishment may occur immediately after a disturbance or take several decades (Shatford et al., 2009), as it did for the young stands in this study. Seed production (Isaac, 1943), rodents and cone/seed eating insects, competing grasses and shrubs (Conard and Radosevich, 1982), weather extremes, fire (Taylor and Skinner, 2003), and herbivores can all delay seedling establishment for many years in southwestern Oregon.

Shatford et al. (2009) studied natural seedling establishment following stand-replacing fire in the Siskiyous and reported seedling establishment peaking 2–10 years after a fire but lasting up to 19 years. If low-severity surface fire returns in 10–15 years (or longer), as it did in the old-growth stands in this study, many trees and shrubs in the understory, as well as some larger trees, would likely be killed, depending on fire intensity and continuity. This would create growing space for establishment and growth of new trees and growth of larger established trees. A reduction in canopy cover is crucial for shade intolerant species like Douglas-fir to become established, grow quickly into the canopy, and reach fire-resistant sizes. Recruitment during periods with fire is likely to occur only with lower intensity and/or highly variable fires that do not uniformly cover an entire stand (Agee, 1993; Baker and Ehle, 2001). Where fires are frequent and fire intensity is variable, it is likely difficult to relate establishment of any uneven-aged stand of trees to fire, no matter how accurately fire occurrence and tree ages are determined. Indeed, variation in fire occurrence over time (climate and weather), length of fire-free periods (fuel accumulation), and probably spatial pattern (topography and distribution of competing grasses and shrubs), as well as variability in fire intensity and severity, are more important to stand structure and tree establishment than mean fire return interval.

4.4. Major stand types and dynamics

We studied two dominant types of stands (A and C) in southwestern Oregon and their patterns of development as well as comment on a common, contemporary stand type (B). Though we recognize that other types and patterns of development exist in this complex landscape, we hypothesize the following development/dynamics for these three stand types:

Type A – past old-growth stands: These stands were a dominant feature in the landscape prior to 1900 and developed at a low, variable density (Figs. 3 and 4), maintained primarily by periodic, irregular fire occurrence (Table 2, Fig. 7). Regeneration was established periodically (Fig. 2) as fire prepared seedbeds and provided growing space; however, fire also killed seedlings, saplings and some larger trees. Thus, these stands were generally irregular in trees size and distribution. Young trees that escaped fire generally grew rapidly for their first 60–70 years (Fig. 4) to achieve large sizes. The large trees in these stands have large crowns and low H:D ratios. These stands are currently rare in the landscape given policies that led to fire exclusion over the last century.

Type B – contemporary old-growth stands: These stands have been largely created by a century without fire in them and are common in the landscape. They followed a similar developmental pathway as Type A until about 1900 and still contain irregular large tree sizes and spacing, large crowns and low H:D ratios. They are currently denser overall, generally, with a well-developed and continuous understory of shrubs, and some hardwood and conifer trees (Parsons and DeBenedetti, 1979), as well as uncharacteristically high fuel accumulations. They are likely much more susceptible to severe fires and insects outbreaks than Type A stands. If stand-replacing fire can continue to be excluded, which is becoming a major challenge to forest managers, then these stands will likely provide important, structurally-complex wildlife habitat.

Type C – young stands: These stands developed with abundant natural regeneration following stand-replacing fire and/or harvesting and mining. Seedlings established at high densities (Table 1, Figs. 1 and 3) over a relative short period (in contrast to Types A and B) creating relatively even-aged/sized stands. Type C stands accumulate volume rapidly on an area basis, although individual tree growth has been predominantly slow after the initial two decades (Fig. 4). These stands have a sparse understory for decades (Bailey et al., 1998; Bailey and Tappeiner, 1998) and are susceptible to insect outbreaks and stand-replacing fire. Trees have small crowns and stems, as well as high H:D ratios. If stand-replacing fire can be excluded from these stands, then they will likely produce high levels of biomass over time but on relatively small stems (Table 1).

4.4.1. Management implications

Type A stands can be sustained with repeated fire and/or an uneven-/multi-aged silvicultural system designed to retain a range of closed and open conditions with a range of tree sizes growing at relatively low, variable densities. Lower density areas within stands provide early seral conditions for the establishment and growth of conifers, shrubs and hardwoods among large overstory trees. Spatially regulating ladder fuels (understory trees and shrubs) and surface fuels (slash and natural deposition) will be important in order to lower the probability of stand-replacing fire.

Vigor of large, old trees (McDowell et al., 2003; Latham and Tappeiner, 2002) would likely be higher and mortality lower than in Type B stands. Frequency and distribution of fire and other treatments would be dictated by within-stand fuel variability (Graham et al., 1999), and areas treated would vary among stands. In some parts of a stand, relatively long-fire free periods (three or more decades) might be needed to establish and promote regeneration and/or maintain large trees.

Type B stands would generally require little within-stand management other than active fire suppression to maintain their current condition and provide structurally-complex habitat. Periodically creating areas of low density in some parts of some stands might be needed to encourage continued development of some large trees with large crowns (i.e., low-density stand dynamics within a high-density stand). These treatments are suggested as ways to maintain Type B stands, but they will continue to accumulate fuels and have an uncertain future given limits to our ability to protect them from landscape-scale wildland fire in southwest Oregon. A well-planned and executed landscape fire management program focused on conserving these stands is needed (Weatherspoon and Skinner, 1995). Alternatively, Type B stands can be converted to Type A stands with aggressive proactive management; for example, Thomas and Agee (1986) found multiple thinning and prescribed fire treatments could restore sustainable density and structure in the Cascades near our study sites. It is advisable to reduce heavy concentrations of ladder and surface fuels in parts or all of these stands, but to balance these actions against the need for habitat associated with understory vegetation and multiple tree layers. We conclude that these contemporary Type B old-growth stands are different from what they were at the beginning of the 20th century; we wonder if they were habitat for the same range of taxa as currently.

Thinning in Type C stands provides growing space among the crowns of larger trees and would maintain or improve growth rates, crown size and tree stability (Tappeiner, 2009). It would also likely reduce climate-induced drought stress, the probability of insect outbreak, as well as the threat of uniform, stand-replacing fire. Surface fuel treatments to regulate understory development and reduce fire hazard, combined with some crown thinning, can reduce the probability of high-severity fire in these stands (Weatherspoon and Skinner, 1995; Martin, 1990; Graham et al., 1999). Such management would produce commercial wood and support a number of current objectives on federal forest lands. If, however, the intention is to promote old-growth characteristics in Type C stands, then it would be best to grow young stands at densities much lower than those we report in this study, possibly beginning with 100–150 tree/ha, for several decades and then maintaining a range of lower densities as tree size and inter-tree competition increase. The ranges of trees/ac (Table 1), live crown and H:D ratios (Fig. 6), as well as diameter growth rates (Fig. 4), that we report for old-growth stands can be used as goals for managing young stands in southwestern Oregon to achieve desired tree and stand characteristics. Heavy thinning would maintain rapid growth of young trees for many decades, ensuring future large-tree stand components (Fig. 5, Poage and Tappeiner, 2002) including large dead wood. However, such treatment also encourages development of an understory of hardwoods and shrubs as well as a mid-story of hardwoods and conifers (Bailey and Tappeiner, 1998; Muir et al., 2002) that might be a goal for Type B but not Type A old-growth stands.

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