Influences of climate, fire, and topography on contemporary age structure patterns of Douglas-fir at 205 old forest sites in western Oregon

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Abstract: Knowledge of forest development is basic to understanding the ecology, dynamics, and management of forest ecosystems. We hypothesized that the age structure patterns of Douglas-fir at 205 old forest sites in western Oregon are extremely variable with long and (or) multiple establishment periods common, and that these patterns reflect variation in regional-scale climate, landscape-scale topography, and landscape-scale fire history. We used establishment dates for 5892 individual Douglas-firs from these sites to test these hypotheses. We identified four groups of old forest sites with fundamentally different Douglas-fir age structure patterns. Long and (or) multiple establishment periods were common to all groups. One group described old forests characterized by substantial establishment from the early 1500s to the mid-1600s, with decreasing establishment thereafter. Another group was characterized by peaks of establishment in the middle to late 1600s and in the late 1800s and early 1900s. A third group was characterized by a small peak of establishment in the mid-1500s and a larger peak in the middle to late 1800s. Characteristic of the fourth group was the extended period of Douglas-fir establishment from the late 1600s to the late 1800s. Group membership was explained moderately well by contemporary, regional climatic variables and landscape-scale fire history, but only weakly by landscape-scale topography.

Résumé : La connaissance du développement des forêts est fondamentale pour comprendre l'écologie, la dynamique et l'aménagement des écosystèmes forestiers. Nous avons posé les hypothèses que les patrons de structure d'âge du douglas de Menzies établi sur des stations forestières âgées de 205 ans de l'ouest de l'Oregon, aux États-Unis, sont extrêmement variables, ayant généralement des périodes d'établissement longues ou multiples, et que ces patrons reflètent les variations du climat à l'échelle régionale, de la topographie à l'échelle du paysage et de l'historique des feux à l'échelle du paysage. Pour tester ces hypothèses, nous avons utilisé les dates d'établissement de 5892 tiges de douglas de Menzies croissant sur ces stations. Nous avons identifié quatre groupes de vieilles stations forestières où les patrons de structure d'âge des douglas de Menzies étaient fondamentalement différents. Des périodes d'établissement longues ou multiples étaient communes à tous les groupes. Un groupe correspondait aux vieilles forêts caractérisées par un établissement substantiel à partir du début des années 1500 jusqu'au milieu des années 1600, période suivie par un établissement décroissant. Un autre groupe était caractérisé par des pics d'établissement à partir du milieu jusqu'à la fin des années 1600 et à partir de la fin des années 1800 jusqu'au début des années 1900. Un troisième groupe était caractérisé par un faible pic d'établissement au milieu des années 1500 et par un pic plus important à partir du milieu jusqu'à la fin des années 1800. Le quatrième groupe était caractérisé par une longue période d'établissement à partir de la fin des années 1600 jusqu'à la fin des années 1800. Les effectifs de ces groupes étaient modérément bien expliqués par des variables climatiques régionales contemporaines et par l'historique des feux à l'échelle du paysage, mais ils étaient faiblement expliqués par la topographie à l'échelle du paysage.

[Traduit par la Rédaction]

Introduction

We believe that forest ecologists should consider the possibility of multiple disturbances as a major factor in the development of forests with old-growth structural charac-teristics. As a dominant canopy tree species, Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) forms the structural backbone of many old forests in western British Columbia, Washington, Oregon, and northwest California (Franklin and Dyrness 1973; Spies and Franklin

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Table 1. Studies, number of sites included from each study (*n*), site numbers, and sampling methods employed in the studies from which the Douglas-fir establishment data for the 205 Oregon old forest sites were drawn.

Study	*n*	Site numbers[a]	Sampling method
a - Impara 1998	90	1–4, 14–18, 20–36, 38–39, 41–44, 46–103	In the first season, all stumps were measured in three 0.05 ha circular plots; one plot was randomly located at each of three hill slope positions (upper, middle, and lower). In the second season, one-third of all stumps were sampled in one 10 m wide belt transect extending across upper, middle, and lower hill slope positions.
b - Poage 1995	1	11	Increment cores extracted and measured from a sample of trees across the range of tree diameters (≥5 cm) in one 2.00 ha rectangular plot (100 m × 200 m).
c - Poage 2001	22	7–8, 12–13, 19, 37, 40, 45, 105, 108–109, 117–124, 191–193	All stumps measured in three to four randomly located 0.10 ha circular plots.
d - Means 1982	1	184	Increment cores extracted and measured from all trees ≥50 cm diameter and 35% of trees with diameters between 5 and 50 cm in one 0.75 ha rectangular plot (75 m × 100 m).
e - Sensenig 2003	18	111–116, 194–205	All stumps measured in three randomly located 0.10 ha circular plots.
f - Tappeiner et al. 1997	8	5–6, 9–10, 104, 106–107, 110	All stumps measured in four to six randomly located 0.10 ha circular plots.
g - Weisberg 1998	65	125–183, 185–190	All stumps measured in four 0.10 ha circular plots located at corners of a 4 ha square (200 m × 200 m).

[a]Sites were numbered first by sorting sites west and east of 123°07′30″W (approximate longitude of Eugene, Oregon). The West (*n* = 116) and East (*n* = 89) sites were then sorted by latitude and study and numbered from north to south, by decreasing latitude. West sites are 1–116 and East sites are 117–205. Sites 1 and 117 are the northern-most West and East sites, respectively. Site numbers listed in Table 1 are used consistently throughout the text, figures, and tables.

1991). Previous work has reported great variability in overstory tree size and age structure of Douglas-fir in old forests in western Oregon (Spies and Franklin 1991; Tappeiner et al. 1997; Poage and Tappeiner 2002, 2005). Douglas-fir in western Oregon is a shade-intolerant species that does not establish under closed overstory canopies (Hermann and Lavender 1990). It is dependent on disturbances to create openings in which it can regenerate and grow (Gray and Spies 1996, 1997). This suggests that the establishment of Douglas-fir in these old forests may have occurred over long periods of time after one disturbance (Franklin et al. 2002) and (or) that new cohorts established after multiple disturbances.

Climate, topography, and disturbance type, intensity, and frequency can all influence the establishment patterns of Douglas-fir. Prior to logging, disturbances responsible for the regeneration of Douglas-fir included fire (ignited by lightning or humans), wind, insects, and pathogens (Agee 1991, 1993; Huff 1995; Weisberg 2004). So tightly coupled is the historical relationship between fire and Douglas-fir establishment, for example, that Douglas-fir age structure is often taken as a surrogate for fire history (Morris 1934; Isaac 1940; Munger 1940; Franklin and Dyrness 1973; Hermann and Lavender 1990; Morrison and Swanson 1990; Agee 1991, 1993; Huff 1995; Poage 1995; Agee and Krusemark 2001; Franklin et al. 2002; Winter et al. 2002; Curtis et al. 2007).

Understanding how old forest structures have developed is important for ecologists interested in forest development and for managers interested in accelerating the development of late-successional structural characteristics within young stands (Poage and Tappeiner 2002). This is particularly relevant in western Oregon and Washington given management objectives set forth under the Northwest Forest Plan (USDA

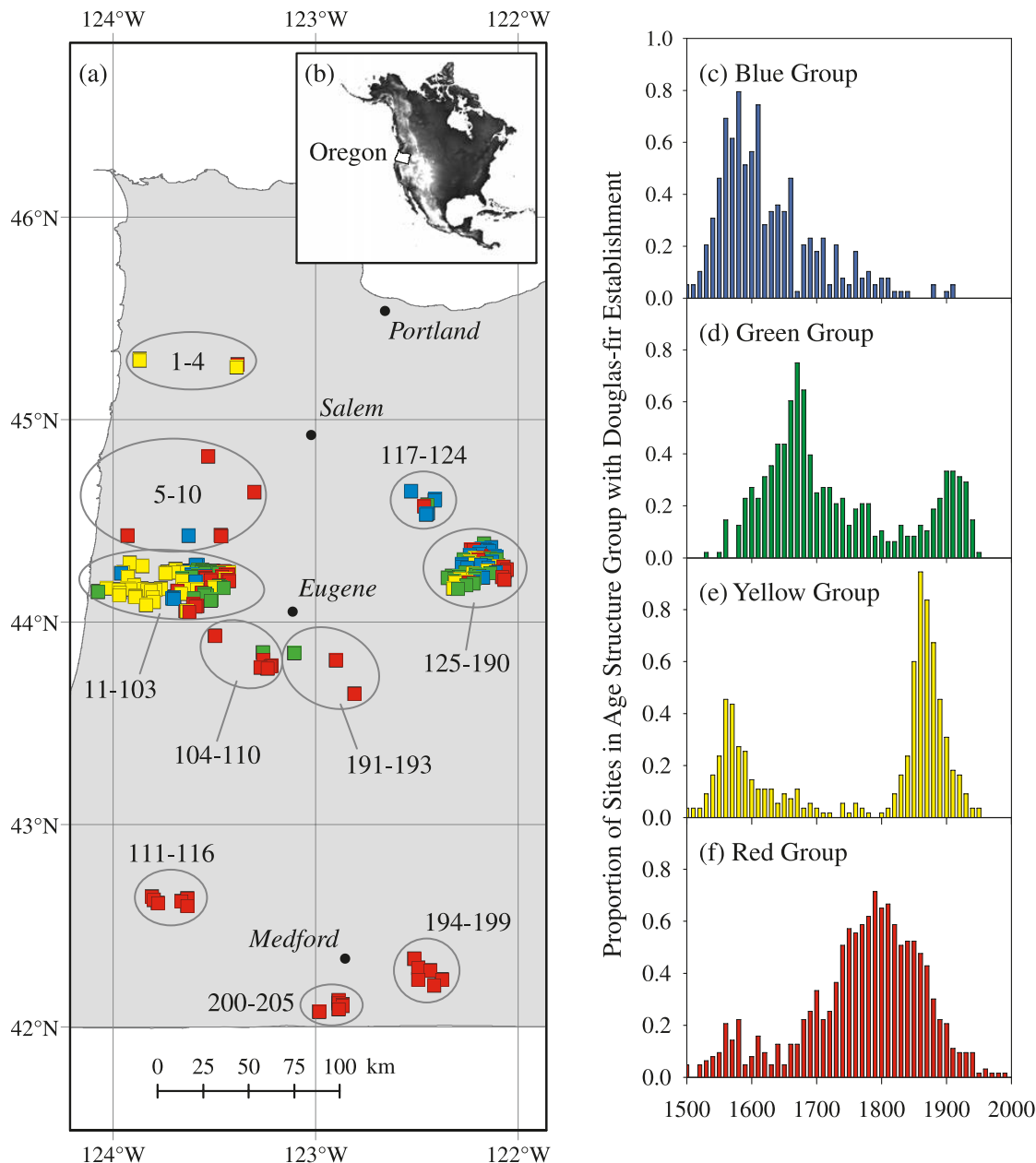Forest Service and USDI Bureau of Land Management 1994).

We addressed two hypotheses. (*i*) The age structure patterns of Douglas-fir at 205 old forest sites in western Oregon are extremely variable, with long and (or) multiple establishment periods being common. (*ii*) The differences in age structure patterns reflect variation in regional-scale climate, landscape-scale topography, and landscape-scale fire history.

Methods

We used establishment dates reported for 5892 individual Douglas-fir trees from seven previously published studies to characterize the contemporary age structure of Douglas-fir at 205 old forest sites in western Oregon (Table 1). The number of sites contributed to our meta-analysis varied among studies. For example, the studies of Impara (1998) and Weisberg (1998) contributed 90 and 65 sites, respectively. In contrast, the studies of Means (1982) and Poage (1995) each contributed one site. To our knowledge, the data from these 205 sites constitute the largest collection of contemporary Douglas-fir age structure information ever assembled and analyzed for old forests in western Oregon.

A total of 116 of the 205 sites were located in the western half of our study area; 89 sites were located in the eastern half (Figs. 1*a*, and 1*b*). The "West" sites were located in the Coast Range and western margin of the Willamette Valley, west of 123°07′30″W (the approximate longitude of Eugene, Oregon). The "East" sites were located east of 123°07′30″W in the western Cascades, eastern margin of the Willamette Valley, and Klamath Mountains of southern Oregon. The elevation range of the 205 sites was approximately 100–1400 m. This area encompasses broad climatic gradients, with 630–5080 mm annual precipitation, 80–240 frost-free days, mean winter temperatures between –3 and +10 °C, and

Fig. 1. (*a*) Locations of the 205 old forest sites in western Oregon. Symbol color indicates age structure group (blue, green, yellow, and red; see text for details). (*b*) Location of Oregon. (*c–f*) Proportion of sites in each age structure group with evidence of Douglas-fir establishment by decade. Site numbers shown on map appear in Fig. 2 and are referred to in the text. Source studies for site numbers are identified in Table 1.

mean summer temperatures between +7 and +30 °C (Pater et al. 1998).

Most sites were originally sampled using two to four randomly located 0.1 ha circular plots (Table 1). Establishment dates were determined from ring counts made on the surfaces of stumps in clearcuts at all sites except the single sites of Means (1982) and Poage (1995) where establishment dates were determined from increment cores extracted from trees.
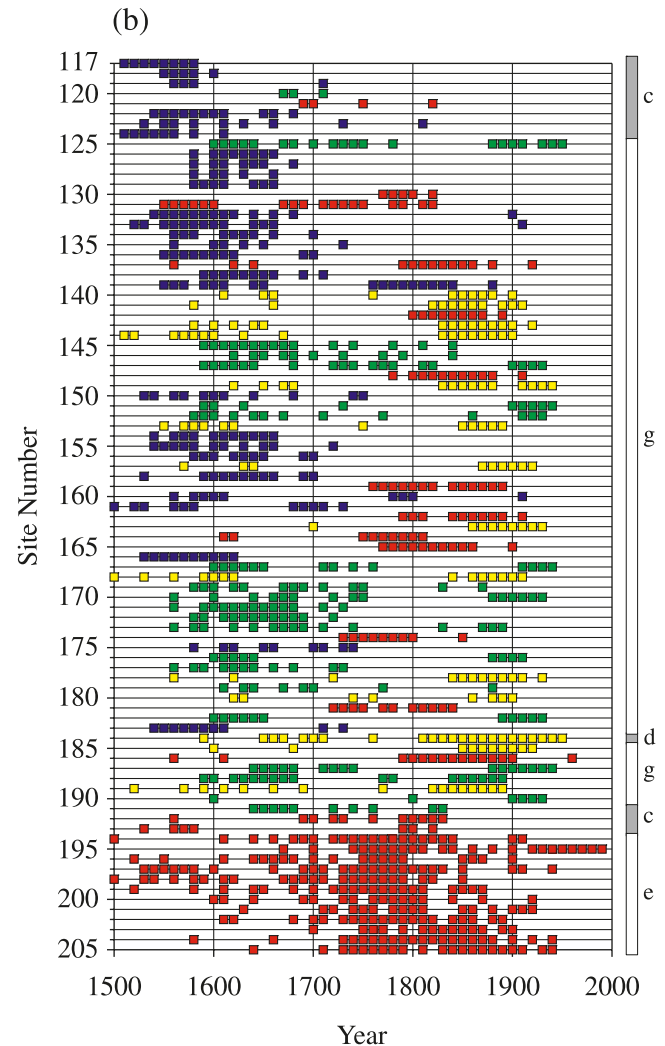
We included sites that met four criteria in our meta-analysis

1. The location of each site was known and could be assigned precise geographic coordinates.

2. Individual Douglas-fir trees (living or recently cut) were sampled or inventoried over a study area ranging from 0.5 to 20.0 ha at each site.

3. Establishment dates were determined for 10 or more individual Douglas-fir trees at each site.

4. At least one of the dated Douglas-fir trees at each site established prior to 1810.

The mean number of establishment dates per site was 28.7 (SD = 13.2), with a range of 10–124. Over 99% of the 5892 trees established in or after 1500; only 36 of 5892 trees established before 1500.

Since establishment dates were only available to the nearest decade for several of the studies, we assigned each tree

Fig. 2. Douglas-fir establishment data for the 205 Oregon old forest sites for the years 1500–2000. Decades for which evidence of Douglas-fir establishment was observed are shown as colored squares for (*a*) West sites (site numbers 1–116) and (*b*) East sites (site numbers 117–205). Symbol color indicates age structure group. Source studies for each site number are indicated by the vertical bars and letters on the right side; see Table 1 for source of each study.

to an establishment decade. For example, we assigned a tree that established in 1563 to the 1560 (1560–1569) establishment decade. This approach is imprecise in that trees assigned to two consecutive decades could have established as few as one and as many as 19 years apart. Despite the potential for within-decade variability, we avoided biasing our results by systematically assigning trees to establishment decades. This also addresses the problem of imprecision in dating due to the use of non-cross-dated studies (Weisberg and Swanson 2001) and the use of tree age estimates taken above the root crown (Lorimer 1985).

We characterized the contemporary age structure patterns

of Douglas-fir and described the geographic distribution of these patterns regionally by mapping the 205 old forest sites (Fig. 1*a*) and plotting the decades in which Douglas-fir established at each site (Fig. 2). For example, site 1 in Fig. 2*a* had six decades for which evidence of Douglas-fir establishment survived to the present. The earliest observed Douglas-fir establishment at site 1 (one of the northern Oregon Coast Range sites from Impara (1998)) occurred in the 1580s (1580–1589). The studies from which the sites were drawn are shown in Table 1.

We identified four age structure groups of old forest sites based on similar patterns of contemporary Douglas-fir age

structure using cluster analysis in the multivariate analysis software PC-ORD, version 4.34 (MjM Software Design, Gleneden Beach, Oregon). We used the presence–absence of Douglas-fir establishment by decade to cluster the groups into age structure groups. For the cluster analysis, we implemented a hierarchical agglomerative approach and used Sorenson's distance measure and a flexible β group linkage method with β set to –0.25 to reduce the amount of chaining (McCune et al. 2002). Preliminary analysis suggested that four age structure groups of sites identified by cluster analysis gave the most interpretable results. We color coded these groups as blue, green, yellow, and red and used this color coding consistently throughout the paper to facilitate interpretation and discussion of results. (The color-coded dendrogram resulting from the cluster analysis is shown in Appendix A.) The proportions of sites in each age structure group with evidence of Douglas-fir establishment are shown by decade in Figs. 1c–1f. For example, Douglas-fir established and survived to the present at 80% of the blue group sites in the 1580–1589 decade (Fig. 1c).

We determined the proportion of total trees at each site that established in each decade. We calculated the mean proportion of trees established in each decade for each age structure group. For each decade, we made pair-wise comparisons among the age structure groups of the mean proportion of trees established in each decade using the Tukey's studentized range test option of the ANOVA procedure of the statistical software SAS, version 9.1 (SAS Institute Inc., Cary, North Carolina). We also calculated the cumulative mean proportion of trees established by decade for each age structure group.

We compared the four age structure groups in terms of regional climate gradients using contemporary (1961–1990) estimates for climatic variables obtained from the Moscow Forestry Sciences Laboratory's Current and Future Climate Web site (Rehfeldt 2006; Crookston 2008). Climatic variables included mean annual precipitation, April–September precipitation, mean annual temperature, mean minimum temperature in the coldest month, mean maximum temperature in the warmest month, the Julian date when the sum of degree days >5 °C equals 100, and a summer dryness index. Degree days >5 °C for each day are calculated by subtracting 5 °C from the day's mean temperature; negative values are set to 0 (Rehfeldt 2006). The summer dryness index is calculated by dividing the sum of degree days >5 °C for April–September by total precipitation for April–September (Crookston 2008). Climate estimates for each site were based on the site's latitude, longitude, and elevation. We used the latitude and longitude of the approximate center of each old forest site and the geographic information system (GIS) software ArcGIS, version 9.2 (Environmental Systems Research Institute, Inc., Redlands, California) to extract the site's elevation, aspect, and slope from a 10 m digital elevation model (DEM).

We made pair-wise comparisons of differences in the climatic variables among age structure groups using Hotelling's T-squared test in S-PLUS, version 6.2 (Insightful Corp., Seattle, Washington). We determined which climatic variables best distinguished age structure groups by comparing simultaneous confidence intervals of differences in group means. We corrected for multiple comparisons by using Sidak's

method to calculate appropriate critical values for tests of the null hypothesis that the confidence interval for difference in group means includes zero (Sidak 1967). We calculated the Mahalanobis distances between group centers in the multidimensional space defined by the climatic variables and used these distances to estimate the overall relative differences among the groups in terms of climate.
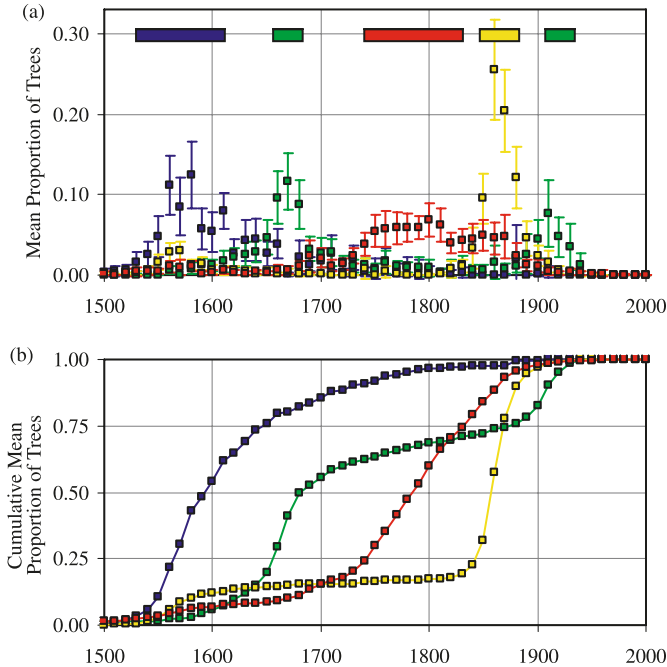
We determined whether the age structure patterns reflected landscape-scale topography and fire history by focusing on two landscape-scale areas with particularly high concentrations of old forest sites. One landscape-scale area is located in the Coast Range west of Eugene and is referred to as the Coast-Impara sites because of the large number drawn from the study by Impara (1998) (sites 11–103 in Figs. 1a and 2a). The other landscape-scale area is located in the Cascades east of Eugene and is referred to as the Cascade-Weisberg sites because of the large number drawn from the study by Weisberg (1998) (sites 125–190 in Figs. 1a and 2b). The Coast-Impara landscape analysis area contains 93 of the 205 old forest sites; the Cascade-Weisberg landscape analysis area contains 66 sites.

We made pair-wise comparisons of the mean elevations and slopes of the four age structure groups in the Coast-Impara area and in the Cascade-Weisberg area using the Tukey's studentized range test option of the ANOVA procedure of SAS. We used polar plots to assess visually differences in aspect and slope among the age structure groups in the Coast-Impara and in the Cascade-Weisberg areas. We used ArcGIS to extract fire history data from different GIS coverages for the Coast-Impara and Cascade-Weisberg sites. We were forced to used different fire history data for the two landscape-scale analysis areas because, to our knowledge, no comprehensive, spatially explicit fire history exists for the portion of western Oregon that includes the Coast-Impara and Cascade-Weisberg sites.

For sites in the Coast-Impara area, we used a fire history and forest age coverage created from Teensma et al. (1991) to determine whether each site had or had not been burned in the mid-1800s (i.e., in or shortly before 1850). We assigned each site that overlapped a polygon of the mid-1800s fire history and forest age coverage (90 of 93 sites) to one of two mid-1800s fire history classes: burned in mid-1800s (43 of 90 sites) or not burned in mid-1800s (47 of 90 sites). We used the fire history and forest age coverage to further classify sites not burned in the mid-1800s into one of two mid-1800s forest age classes: ≥200 years old in mid-1800s (46 sites) or 100–199 years old in mid-1800s (1 site). We used a χ^2 test to test the null hypothesis that the age structure groups were randomly associated with the mid-1800s fire history classes. Using ArcGIS, we visually assessed the spatial associations among the age structure groups and areas burned and not burned in the mid-1800s in the Coast-Impara area.

For sites in the Cascade-Weisberg area, we assigned to each site the dates of fires detected by Weisberg (1998) for the period 1588–1976. We made pair-wise comparisons among the age structure groups of the mean number of fires detected for the full period (1588–1976) using the Tukey's studentized range test option of the ANOVA procedure of SAS. We also made pair-wise comparisons for the periods 1588–1599, 1600–1699, 1700–1799, 1800–1899, and 1900–

Fig. 3. (*a*) Mean proportion of total trees established in each decade for each age structure group for the years 1500–2000. Symbol color indicates age structure group. Vertical bars indicate upper and lower 95% confidence intervals for the mean. Horizontal bars near the top of the graph indicate decades in which the mean proportion of total trees established was significantly greater for the age structure group indicated by the color of the horizontal bar than the means of the other three age structure groups (Tukey's studentized range test, $p < 0.05$). (*b*) Cumulative mean proportion of total trees established for each age structure group.

Table 2. Earliest Douglas-fir establishment dates by age structure group and study.

	n	Mean	SD	Range
All sites	205	1595.6	91.7	1280–1800
Blue group	39	1548.7	29.9	1460–1610
Green group	48	1614.8	82.5	1280–1800
Yellow group	63	1625.2	126.7	1320–1800
Red group	55	1578.0	59.2	1490–1800
Impara 1998	90	1615.2	82.1	1480–1800
Poage 1995	1	1560.0	—	1560–1560
Poage 2001	22	1559.1	93.2	1280–1750
Means 1982	1	1590.0	—	1590–1590
Sensenig 2003	18	1542.8	129.5	1320–1730
Tappeiner et al. 1997	8	1680.0	91.8	1570–1800
Weisberg 1998	65	1585.5	80.0	1320–1800

1976. Using ArcGIS, we visually assessed the spatial associations among the four age structure groups and different fires.

Results

The contemporary Douglas-fir age structure patterns of the 205 old forest sites in western Oregon included in our meta-analysis are extremely variable (Figs. 2 and 3), providing support for our first hypothesis. In characterizing the four age structure groups (blue, green, yellow, and red) identified using cluster analysis, we focused on Douglas-fir establishment and survival from 1500 to the present because over 99% of the 5892 Douglas-fir trees included in our study established in, or after, 1500. At more than 92% of the 205 sites, all Douglas-fir that established and survived to the present established in or after 1500. The average earliest establishment date for each of the four age structure groups fell within the range 1548–1626 (Table 2).

The four age structure groups were distinguished from one another by differences in their temporal patterns of Douglas-fir establishment and survival. The blue group ($n = 39$ of 205 sites) described old forest sites characterized by substantial establishment from the early 1500s to the mid-1600s (Figs. 1*c* and 3). The mean proportion of total trees established at blue group sites was significantly greater for the decades 1530–1610 than for other age structure groups (Tukey's studentized range test; $p < 0.05$; Fig. 3*a*). The
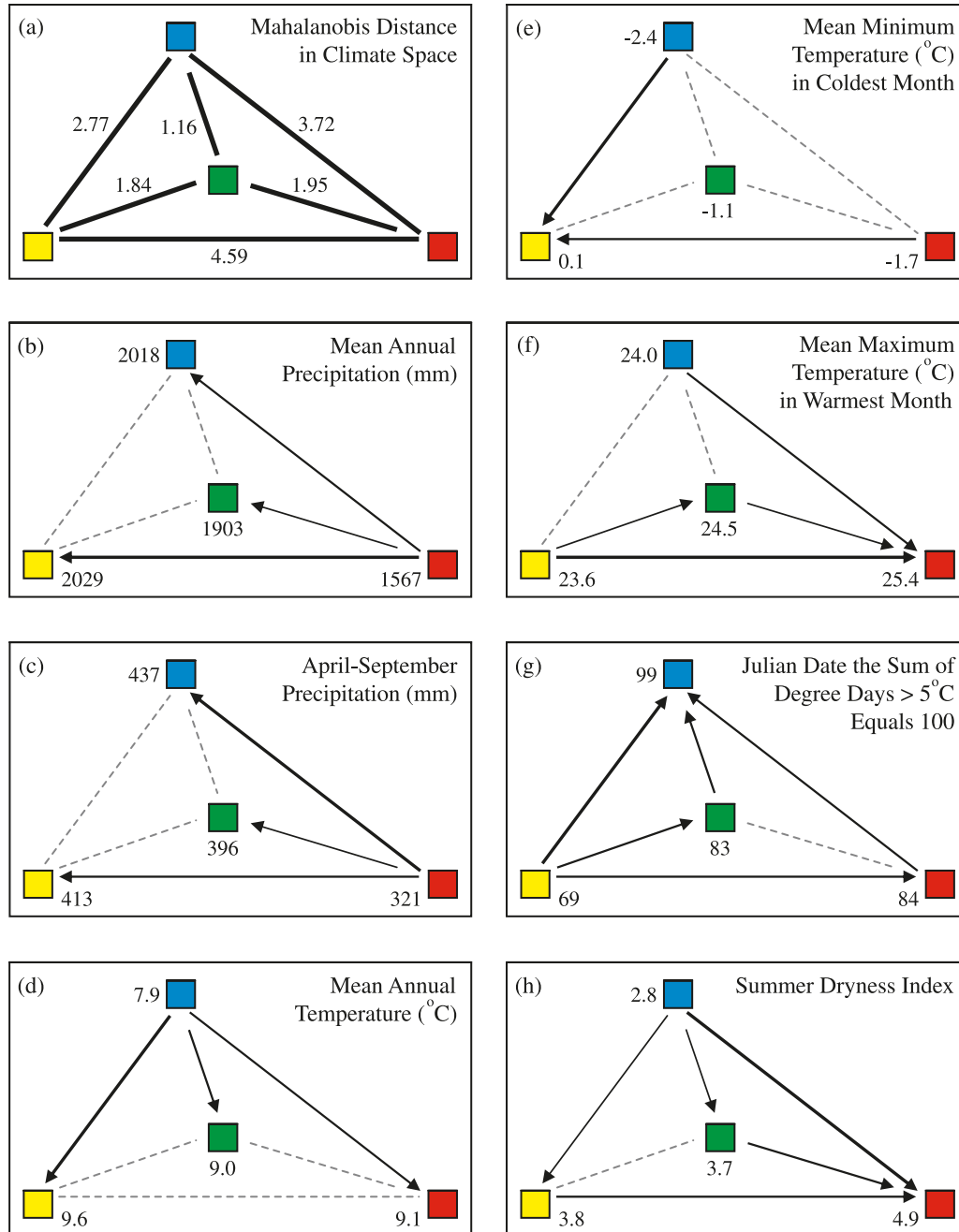
green group ($n = 48$) was characterized by two peaks of establishment, one in the middle to late 1600s and one in the late 1800s and early 1900s (Figs. 1*d* and 3). The mean proportion of total trees established at green group sites was significantly greater for the decades 1660–1680 and 1910–1930 than for other age structure groups (Tukey's studentized range test; $p < 0.05$; Fig. 3*a*). The initial green peak of establishment was shorter than the initial peak of the blue group, although the maximum proportion of total trees established in a single decade was similar for both the blue and green groups (i.e., 0.11–0.13/decade). The second peak of establishment occurred at the green group sites ~200 years after the initial peak of establishment. A bimodal distribution of surviving Douglas-fir establishment also characterized the yellow group ($n = 55$), suggesting that two distinct establishment periods occurred ~300 years apart (Figs. 1*e* and 3). In contrast with the green group, the second establishment peak of the yellow group was considerably larger than the first (in terms of trees surviving to the present). The mean proportion of total trees established at yellow group sites was significantly greater for the decades 1850–1880 than for other age structure groups (Tukey's studentized range test; $p < 0.05$; Fig. 3*a*). The apparent increase in mean proportion of total trees established at yellow group sites in the middle to late 1500s was not significantly greater than for the other age structure groups. The developmental pathway characterized by the red group was markedly different than those of the other age structure groups (Fig. 3). Characteristic of the red group ($n = 63$) was the extended period of Douglas-fir establishment from the late 1600s to the late 1800s (Figs. 1*f* and 3). Compared with the other age structure groups, the peak period of Douglas-fir establishment for the red group was much longer (~160 years), and the proportion of total trees established each decade was lower (0.02–0.06/decade). The mean proportion of total trees established at red group sites was significantly greater for the decades 1740–1830 than for other age structure groups (Tukey's studentized range test; $p < 0.05$; Fig. 3*a*).

Differences existed between the Douglas-fir age structure groups in terms of the climatic variables compared at regional scales, providing support for the hypothesis that differences in age structure patterns reflect variation in regional-scale climate (Fig. 4). Overall climatic differences
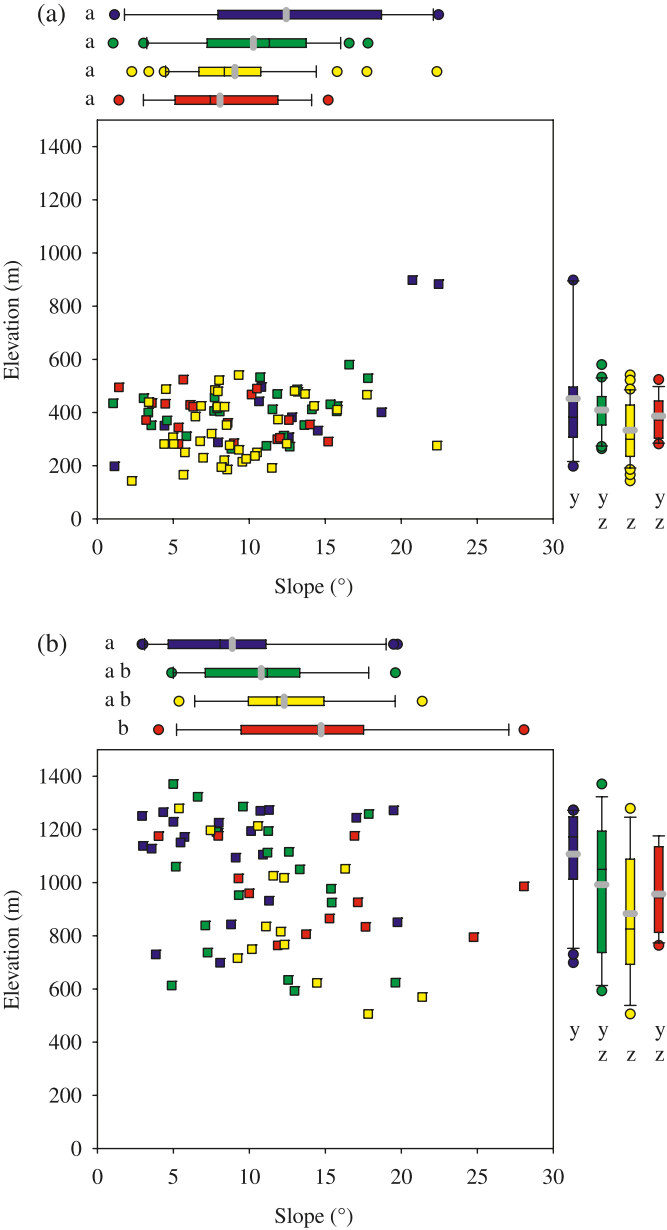
Fig. 4. Differences among age structure groups in terms of climatic variables. Symbol color indicates age structure group. (*a*) Mahalanobis distances between group centroids in climate space. (*b–h*) Group means for seven different climatic variables. Significant differences between group means are indicated by solid arrows, the heads of which point to the larger of the two groups means being compared (Hotelling's T-squared test corrected for multiple comparisons using Sidak's method, $p < 0.05$). Arrow widths are proportional to the differences among group means for a given climatic variable (i.e., larger differences are indicated by wider arrows). Broken lines indicate nonsignificant differences between group means.

between the groups were indicated by the Mahalanobis distances between group centers in the resulting *n*-dimensional contemporary climate space (Fig. 4*a*). *F* tests of the Mahalanobis distances indicate that the groups differed significantly from one another in terms of the pooled climate variables ($p < 0.02$ in all comparisons). The blue, yellow, and red groups differed most from each other in terms of contemporary climate. The green group fell between the other three groups climatically, but was most similar to the blue group.
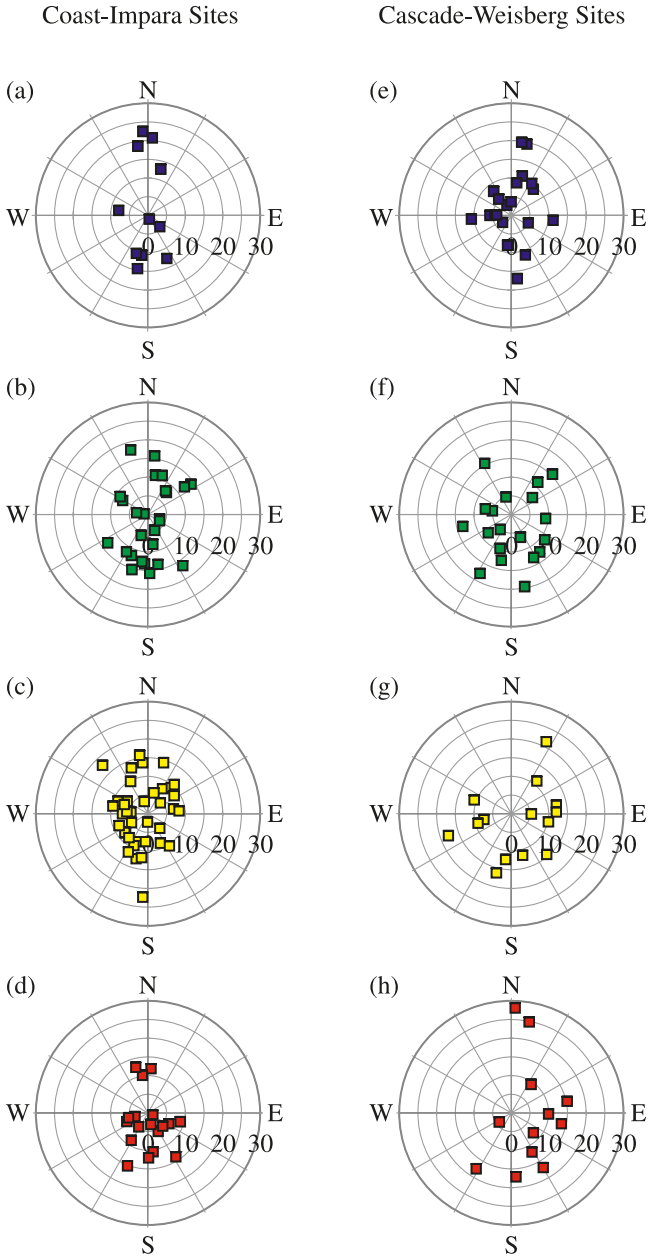
The red group sites generally occurred in drier, warmer environments than sites in the other groups (Figs. 4*b* and 4*c*). The blue group had the lowest mean annual temperature (Fig. 4*d*). Mean winter temperature was greatest for the yellow group (Fig. 4*e*). Mean summer temperature was greatest for the red group (Fig. 4*f*). Growing season began earliest for the yellow group and latest for the blue group (Fig. 4*g*). On average, the red group was the most droughty and the blue group the least droughty of the four age structure groups (Fig. 4*h*).

Fig. 5. Elevations and slopes for sites in the (*a*) Coast-Impara (site numbers 11–103) and (*b*) Cascade-Weisberg (site numbers 125–190) areas. Symbol color indicates age structure group. Group means within each area are indicated by the grey bars on each box-and-whisker plot. Similar letters indicate group means within each area that do not differ significantly (Tukey's studentized range test, $p \geq 0.05$).

Fig. 6. Slopes and aspects for sites in the (*a–d*) Coast-Impara (site numbers 11–103) and (*e–h*) Cascade-Weisberg (site numbers 125–190) areas. Symbol color indicates age structure group. Slope (degrees) increases with distance from the center of each polar plot.

Coast-Impara Sites   Cascade-Weisberg Sites

The age structure groups were weakly associated with topographic variables at landscape scales. The blue group sites at the Coast-Impara area (Fig. 5*a*) and Cascade-Weisberg area (Fig. 5*b*) were significantly higher in elevation than the yellow group sites, but were not significantly different in elevation from the green and red group sites in their respective areas. Although no difference in slope existed between the age structure groups at the Coast-Impara area (Fig. 5*a*), the blue group sites at the Cascade-Weisberg area were generally on flatter ground than the red group sites (Fig. 5*b*). Other than a weak association between the red group sites and south-facing slopes at the

Coast-Impara area, the age structure groups were not strongly associated with the combination of slope and aspect at either the Coast-Impara or Cascade-Weisberg areas (Figs. 6*a* and 6*b*).

The age structure groups were strongly associated with landscape-scale fire history at the Coast-Impara area. The distribution of Coast-Impara sites classified as burned in the mid-1800s (43 of 90 sites) was nonrandom with respect to the age structure groups ($\chi^2 = 30.9$, df = 3, $p < 0.0005$). Over 80% of yellow group sites burned in the mid-1800s (Table 3). In contrast, only 12% of green group sites burned in the mid-1800s. Slightly more than one-third of blue

Table 3. Number of Coast-Impara sites by age structure group and mid-1800s fire history class estimated from Teensma et al. (1991).

Mid-1800s fire history class	Blue	Green	Yellow	Red	Total
Burned	4	3	30	6	43
Not burned	7	22	7	11	47
Total	11	25	37	17	90

(36%) and red (35%) group sites burned in the mid-1800s. Of the sites not burned in the mid-1800s, 46 of 47 sites were classified as forest ≥200 years old in the mid-1800s and 1 of 47 sites was classified as forest 100–199 years old in the mid-1800s (1 site).

The clear spatial association of yellow group sites with the large burned area in the west half of Coast-Impara area is striking (Fig. 7a). In contrast, the majority of blue and green group sites, located in the east and northeast portions of the Coast-Impara area, were in landscape areas reconstructed as having forests ≥200 years old in the mid-1800s. The blue and green group sites classified as burned in the mid-1800s were located close to the edges of the burned areas in the Coast-Impara area. The red group sites in the Coast-Impara area tended to be located near the edges of burned areas.

The age structure groups were less strongly associated with landscape-scale fire history at the Cascade-Weisberg area. There, 65 of 66 (98%) sites were located in landscape areas where two or more fires were identified for the 1588–1976 period (Fig. 7b). Almost 80% of the sites (52 of 66) were in areas that burned four or more times during this period of almost four centuries. Although the age structure groups did not differ significantly in terms of the total number of times burned during the 1588–1976 period, they differed in terms of when they burned during this period (Table 4). The blue group sites were characterized by fewer fires during the 1700s, 1800s, and 1900s, relative to sites in at least one other age structure group. The green group sites were characterized by more fires during the late 1500s and 1900s and fewer fires during the 1800s. The yellow group sites were characterized by more fires during the 1800s. The red group sites were characterized by more fires during the 1700s and fewer fires during the late 1500s. All of the red group sites burned four or more times during the 1588–1976 period (Table 4).
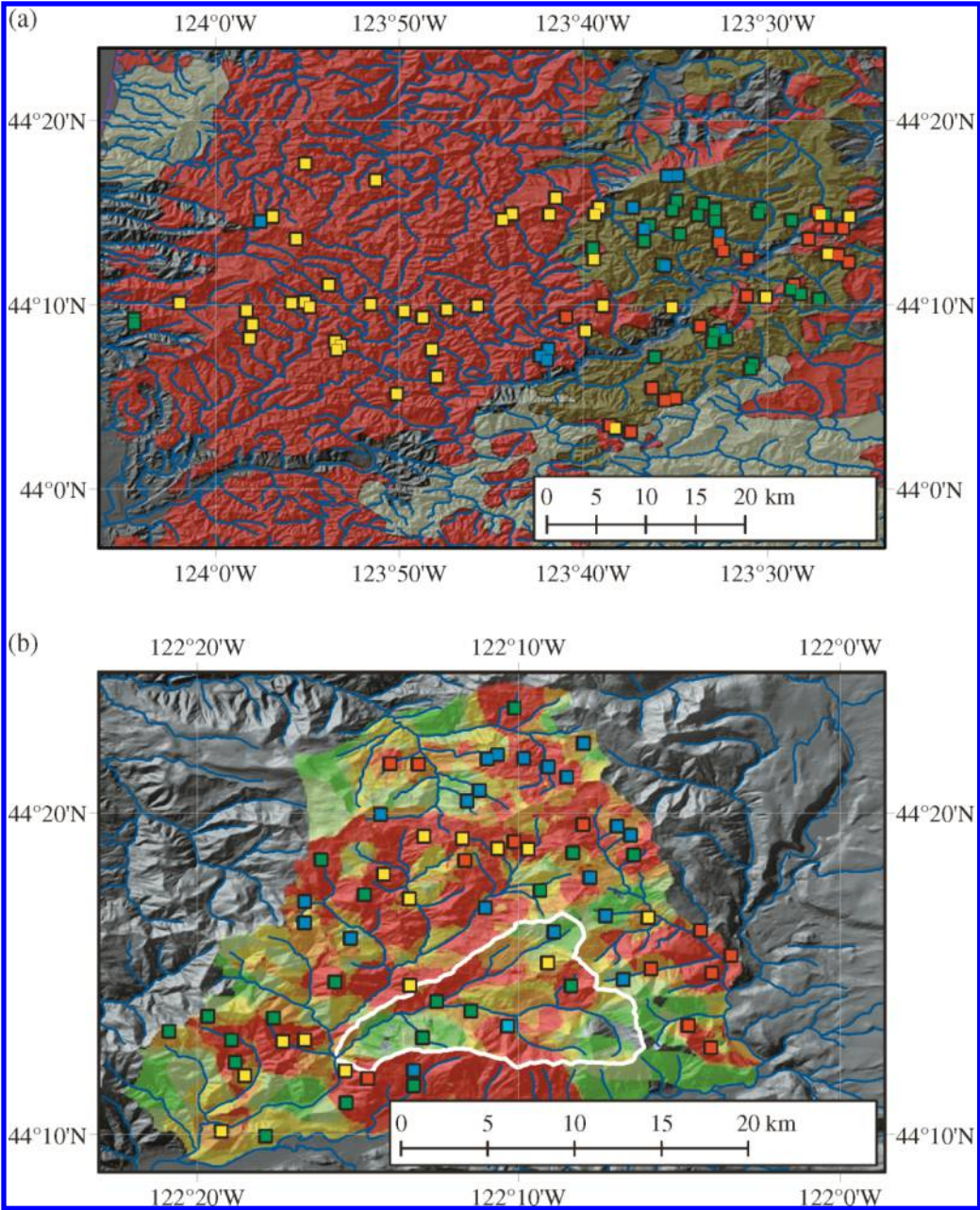
Discussion

The great variability in the age structures of Douglas-fir trees observed at the 205 old forest sites in western Oregon resulted from long and (or) multiple establishment periods. The developmental pathway characterized by the blue age structure group suggests an initial establishment period during which a large percentage (e.g., 70%) of trees established during a period of ~80 years (Fig. 3). This pattern is consistent with prolonged establishment following a single large disturbance, such as fire, but at a sufficiently low density to allow trees to establish over decades. Protracted periods of Douglas-fir establishment following individual fires do occur

Table 4. Number of fires identified in the Cascade-Weisberg area (1998) by age structure group for different periods.

Group	1588–1976 Mean	SE	Range	1588–1599 Mean	SE	Range	1600–1699 Mean	SE	Range	1700–1799 Mean	SE	Range	1800–1899 Mean	SE	Range	1900–1976 Mean	SE	Range
Blue	3.86a	0.33	1–6	0.52ab	0.11	0–1	0.95a	0.20	0–3	0.76b	0.15	0–2	1.33b	0.24	0–3	0.29b	0.10	0–1
Green	5.11a	0.40	2–8	0.79a	0.10	0–1	0.89a	0.15	0–2	0.84ab	0.18	0–3	1.63b	0.26	0–3	0.95a	0.18	0–2
Yellow	5.07a	0.41	3–8	0.57ab	0.14	0–1	0.79a	0.21	0–2	0.43b	0.14	0–1	2.64a	0.27	1–4	0.64ab	0.23	0–3
Red	4.75a	0.28	4–7	0.25b	0.13	0–1	0.58a	0.19	0–2	1.50a	0.23	0–3	2.08ab	0.26	0–3	0.33ab	0.19	0–2
All sites	4.64	0.19	1–8	0.56	0.06	0–1	0.83	0.10	0–3	0.85	0.09	0–3	1.83	0.14	0–4	0.56	0.09	0–3

Note: Number of sites in each age structure group: blue, 21; green, 19; yellow, 14; red, 12. Similar letters indicate statistically similar group means (Tukey's studentized range test; $p < 0.05$).

Fig. 7. (*a*) Locations of sites in the Coast-Impara area (site numbers 11–103) imposed on the mid-1800s fire history class estimates of Teensma et al. (1991). Area color indicates age structure group. Red areas burned in or shortly before 1850. Tan areas indicate forests that were 100–199 years old in 1850. Olive green areas indicate forests that were ≥200 years old in 1850. (*b*) Locations of sites in the Cascade-Weisberg area (site numbers 125–190) imposed on the total number of fires identified by Weisberg (1998) for the period 1588–1976. Area color indicates age structure group: dark green, one fire; light green, two fires; yellow, three fires; orange, four fires; and red, five or more fires. The boundary of the H.J. Andrews Experimental Forest is shown in white.

(Yamaguchi 1986). Alternatively, multiple disturbances during this initial establishment period may have enabled several cohorts to have established during a relatively short period. The remaining 30% of Douglas-fir at blue group sites established over the next ∼300 years at a far slower rate, presumably because disturbances of sufficient magnitude to enable widespread establishment did not occur. Small groups of trees or individual trees establishing following small-scale disturbances may have been the norm during this period.

The developmental pathway characterized by the green group may have initially resembled that of the blue group,

but with an initial peak occurring ∼100 years after that of the blue group (Fig. 3). If the green group sites had been initially disturbed at the same time as the blue group sites, the delay in the green group peak may have been due to more severe subsequent disturbances that eliminated a large proportion of earlier establishment. The second peak of establishment at green group sites suggests one or more closely spaced disturbances of sufficient magnitude to enable the establishment of new Douglas-fir but not so great as to remove as many of the 200- to 300-year-old trees established during the initial peak of establishment.

The developmental pathway of the yellow group might be viewed as characteristic of forests with two age classes, in which many younger trees establish amid a small number of remnants. The maximum proportion of total trees established in a single decade at yellow group sites (>0.25/decade) was larger than for other age structure groups, suggesting that the disturbance(s) leading to the much larger second establishment peak may also have been larger than those experienced by the other age structure groups. For example, the yellow sites in the west half of the Coast-Impara area (Fig. 7a) likely established following the fires that burned over much of the Coast Range during the mid-1800s (Morris 1934; Impara 1998). The yellow group sites in the Cascade-Weisberg area experienced significantly more fires during the 1800s than did the blue or green group sites (Table 4).

The long runs of Douglas-fir establishment and survival evident for many of the red group sites (Fig. 2) are characteristic of the age structures often associated with western pine forests and frequent, low intensity fires (Franklin and Van Pelt 2004). Sensenig (2003), whose 18 red group sites account for the southern-most of the 205 old forest sites, reported that fire occurred at these 18 sites in at least two out of three decades during the period 1700–1900. The red group sites tended to be located in areas that were droughtier and, presumably, inherently more fire-prone than sites in the other age structure groups.

Our results suggest that disturbance, in particular fire, was common on our sites and played a key role in defining the four developmental pathways we describe for the 205 old forest sites we studied. Both Impara (1998) and Weisberg (1998) have unequivocally shown that multiple fires were the rule rather than the exception in the Coast-Impara and Cascade-Weisberg areas. It is clear that multiple fires can lead to multiple periods of Douglas-fir establishment and, consequently, a variety of old forest age structures. In all four age structure groups there was a pronounced lack of tree recruitment after the 1930s, presumably because of fire suppression efforts (Sensenig 2003). This suggests that today's old forests are quite different and may function in quite a different manner than they did in the decades before the mid-1900s.

For managers interested in developing late-successional characteristics within young stands and ecologists interested in forest development, the four age structure groups represent different models of old forest development in forests dominated by Douglas-fir. Forest ecologists and managers should be aware that disturbances severe enough to initiate new cohorts of trees may be an important aspect of old forest development. Such disturbances would likely establish new cohorts of trees that would grow to become part of the main canopy, as well as promote snags and logs on the forest floor.

Finally, we note that the developmental pathways characterized by the blue, green, yellow, and red age structure groups are based on establishment dates determined largely from the stumps of trees cut during the past two to three decades. As in previous retrospective studies (e.g., Poage and Tappeiner 2005), the question arose of whether these 205 old forests might represent structural anomalies relative to the historic range of structural variability observed in old forests. In other words, had these forests been passed over earlier because, for example, they had had too few large-diameter overstory trees or were located in less accessible areas? We acknowledge that this is a possibility and that the developmental pathways we describe for the 205 old forest sites we studied represent some unknown fraction of the full range of possible developmental pathways. If true, this strengthens further our conclusion that multiple developmental pathways existed for old forests in western Oregon.
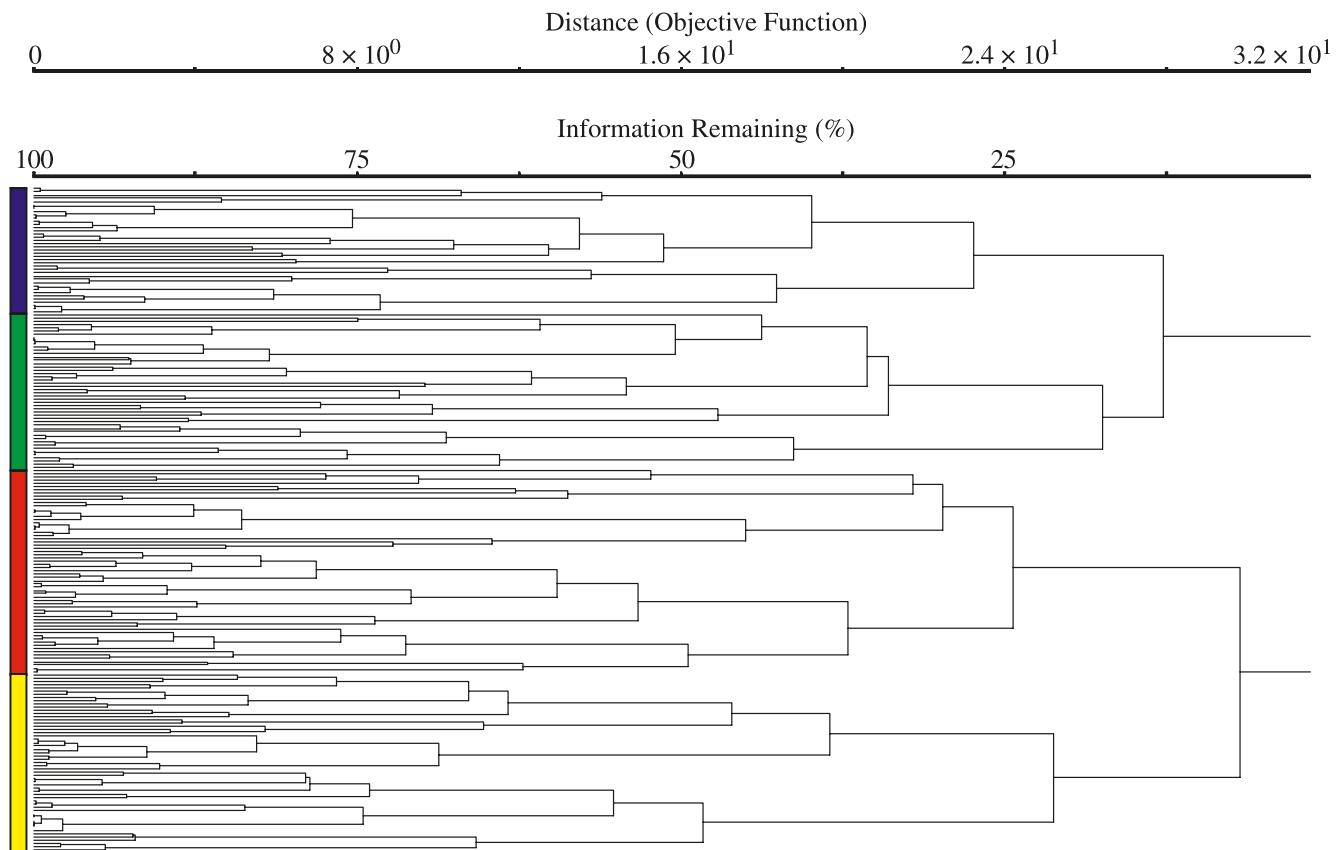
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Appendix A

Fig. A1 appears on the following page.

Fig. A1. Dendrogram resulting from cluster analysis of Douglas-fir establishment by decade for the 205 old forest sites in western Oregon. Symbol color indicates age structure group (blue, green, yellow, and red; see text for details).

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