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Post-fire tree establishment and early cohort development in conifer forests of the western Cascades of Oregon, USA

Alan J. Tepley,[1,3,]† Frederick J. Swanson,[2] and Thomas A. Spies[2]

[1]Departments of Geosciences and Forest Ecosystems and Society, Oregon State University, Corvallis, Oregon 97331-5506 USA
[2]US Forest Service, Pacific Northwest Research Station, USDA Forest Service, Corvallis, Oregon 97331 USA

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Abstract. Early-seral ecosystems make important contributions to regional biodiversity by supporting high abundance and diversity of many plant and animal species that are otherwise rare or absent from closed-canopy forests. Therefore, the period of post-fire tree establishment is a key stage in forest stand and ecosystem development that can be viewed in the context of competing management interests in diverse early-seral ecosystems vs. rapid forest development for ecological or commercial objectives. Previous work in Douglas-fir/western hemlock forests of the Pacific Northwest suggests stands initiate either with abrupt establishment (<20 years) or by protracted establishment with low tree density persisting >100 years. To improve understanding of how post-fire tree establishment and early cohort development have varied in space and over time and elucidate some of the factors contributing to that variation, we analyzed forest structure, tree ages, and Douglas-fir growth across the central western Cascades of Oregon where cohort ages span nearly eight centuries. The number of post-fire cohorts was estimated per stand, and establishment trajectories were evaluated by cohort. On average, it took 43.5 years to reach establishment of 90% of the trees per cohort. The rate and duration of establishment were surprisingly consistent across variation in topography (elevation, slope position, and aspect), among cohorts initiated from the late 12th to the early 20th century, and regardless of the severity of the cohort-initiating fire or the timing of establishment by shade-tolerant species. Only 8% of cohorts completed establishment within 20 years and 12% had establishment lasting >80 years. Douglas-fir growth (basal area increment) exhibits high plasticity in relation to different competitive interactions within uni-specific and multi-species cohorts and between cohorts of different age, suggesting wide variation in the structure and dynamics of early-seral ecosystems and an ability to tolerate moderate competition when young. This study illustrates that post-fire establishment in Douglas-fir/western hemlock forests of the central western Cascades historically was a multi-decadal process. Limited regeneration in a short window did not necessarily lead to persistent shrublands. In fact, post-fire forest development appears resilient to considerable variation in the fire regime and climatic and biotic constraints on tree establishment.

Key words: Douglas-fir; early-seral ecosystems; forest succession; initial floristics; Oregon Cascades; post-fire cohort; post-fire establishment; relay floristics.

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[3] Present address: Department of Geography, University of Colorado at Boulder, Campus Box 260, Boulder, Colorado 80309-0260 USA.

† **E-mail:** Alan.Tepley@Colorado.edu

Introduction

Early-seral ecosystems are among the most biologically diverse and structurally complex stages of forest development. Many plant and animal species reach their greatest abundance in the interval before the developing forest ecosystem reaches tree canopy closure (Swanson et al. 2011). Yet, early-seral ecosystems that have not been subject to management may be one of the more poorly represented development stages in regions where fire historically was infrequent and fire suppression has further reduced fire occurrence, and where post-fire management and plantation forestry greatly reduce the length of the pre-canopy-closure period (Hansen et al. 1991). Knowledge about the trajectories and rates of post-disturbance tree establishment and the time to canopy closure is needed if we are to improve our understanding of the biologically-rich, early-seral stage and develop management plans and practices that seek to sustain the early-seral component of forest landscapes.

Although interest in early-seral ecosystems is growing from a conservation perspective (Swanson et al. 2011), there is concern that only a short window is available for successful tree regeneration in the face of competing vegetation and natural regeneration processes might not consistently produce well-stocked stands (Oregon Revised Statutes 527.745; https://oregonlegislature.gov//bills_laws/lawsstatutes/2013ors527.html). Also, failure to achieve a minimum seedling density in this window could postpone ecological values associated with older forests (e.g., wildlife habitat or carbon storage). Furthermore, the early-seral communities of some regions may be prone to repeated burning (Agee and Huff 1987, Thompson et al. 2007). These concerns could be exacerbated under a warming climate through adverse effects on tree establishment and growth (Tercero-Bucardo et al. 2007) and a greater frequency of weather conducive to re-burning of early-seral vegetation. Better understanding of historical post-disturbance tree establishment could aid in assessing the degree to which post-disturbance vegetation dynamics have been altered by recent climate- or management-driven changes to disturbance regimes (Savage et al. 2013), and thus, assist in weighing management alternatives in the key period shortly after disturbances.

Studies of forests dominated by Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) in the Pacific Northwest (PNW) of the United States have long contributed to concepts and management policy regarding old-growth forests and native forests in general (Spies and Duncan 2009). Yet, much remains unknown about the stand initiation and development trajectories through which their old-growth characteristics developed. In this region, Douglas-fir is a relatively shade-intolerant species whose regeneration depends on disturbances that open the canopy, and fire is the primary disturbance agent responsible for such openings (Spies and Franklin 1989). Thus, it generally is perceived to form even-aged stands that establish after fire, but the duration of the stand initiation period is debated.

Observations following early 20th-century fires and the relatively few stand-history reconstructions suggest two pathways of stand initiation (Donato et al. 2012): one with abrupt establishment leading to canopy closure in about two decades (Winter et al. 2002) and the other characterized by protracted establishment and low tree density persisting for >100 years (Tappeiner et al. 1997, Poage and Tappeiner 2002). However, it is not known if poor regeneration in a very short window necessarily means it will take >100 years to re-establish forest cover or if these pathways only represent the endpoints of a continuum of stand initiation patterns represented across the region. Also, little is known about the causes of variation in stand initiation or how the representation of different pathways has varied in space or over time.

Discussion on post-fire establishment in Douglas-fir/western hemlock forests has focused largely on conditions following stand-replacing fire or harvest, and establishment of Douglas-fir only (Tappeiner et al. 1997, Poage and Tappeiner 2002, Freund et al. 2014). As recognition increases that the representation of non-stand-replacing fire tends to increase with decreasing annual precipitation across the distribution of Douglas-fir/western hemlock forests (Tepley et al. 2013), it is important to broaden our perspective on the diversity of post-fire conditions and cohort initiation pathways. Also, it is important to consider post-fire establishment by shade-tolerant species and whether they establish along with Douglas-fir (Winter et al. 2002) or lagged several decades after Douglas-fir (Wimberly and Spies 2001).

To better understand historical variation in post-fire tree establishment and early cohort development, we evaluate stand structure, the ages of Douglas-fir and shade-tolerant species, and Douglas-fir growth across the central western Cascades of Oregon, which is representative of a large portion of the Douglas-fir/western hemlock region and includes cohort ages spanning nearly eight centuries. We address the following questions: (1) what was the variability in establishment trajectories and the relative frequency of rapid vs. protracted post-fire establishment by Douglas-fir?, (2) to what degree do the effects of topographically-constrained microclimate on seedling establishment and persistence influence trajectories of post-fire establishment by Douglas-fir?, (3) how has the duration of post-fire establishment by Douglas-fir varied with the timing of cohort initiation during periods of widespread fire and periods with limited burning?, and (4) in what ways do Douglas-fir establishment and growth vary in relation to the severity of the cohort-initiating fire and the timing and rate of establishment by shade-tolerant species?

Methods

Study area

Sampling was conducted in two study areas in the central western Cascades of Oregon (Fig. 1). The Blue River study area includes the 240-km^2 Blue River watershed plus 33 km^2 to the north. It has deeply dissected terrain characteristic of the eastern part of the western Cascade Range. Elevation ranges from 316 to 1,753 m and most major ridges are higher than 1,200 m. The Fall Creek study area is the eastern 300 km^2 of the Fall Creek watershed. It has lower topographic relief characteristic of the western part of the western Cascades. Elevation ranges from 254 to 1,519 m, but only the highest ridges that form the southern perimeter of the study area are higher than 1,200 m. Annual precipitation averages 233 cm in the Blue River study area and 182 cm at Fall Creek (Daly et al. 2008).

Two Vegetation Zones of Franklin and Dyrness (1988) comprise almost the entire extent of both study areas. The Western Hemlock zone accounts for nearly all terrain below ca. 1,200 m. Forests are dominated by Douglas-fir, with western hemlock and western redcedar (*Thuja plicata* Donn ex D. Don) as the major shade-tolerant associates. The Pacific Silver Fir zone is found along most major ridgetops of the Blue River study area and the high ridges along the southern perimeter of the Fall Creek study area. Major tree species are Douglas-fir, noble fir (*Abies procera* Rehd.), Pacific silver fir (*Abies amabilis* (Dougl. ex Loud.) Dougl. ex Forbes), western hemlock, and mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.). The Mountain Hemlock zone is represented on the highest ridges of the Blue River study area, and the Douglas-fir climax type is found in the harshest sites (e.g., rocky outcrops and steep slopes with thin soil).

Data collection and processing

Sample sites were selected using a stratified random approach that distributes sampling effort across both study areas while accounting for most of the physiographic variation. Sampling was conducted at the upper, mid, and lower slope position of one randomly selected slope facet within each 25-km^2 grid cell across each study area following the methods of Tepley et al. (2013). Forest structure and tree ages were sampled in one 120 m long transect randomly located at each slope position of the selected slope facets. Altogether, 124 transects were sampled: 71 in the Blue River study area and 53 at Fall Creek. Each transect consists of 5, 0.02-ha circular plots at 30-m intervals, and the entire transect is treated as one sample unit. Sampling effort was spread over 120 m to ensure tree ages represent broadly-distributed age classes likely to represent regeneration in response to widespread disturbances rather than local treefall gaps.

In the five plots along each transect, diameter at breast height (dbh) was recorded for all trees $>$15 cm dbh and increment cores were collected from a subset of the live trees. The subset was determined by dividing each 0.02-ha plot into four quadrants and coring the largest tree of each species in each quadrant. Selecting the largest tree increases the likelihood that the oldest trees are sampled, but sampling one tree per species

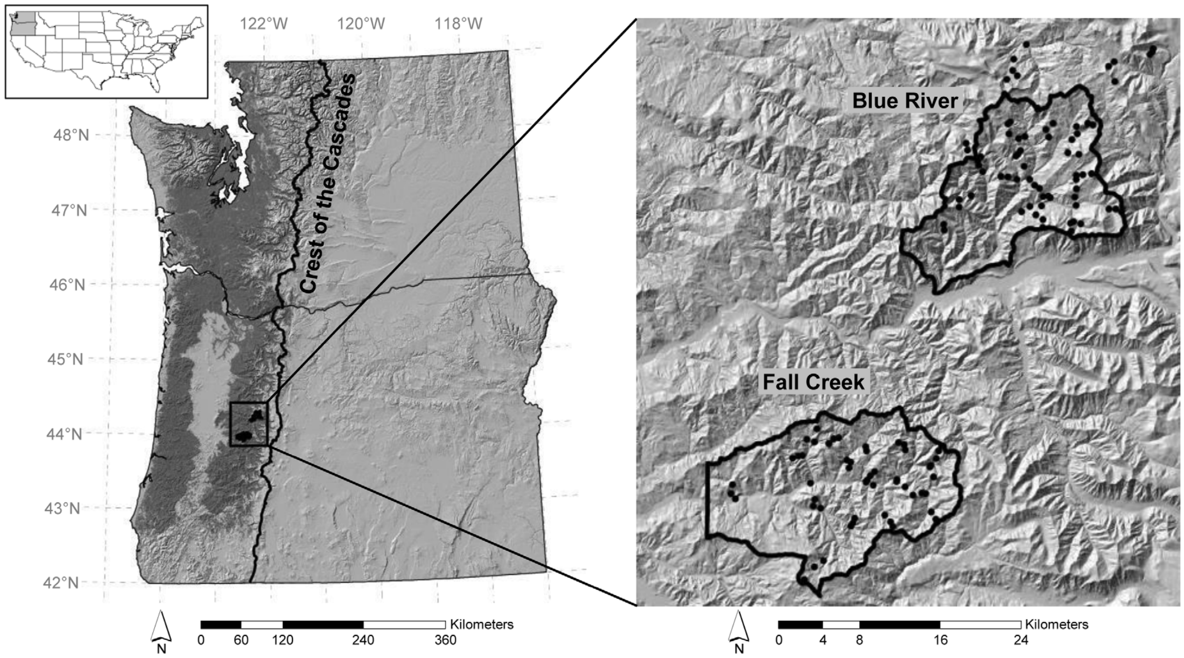

Fig. 1. Study areas and sampled transects in relation to the extent of Douglas-fir/western hemlock forests (dark shading; GIS data available at www.landfire.gov).

per quadrant ensures that a broad range of sizes is sampled for each species. Trees were cored as close to the ground as possible, and the height of core extraction was recorded. Altogether, 3,277 tree cores were collected, representing an average of 27 trees per transect, or 76% of the live trees.

Initial cross-dating was conducted by skeleton plotting and the list-year method (Speer 2012). Then, a master chronology was developed by measuring the ring width of >200 Douglas-fir cores to the nearest 0.001 mm using a Velmex sliding-stage micrometer. The remaining cores were cross-dated by comparison to the master chronology. Eighty-five percent of all cores were cross-dated, including 99% of the Douglas-fir cores. Cores that could not be cross-dated are primarily from angiosperms and shade-tolerant conifers with strongly suppressed growth.

The year of tree establishment was estimated for 3,038 trees (1,084 Douglas-fir trees), limited to cores that intersect the pith or where the innermost ring forms a complete arc. For off-center cores, an average of seven years to the pith was estimated following Duncan (1989). An average of four years to reach coring height was estimated using the equation of Morrison and Swanson (1990). The estimated year of tree establishment after adjusting for off-center cores and estimating the time to reach coring height hereafter is referred to as the establishment date.

Analyses

Duration of post-fire establishment.—In the western Cascades of Oregon, Douglas-fir regeneration generally is initiated by disturbances that open the canopy (Spies and Franklin 1989), it ceases following canopy closure (Winter et al. 2002), and does not begin again until the next canopy-opening disturbance. Thus, the range of Douglas-fir ages within a cohort provides our best estimate of the interval from disturbance to canopy closure. The range of all Douglas-fir ages within a stand, however, may over-estimate the duration of post-fire establishment because stands may contain two or more post-fire cohorts (Tepley et al. 2013). Therefore, we first estimate the number of cohorts per stand, and then evaluate establishment duration by cohort.

Our ability to determine the number of cohorts per stand is complicated by the poor recording and preservation of fire scars by Douglas-fir in this region compared to ponderosa pine (*Pinus*

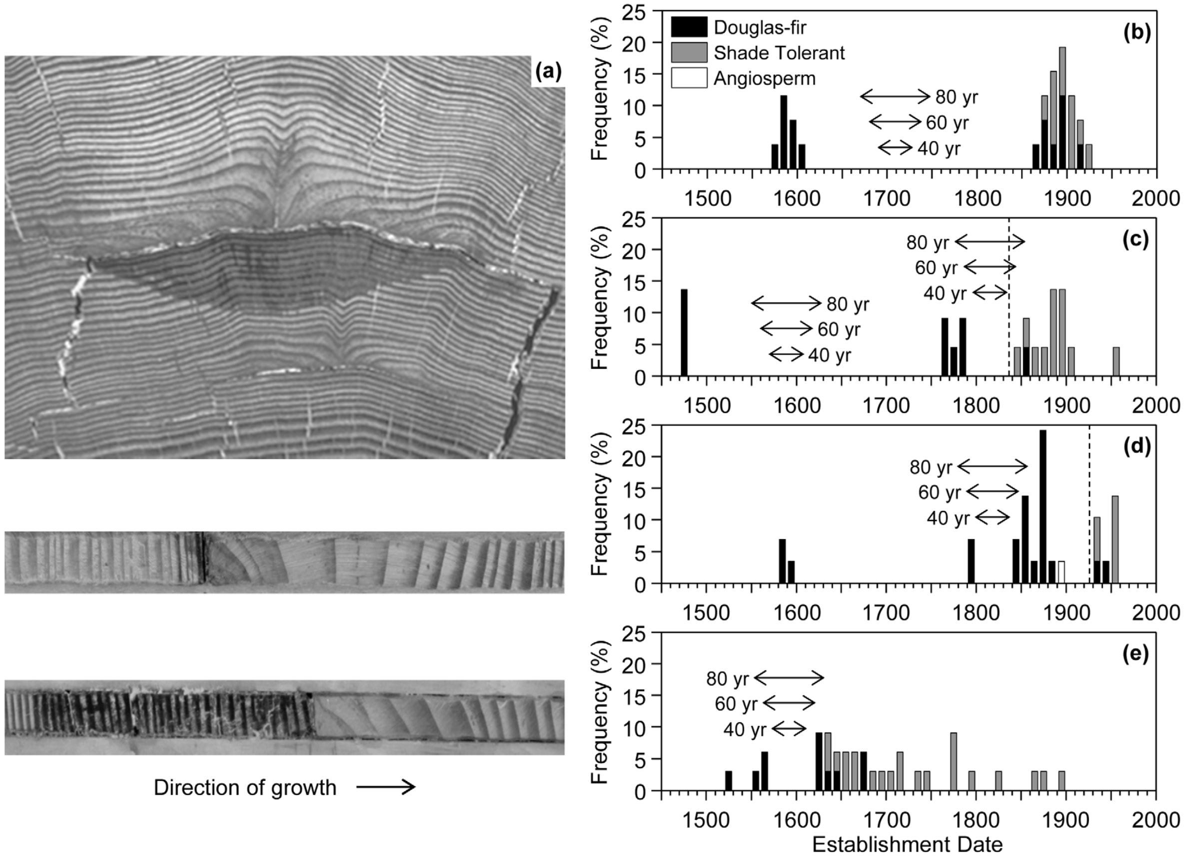

Fig. 2. Illustration of (a) healed fire scars in a Douglas-fir stump (photo by Peter Weisberg) and increment cores. In (b–e), age-structure data for four representative transects illustrate how windows of 40, 60, and 80 years with no record of establishment were used to estimate the number of cohorts per stand. Example (b) is the most common scenario, where two cohorts are identified regardless of window width. The youngest cohort in (c) and (d) was identified based on healed fire scars (vertical dashed lines). Examples (d) and (e) illustrate how using a 40-year window can lead to identification of a greater number of cohorts than 60- or 80-year windows.

ponderosa Douglas ex P. Lawson & C. Lawson) in drier regions. Fire-caused wounds that affect more than ~10% of Douglas-fir bole circumference tend to rot. Only the small scars that form beneath bark fissures and heal in 10–15 years are likely to be preserved (Morrison and Swanson 1990, Skinner and Taylor 2006). These wounds are unavailable for sampling except shortly after harvest, when full cross-sections of numerous stumps are visible and before they decay (Fig. 2a).

In the face of an incomplete fire record, the number of cohorts per stand was estimated by labeling each time a Douglas-fir establishment date is preceded by a gap in the age distribution wider than a critical window as the initiation of a new cohort (Fig. 2). To address sensitivity of results to the rule for identifying cohorts, the duration of post-fire establishment is compared when cohorts are identified using increasingly conservative windows (40, 60, and 80 years). The identification of cohorts proceeds by treating the establishment date of the oldest Douglas-fir tree per stand as the initiation year for the oldest cohort. Additional Douglas-fir trees are identified as belonging to the same cohort as long as at least one establishment date for any species is recorded within the critical window before its establishment. When a gap in the age distribution exceeds the window width, the first Douglas-fir establishment date after the gap is considered the initiation year of a new cohort

(Fig. 2b). The narrowest window (40 years) is most likely to identify all cohorts per stand, but it has the greatest potential to falsely separate a long period of establishment into two cohorts. The widest window (80 years) is least likely to falsely divide one period of establishment into two cohorts, but it has the greatest potential to treat two pulses of post-fire establishment as a single cohort (Fig. 2d, e).

In the rare cases when healed fire scars were found in increment cores (Fig. 2a), the trees that predate the scar were treated as a separate cohort from those that established after it, regardless of the width of gaps in the age distribution (Fig. 2c, d). To be considered a fire scar, an increment core had to have a break, usually preceded by a pitch deposit (representing compartmentalization of the wound), one or more locally absent rings after the break (representing the time for the wound to heal), and wider slanted or curled rings following the break (representing closure of the wound) (Fig. 2a).

After estimating the number of cohorts per stand, we calculated the cumulative percentage of Douglas-fir trees that established over time since the initiation of each cohort. Variation in the number of trees per cohort (1–27 trees) raises concern that we could underestimate the duration of post-fire establishment in cohorts represented by a small number of trees. To address this concern, first cohorts represented by <5 trees were excluded from all analyses. The remaining cohorts were then placed into groups of different sample size: 5, 6, 7–9, 10–13, and 14–27 trees. A Kruskal-Wallis test was applied to the cumulative percentage of trees established by the end of each of the first six decades following cohort initiation to determine whether the rate of establishment differs in relation to cohort sample size.

If statistically significant differences ($p < 0.05$) were found for any decade, multiple comparisons were conducted with a one-tailed Dunn's test using package 'pgirmess' in R version 3.0.0 (R Core Team 2013). This test compares multiple treatments to one control, where the group of the largest sample size (14–27 trees per cohort) was the control and each group represented by <14 trees per cohort was considered a treatment. A one-tailed test was used because we were interested only in whether the treatments show a faster rate of establishment (i.e., higher cumulative establishment by the end of the decade) than the control. If a given sample size showed faster establishment than the group of the largest sample size, cohorts of that sample size were excluded from subsequent analyses.

Influences of topography.—Variation in post-fire establishment by Douglas-fir was evaluated along gradients of elevation, slope position, and aspect as an exploratory analysis to assess the degree that topographically-moderated microclimate affects the rate and duration of establishment. Aspect was transformed to a continuous variable ranging from 0 (southwest) to 2 (northeast) (Beers et al. 1966). Slope position was calculated as transect elevation above the valley bottom divided by the total elevation range from ridgetop to valley bottom, providing values from 0 (valley bottom) to 1 (ridgetop). Although sample sites at the highest and lowest elevations of the dataset tend to be located at upper and lower slope positions, respectively, elevation and slope position otherwise are largely independent topographic factors in this topographically complex landscape. For the 70% of transects at elevations between 600 and 1,200 m, the correlation between elevation and slope position is relatively low ($r = 0.31$).

Variation in the cumulative percentage of trees established as a function of time since cohort initiation was modeled across the range of each topography variable and compared to the average establishment trajectory irrespective of topography. Establishment trajectories were modeled using Non-Parametric Multiplicative Regression (NPMR; McCune 2006) in HyperNiche version 1.12 (McCune and Mefford 2004). Models combining more than one topography variable are not presented because model fit was not improved relative to models using topography variables individually.

NPMR models a local response for a particular region of sample space, allowing the modeled establishment trajectory to vary continuously across the range of each topography variable. The Local Mean form of NPMR was used, where the response at each target point (each combination of the value of a topography variable and the time since cohort initiation) is calculated as the mean of measured responses at sample sites weighted by the product of the weights for each predictor (McCune 2006). Weights for predictors are assigned according to their difference from the target point, where the rate at which weights diminish with distance along the environmental gradient from the target point is based on a Gaussian kernel centered on the target point. The standard deviation of the Gaussian kernel (referred to as the tolerance) is tuned for each predictor (McCune 2006). A narrow tolerance for aspect, for instance, would mean the modeled response is influenced only by sample sites at similar aspect to the target point, allowing for a markedly different response on north vs. south aspects.

A cross-validated measure of model fit (xR^2) was calculated, where the data for each sample site are excluded from the estimated response at that point, providing a built-in method of cross-validation that helps guard against over-fitting (McCune 2006). Statistical significance was evaluated using a Monte Carlo simulation with 499 replications.

Timing of cohort initiation.—Trajectories of post-fire establishment by Douglas-fir were compared among cohorts initiated in four periods (in years AD): (1) 1170–1350, (2) 1470–1610, (3) 1610–1780, and (4) 1780–1940. The second and fourth periods correspond to the two periods of extensive fire identified in a synthesis of 10 fire-history studies west of the crest of the Cascades in Oregon and Washington (Weisberg and Swanson 2003). The synthesis identified the third period as a period of limited burning. The earliest period may represent another period of widespread burning based on evidence of fire in several study areas at this time (Hemstrom and Franklin 1982, Yamaguchi 1993, Agee and Krusemark 2001). The interval from 1350 to 1470 may represent another period of limited burning. No cohorts of the present study area initiated in this period, and the limited data from other studies do not suggest fire was widespread elsewhere in the region during this interval.

The rate of post-fire establishment was compared based on the time to reach establishment of 30, 60, and 90% of the Douglas-fir trees in a cohort. A Mann-Whitney U test was used to determine whether these values differ significantly for cohorts initiated in the two periods of widespread burning (1470–1610 and 1780–1940). The other two periods are not compared quantitatively due to the small number of cohorts initiated in those periods.

Pathways of cohort initiation.—To evaluate how competitive interactions within uni-specific and multi-species cohorts and across cohorts of different age affect early cohort development, establishment and growth of Douglas-fir were compared among cohorts that followed (1) initial floristics (concurrent establishment of Douglas-fir and shade-tolerant species) and (2) relay floristics (establishment of shade-tolerant species lagged several decades behind Douglas-fir) pathways after high-severity fire, and (3) cohorts that initiated in response to moderate-severity fire. We limit this analysis to the youngest cohort per stand to avoid the loss of evidence of cohort initiation caused by subsequent disturbances. Also, we limit the analysis to cohorts that initiated after 1780 because non-fire disturbances and limitations posed by the longevity of shade-tolerant species complicate interpretations of the initiation of older cohorts.

Classification of cohorts as initiated following moderate- or high-severity fire used two of the age-structure types and corresponding stand development interpretations of Tepley et al. (2013). Age-structure type 4 has two Douglas-fir cohorts, where trees of the older cohort have charcoal on their bark and are present at a density (45 trees/ha) about two-thirds that in unburned stands of similar age (62 trees/ha in type 1), suggesting the younger cohort initiated after moderate-severity fire. Age-structure type 5 has a cohort initiated after 1780, and older trees are either absent or present at a very low density (average 9 trees/ha), suggesting the cohort initiated after high-severity fire (Tepley et al. 2013). Cohorts that initiated after high-severity fire were classified as following an initial floristics pathway (Connell and Slatyer 1977) if establishment dates for at least 50% of the shade-tolerant trees fall within the period of establishment by Douglas-fir. Otherwise they were classified as following a relay floristics pathway.

The cumulative percentage of Douglas-fir trees that established by the end of the first six decades following cohort initiation was evaluated using a Kruskal-Wallis test. Multiple comparisons were conducted by applying a Mann-Whitney test to each pair of pathways and using the Bonferroni correction to account for the total number of

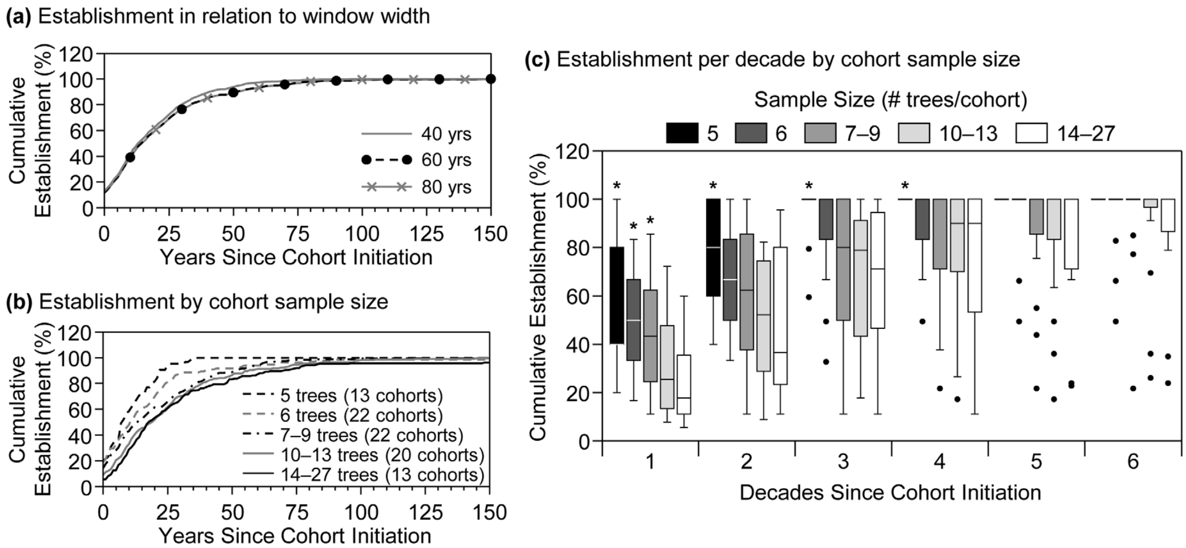

Fig. 3. Comparison of establishment trajectories for Douglas-fir trees in relation to (a) the window width used to estimate the number of cohorts per stand, and (b) the number of trees representing each cohort for cohorts identified using an 80-year window. In (c), cumulative establishment by the end of the first six decades for cohorts identified with the 80-year window is compared across cohorts represented by different numbers of trees. Asterisks indicate a statistically greater percentage of trees established ($p < 0.05$) than in the group of the largest sample size (14–27 trees) based on a one-tailed Dunn's test conducted after a Kruskal-Wallis test.

comparisons (Holm 1979).

Annual basal area increment (BAI) of Douglas-fir trees over their first 150 years of growth was compared among the three pathways of cohort initiation. BAI was calculated using measured ring widths plus the estimated radius and number rings from the pith to the first complete ring for off-center cores (Duncan 1989). BAI values were relativized by converting values to z-scores to equalize the mean and variance among trees so that all trees are given equal weight in calculating an average growth trajectory for each cohort initiation pathway.

Results

Duration of post-fire establishment

Post-fire establishment occurred primarily over four decades following cohort initiation regardless of the window applied to identify cohorts. The percentage of trees that established within 40 years of cohort initiation ranged from 89.6% when cohorts were identified with a 40-year window, to 85.3% and 85.1% using 60- and 80-year windows, respectively (Fig. 3a). Due to uncertainty in fire history and the minor differences in the establishment trajectories identified using different window widths, all further analyses are conducted using cohorts identified with the most conservative window (80 years).

After comparing establishment trajectories in relation to the number of Douglas-fir trees per cohort (Fig. 3b), only those cohorts represented by at least six trees were retained in further analyses. Cohorts represented by five trees showed significantly greater cumulative establishment than cohorts of the largest sample size (14–27 trees) by the end of each of the first four decades (Fig. 3c). Thus, it is likely that more gradual establishment would have been found had more trees been sampled. By contrast, cohorts represented by 6 and 7–9 trees showed only a significantly greater percentage of trees established than cohorts of 14–27 trees in the first decade. Cumulative establishment in cohorts of 10–13 trees did not differ significantly from that in cohorts of the largest sample size in any decade (Fig. 3c). Therefore, after identifying cohorts using the 80-year window and excluding

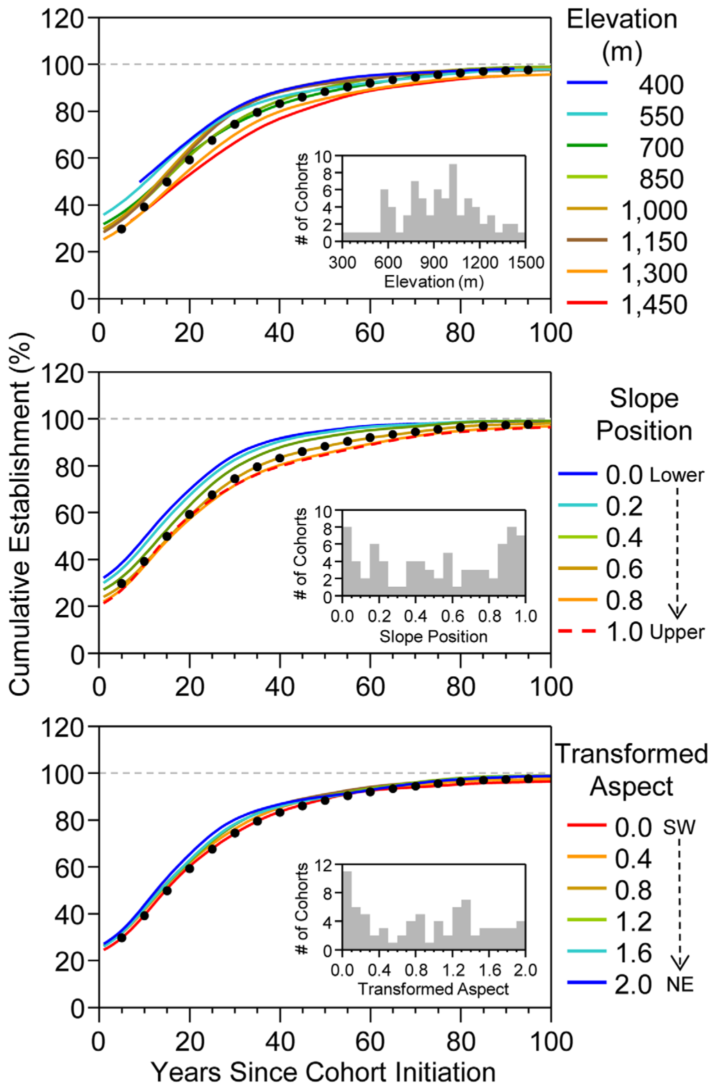

Fig. 4. Comparison of variation in establishment trajectories for Douglas-fir along gradients of (a) elevation, (b) slope position, and (c) aspect, as modeled using NPMR. Black dots represent the average trajectory across all cohorts irrespective of topography. Colored lines represent slices across a continuous response surface generated by NPMR models. Inset histograms provide the distribution of cohorts in relation to each topography variable.

cohorts represented by <6 trees, the dataset of 1,084 Douglas-fir ages in 124 stands was reduced to 765 ages representing 77 cohorts in 72 stands.

Influences of topography

Trajectories of Douglas-fir establishment varied little with topography. The modeled percentage of trees established as a function of time since cohort initiation and elevation ($xR^2 = 0.569$, $p < 0.002$) provides little improvement in fit over a model of cumulative establishment only as a function of time since cohort initiation ($xR^2 = 0.553$, $p < 0.002$). However, it suggests slower establishment than the average of the study area is only likely near the upper-elevation limit of Douglas-fir (>1,300 m; Fig. 4a). The model of establishment as a function of time since cohort initiation and slope position provides similarly small improvement in model fit ($xR^2 = 0.573$, $p < 0.002$) over the model with no topography

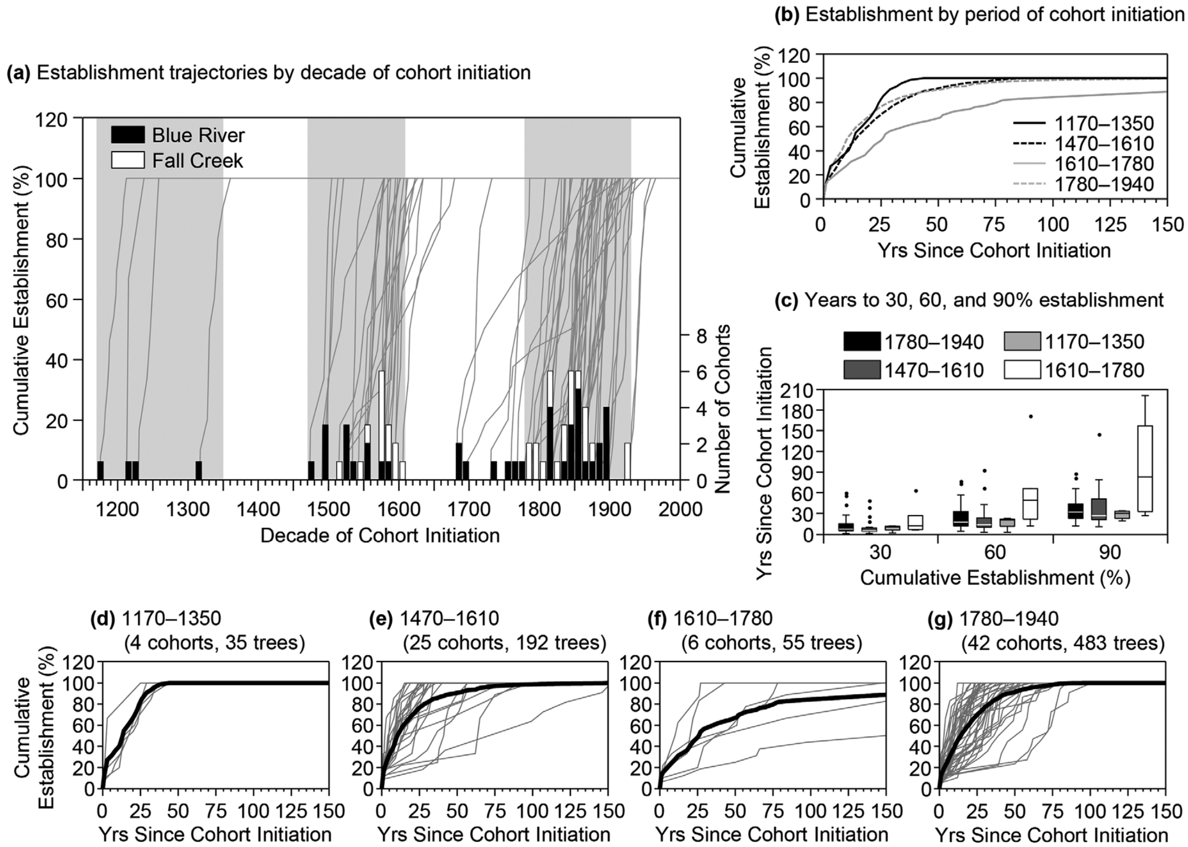

Fig. 5. Comparison of cumulative Douglas-fir establishment in relation to the timing of cohort initiation. In (a), the number of cohorts initiated by decade in the Blue River and Fall Creek study area is compared in relation to the periods of region-wide, extensive burning (1170–1350, 1470–1610, and 1780–1940; gray shading) and limited fire (1610–1780; unshaded). In (b), the average establishment trajectory is compared across the four periods of cohort initiation. The time to reach establishment of 30, 60, and 90% of the trees in the cohort is compared in (c). In (d–g), variation in establishment is compared across the four periods of cohort initiation, where each gray line represents one cohort and the thick black line is the average of the time period.

variables, yet it suggests a tendency for progressively more gradual establishment from lower to upper slopes (Fig. 4b). Near the valley bottom, 90% of trees are predicted to establish within 40 years of cohort initiation, but it is predicted to take 62 years to reach 90% establishment near ridgetops. No difference in establishment was found in relation to aspect (Fig. 4c). Model fit after including aspect ($xR^2 = 0.559$, $p < 0.002$) is essentially unchanged from the model with no topography variables ($xR^2 = 0.553$).

Timing of cohort initiation

Eighty-eight percent of cohorts were initiated in the two intervals (1470–1610 and 1780–1940) previously identified as periods of widespread burning across the region (Weisberg and Swanson 2003): 33% in 1470–1610 and 55% in 1780–1940 (Fig. 5a). No difference in establishment trajectories was evident between these periods, with establishment nearly complete by year 40 in almost all cohorts (Fig. 5b). For cohorts initiated between 1470 and 1610, it took an average of 12 years to reach establishment of 30% of the trees, 22 years to 60%, and 41 years to 90% (Fig. 5c). Cohorts initiated between 1780 and 1940 averaged 13, 24, and 38 years to reach 30, 60, and 90% establishment, respectively. None of these values differ significantly between the two periods ($p >$ 0.05 in all comparisons). It took >70 years to reach 90% establishment in only 3 of 25 cohorts initiated between 1470 and 1610 and 2 of 42 cohorts initiated after 1780 (Fig. 5e, g).

The four cohorts initiated between 1170 and 1350 show a similar establishment trajectory to those initiated in the two periods of widespread fire (Fig. 5b, d). On average, it took 9 years to reach 30% establishment, 17 years to 60%, and 29 years to 90% (Fig. 5c).

The only period when protracted establishment was not limited to a very small portion of cohorts is 1610–1780 (Fig. 5f), the period characterized by Weisberg and Swanson (2003) as having limited fire across the region. On average, it took 22 years to reach 30% establishment, 61 years to 60%, and 98 years to 90% (Fig. 5c). All trees established by year 40 in two of the six cohorts initiated in this period, but it took >100 years to reach 100% establishment in three cohorts (Fig. 5f). These cohorts are found in some of the harshest sites of the study area, including rocky ridgetops, which may be least favorable to seedling establishment and growth, and canopy coverage may be low enough that Douglas-fir can establish in the absence of fire.

Pathways of cohort initiation

Comparisons of Douglas-fir establishment and growth across the three pathways of cohort initiation elucidate the relative influences of intra- (relay floristics) and inter-specific (initial floristics) competition in the post-fire cohort and competition across cohorts of different age following moderate-severity fire. In mature-aged (ca. 80–200-year-old) cohorts that initiated along a relay floristics pathway, the average density of Douglas-fir (344 trees/ha) and shade-tolerant trees (54 trees/ha) are highest and lowest, respectively, of the cohort initiation pathways (Fig. 6a). Initial floristics cohorts have a slightly higher density of shade-tolerant trees (248 trees/ha) than Douglas-fir (225 trees/ha; Fig. 6b). Stands with a cohort initiated after moderate-severity fire have 43 Douglas-fir trees/ha, on average, that predate the fire, and the ratio of Douglas-fir (173 trees/ha) to shade-tolerant trees (241 trees/ha) in the post-fire cohort is the lowest of the three pathways (Fig. 6c).

Little difference was found in the duration of Douglas-fir establishment among pathways. On average, the percentage of Douglas-fir trees that established within 40 years ranged from 87% in cohorts initiated after moderate-severity fire to 95% and 99% in relay and initial floristics pathways, respectively, after high-severity fire (Fig. 6d–f). Cumulative Douglas-fir establishment did not differ significantly among pathways by the end of each of the first six decades ($p > 0.05$ for all comparisons).

Marked differences were found, however, in the establishment of shade-tolerant species. Initial and relay floristics pathways form two distinct groups, with only 4% of establishment dates for shade-tolerant species falling before the completion of Douglas-fir establishment in relay floristics cohorts (Fig. 6d), compared to 80% in initial floristics cohorts (Fig. 6e). Cohorts initiated after moderate-severity fire resembled initial floristics cohorts, with 73% of establishment dates for shade-tolerant trees falling within the pulse of establishment by Douglas-fir (Fig. 6f).

Growth patterns of Douglas-fir trees varied in relation to cohort initiation pathway. In relay floristics cohorts, BAI increases to a distinct peak around age 40, followed by a gradual decline to a nearly constant BAI by age 80–90 (Fig. 6g). The timing of the peak in growth roughly corresponds to the cessation of Douglas-fir establishment (Fig. 6d), suggesting a shift to more intensive competition among Douglas-fir trees corresponding to canopy closure. A similar peak in Douglas-fir growth is evident, but much less distinct in initial floristics cohorts (Fig. 6h). The less distinct peak in growth may reflect less intensive intra-specific competition under the lower density of Douglas-fir trees, where the present density averages only 65% of that found in relay floristic cohorts (Fig. 6a, b). High variation in BAI in initial floristics cohorts after age 80 reflects decreasing sample size due to the young ages of several cohorts (Fig. 6h).

In cohorts initiated following moderate-severity fire, Douglas-fir growth gradually increases over the first 100 years, without a peak followed by a decline in growth as found in the other pathways (Fig. 6i). Slow growth in the first 2–3 decades may be a response to partial shading by the older trees (Fig. 6c). The lack of a peak and then decline in growth suggests less intensive competition among Douglas-fir trees of the post-fire cohort, which are present at the lowest density (173 trees/ha) of the cohort initiation

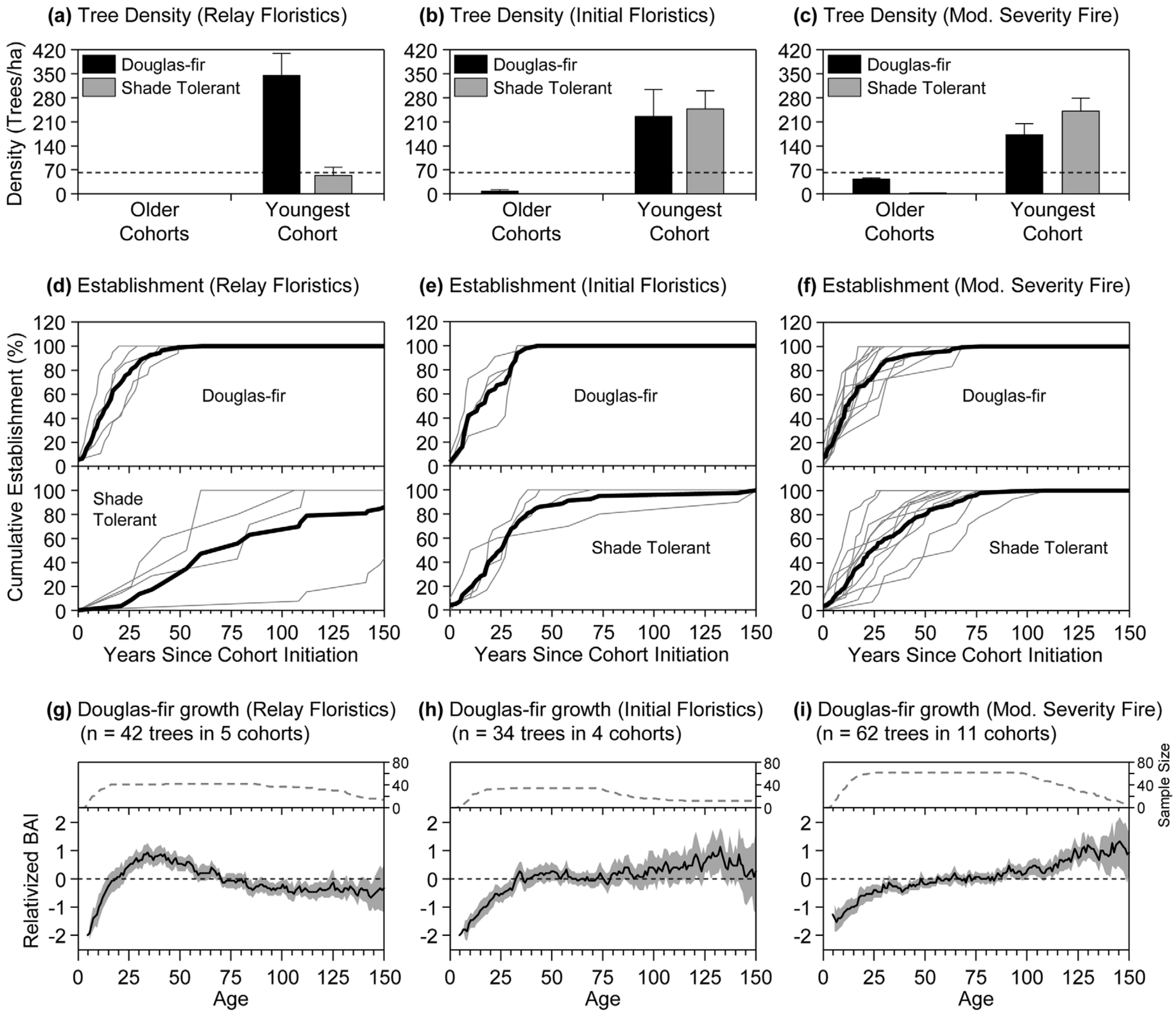

Fig. 6. Comparison of establishment and growth trajectories among cohorts following initial and relay floristics pathways after high-severity fire and in cohorts initiated following moderate-severity fire. In (a–c), the present density (mean + 1 SE) of Douglas-fir and shade-tolerant species in the mature-aged post-fire cohort and in cohorts that predate the most recent fire is compared among the three pathways (the dashed horizontal line represents the density of Douglas-fir trees averaged across 18 stands with no evidence of fire for >400 years; age-structure type 1 of Tepley et al. 2013). Cumulative establishment of Douglas-fir and shade-tolerant trees in the youngest cohort per stand is compared in (d–f), where each thin gray line represents one stand and the thick black line is the average across stands. In (g–i), relativized basal area increment (BAI) for Douglas-fir trees of the youngest cohort is compared among the pathways (gray shading represents 95% confidence intervals).

pathways (Fig. 6a–c).

Discussion

Post-fire establishment

Post-fire establishment by Douglas-fir occurred primarily over four decades (Fig. 3) and remained surprisingly consistent over a broad range of topographic settings (Fig. 4), over nearly eight centuries (Fig. 5), and regardless of the severity of the cohort-initiating fire or the timing of post-fire establishment by shade-tolerant species (Fig. 6). These findings corroborate another recent study of post-fire establishment in Douglas-fir/western hemlock forests (Freund et al. 2014). The present study employs an extensive sampling approach that evaluates establishment in 77 cohorts that span broad variation in cohort ages, topography, and cohort initiation pathways. The other study utilizes a more intensive approach that sampled 18, 100–300-year-old, single-cohort stands that initiated after high-severity fire and have no evidence of subsequent burning, but a larger number of trees were sampled per stand (Freund et al. 2014).

Despite differences in study design, interpretations are remarkably consistent across the two studies. The time (mean ± 95% confidence interval) to reach establishment of 90 and 100% of the trees in a cohort was 43.5 ± 7.0 and 48.4 ± 8.1 years, respectively in this study, compared to 35 ± 7.1 and 60 ± 10.1 years, respectively in the study of Freund et al. (2014). Thus, the smaller number of trees sampled per cohort in this study might not fully account for the tail of the distribution of establishment dates, but otherwise the two studies provide strong validation that establishment is nearly complete (ca. 90%) in about 40 years. Completion of establishment within 20 years was only found in 8% of cohorts in this study and none in the study of Freund et al. (2014), but 22% of cohorts reached 90% establishment by year 20. Establishment lasting >80 years was found in 12% of cohorts in this study and 17% of cohorts sampled by Freund et al. (2014).

Previous interpretations that protracted establishment lasting >100 years was common in the development of older forests of this region were based on counting tree rings on cut stumps in the field and comparing early growth rates of old-growth trees to young trees in stands that regenerated naturally after harvest (Tappeiner et al. 1997, Poage and Tappeiner 2002). Douglas-fir ages were reported to range from 140 to 460 years in four stands in the western Cascades of Oregon and southwestern Washington (Franklin and Hemstrom 1981), from 66 to 364 years in 10 stands of the Oregon Coast Range (Tappeiner et al. 1997), and the range averaged 174 years (maximum 430 years) in 28 stands of the Cascades, Coast Range, and Willamette Valley margin of Oregon (Poage and Tappeiner 2002).

In considering the Douglas-fir age ranges reported in previous studies, it is important to note that the authors did not report on whether the ages represent establishment after a single fire or more than one period of post-fire establishment. The full range of Douglas-fir ages per stand in this study (average 173 years) is similar to that reported in previous work, but we suggest this wide range reflects the occurrence of two or more post-fire cohorts in many stands, each represented by a relatively abrupt pulse of establishment (e.g., Fig. 2b–d). For the 55 out of 124 stands identified as having >1 cohort (the oldest cohort of several stands was excluded from analyses due to the small number of pith dates), the time from the completion of establishment of one cohort to initiation of a younger cohort averaged 217 years. Seventeen percent of cohorts had initiation dates that correspond to a healed scar found in the stand and would have been combined with other cohorts without the use of fire scars (Fig. 2b, c). Additional support for the interpretation that many stands contain more than one post-fire cohort comes from the presence of charred bark on trees of the older but not the younger cohort (Tepley et al. 2013).

The degree that errors associated with aging stumps of old trees in the field affects interpretations of post-fire establishment has been given little consideration. Weisberg and Swanson (2001) aged 26 Douglas-fir stumps in the field (80% were 300–500 years old) and then cross-dated samples from those stumps. Field-counted ages typically were under-estimated, by an average of 25 years, and errors increased with tree age. To assess how counting errors affect interpretations of post-fire establishment, the distribution of counting errors found by Weisberg and Swanson (2001) can be used to simulate counting errors to cross-dated data, and thereby evaluate how it would have been interpreted had it been counted in the field (Appendix A). For instance, cohorts that initiated between 1470 and 1610 took an average of 41 years to reach establishment of 90% of the trees (Fig. 5c, e), but this average increases to 85–96 years after 5 replicates simulating counting errors. Thus, counting errors could lead to the interpretation that establishment over a few decades, as was widespread in this study and in Freund et al. (2014), represents protracted establishment over a century. Similarly, counting errors could blur two pulses of establishment into a single period of protracted establishment.

Douglas-fir tree density and growth do not support the hypothesis that old stands of our study area commonly initiated at low tree densities (e.g., 77–114 trees/ha at age 20) with little self-thinning, as proposed for the Oregon Coast Range (Tappeiner et al. 1997). The present density of Douglas-fir trees in mature-aged stands averages 225 and 344 trees/ha in initial and relay floristics cohorts, respectively, and stands with a cohort initiated after moderate-severity fire have an average of 43 and 173 Douglas-fir trees/ha in the older and younger cohorts, respectively (Fig. 6a–c). These values are similar to the average of 226 Douglas-fir trees/ha found in 71, 82–157-year-old, non-riparian stands in Washington and Oregon (Pollock et al. 2012). Self-thinning was probably most intense in relay floristics cohorts, where a marked reduction in Douglas-fir growth begins at about the time of canopy closure (Fig. 6g). Douglas-fir BAI over the first 100 years of growth in cohorts that initiated between 1470 and 1610 shows little difference from that in cohorts initiated between 1780 and 1940 (Appendix B), suggesting the older cohorts probably experienced a similar range of development pathways to that evident in the present mature cohorts.

Although we do not deny the potential for protracted establishment, we suggest it was much less common than previously believed. Hypotheses for protracted establishment include a loss of seed sources following extensive and severe fires or competition from hardwoods, shrubs, or herbaceous vegetation (Franklin and Hemstrom 1981). Both factors could be exacerbated by repeated burning within the first few decades, which could remove seed sources that survived the initial fire (Isaac and Meagher 1936) and promote expansion of sprouting hardwoods, shrubs, and herbs (Donato et al. 2009*b*). Climate unfavorable to seedling survival also could extend post-fire establishment, either locally in harsh sites, or over broad areas when a fire is followed by years to decades of unfavorable climate. These factors probably extend the duration of post-fire tree establishment, but likely over a few decades rather than a century or more.

The 12% of cohorts with ages spanning >80 years include cohorts located in the harshest sites sampled across the study area and cohorts that would have been divided into two shorter periods of establishment had a less conservative window been used to identify cohorts (e.g., Fig. 2d, e). For example, three of the six cohorts that initiated between 1610 and 1780 show gradual establishment (Fig. 5g) and were located on rocky ridgetops that support the *Pseudotsuga menziesii*/*Holodiscus discolor* plant association (Franklin and Dyrness 1988). Because these cohorts were initiated at a time when there is little evidence that fire was widespread in the study area (Fig. 5a) or more broadly across the region (Weisberg and Swanson 2003), it is improbable that loss of seed sources in extensive fires could have produced protracted establishment. The wide age ranges more likely result from poor seedling survival and growth, possibly in combination with Douglas-fir establishment in the absence of fire under the relatively open tree canopy at these harsh sites. Also, because these are fire-prone sites that burned when fire otherwise was uncommon across the study area (Fig. 5a), an 80-year window might be too conservative to identify all cohorts in the absence of fire scars (Means 1982).

Other than the wide age ranges in cohorts on extremely harsh sites, the rate and duration of post-fire establishment varied little in relation to topography (Fig. 4), consistent with Freund et al. (2014). A tendency for more gradual establishment of Douglas-fir was found only near its upper-elevation limit (Fig. 4a) and at upper slope positions (Fig. 4b), but even these settings reach 90% establishment within about 60 years. Establishment trajectories did not vary by aspect in this study (Fig. 4c), nor did seedling density differ between north and south aspects 14 years after the Warner Creek Fire, 24 km southeast of the Fall Creek study area (Brown et al. 2013). Although repeated sampling following timber harvest revealed that north aspects reached canopy closure 10 years earlier than south aspects (Halpern and Lutz 2013), post-harvest conditions differ from those after wildfire in several important ways. For example, delayed tree mortality (e.g., 55% of trees that were alive the year after the Warner Creek Fire died by year 14) and snags that persist following wildfire provide partial shade that could dampen microclimatic extremes on south aspects (Brown et al. 2013).

Pathways of cohort initiation

Three pathways of cohort initiation led to wide variation in forest composition and structure that persists at least through the mature age class (ca. 80–200 years old). Cohorts that followed the different pathways are distinguished by differences in the present density of Douglas-fir and shade-tolerant trees (Fig. 6a–c), the timing of establishment of shade-tolerant species (Fig. 6 d–f), and the growth trajectory for Douglas-fir trees (Fig. g–i). Yet, Douglas-fir established primarily over four decades in all three pathways (Fig. 6d–f).

The relay floristics pathway is the closest of the three pathways to the plantation model of stand development (Smith et al. 1997), with the main exception that Douglas-fir established over about 40 years (Fig. 6d) rather than all in a single year. At about the time Douglas-fir establishment ceased, Douglas-fir trees reached a peak in BAI followed by a decline to nearly constant BAI over the next 40–50 years (Fig. 6g), a likely response to increasing competition as Douglas-fir tree crowns coalesced to form a canopy dense enough to preclude further Douglas-fir establishment. Probably only a few seedlings or saplings of shade-tolerant species were present at the time of canopy closure, as suggested by their low density (54 trees/ha) in mature-aged stands (Fig. 6a), and only 4% of their establishment dates fall before the cessation of Douglas-fir establishment (Fig. 6d). The present density of Douglas-fir trees (344 trees/ha) is >5 times that in old-growth (>400-year-old) stands of the study area (62 trees/ha; Fig. 6a). Thus, substantial thinning by both density-dependent and density-independent processes (e.g., wind, snow and ice, parasites, insects, and pathogens) is likely to continue over the next 2–3 centuries.

Initial floristics cohorts probably had a lower density of establishing Douglas-fir seedlings and greater structural complexity earlier in development than relay floristics cohorts, as proposed by Donato et al. (2012), but in contrast to predictions, post-fire establishment was no more protracted than in relay floristics cohorts. Both pathways show cessation of Douglas-fir establishment about 40 years after cohort initiation (Fig. 6d, e). In initial floristics cohorts, 88% of the shade-tolerant trees established before cessation of Douglas-fir establishment (Fig. 6e). Because Douglas-fir tends to overtop slower growing western hemlock trees in about 20 years (Wierman and Oliver 1979), a deep canopy with vertical stratification by species (e.g., Douglas-fir in dominant and co-dominant classes and western hemlock limited to intermediate and suppressed classes) probably developed shortly after the canopy grew dense enough to preclude additional Douglas-fir establishment. This stratification becomes more pronounced in the mature age class (Pollock et al. 2012).

Douglas-fir growth patterns support interpretations of Donato et al. (2012) that density-dependent thinning is less intensive in initial than relay floristics cohorts, but initial tree density typically was not so low that the old-growth canopy dominants are determined early in stand development. After Douglas-fir overtopped western hemlock trees to form a vertically stratified canopy, they would have faced less competition (at least for light) than Douglas-fir trees of the denser, mono-specific canopy in relay floristics cohorts. Thus, Douglas-fir trees of initial floristics cohorts do not exhibit as distinct a decline in BAI after canopy closure as was found in relay floristics cohorts (Fig. 6g, h). However, the average density of Douglas-fir trees in mature-aged, initial floristics cohorts (225 trees/ha) is 3.6 times that in old-growth (>400-year-old) stands of the study area (62 trees/ha; Fig. 6b), suggesting these cohorts are likely to continue to thin, either by density-dependent or density-independent processes.

Cohorts that initiated following moderate-severity fire exhibit the greatest structural complexity throughout their development. Douglas-fir trees that survived the fire are present at a density (43 trees/ha) about two-thirds that in unburned old-growth stands of the study area (62 trees/ha; Fig. 6c), and the post-fire cohort exhibits concurrent establishment of Douglas-fir and shade-tolerant trees (Fig. 6f). Thus, the post-fire cohort probably developed vertical stratification of the canopy by species, similar to initial floristics cohorts, with the added influences of older trees on spatial patterns and competitive interactions in the post-fire cohort (Zenner 2000). Douglas-fir trees of the post-fire cohort are likely to be distant from older trees (Goslin 1997), but partial shade from the surviving trees still may have contributed to lower BAI in the first few decades than in cohorts initiated following stand-replacing fire (Fig. 6g–i). For example, Acker et al. (1998) found a 26% decrease in mean annual increment of the younger cohort for every ca. 12 trees/ha present in the older cohort. The present density of Douglas-fir trees in the mature cohort (173 trees/ha) is the lowest of the cohort initiation pathways (Fig. 6c). Relatively weak competition among these trees after they overtopped the shade-tolerant trees could account for the trend of gradually increasing BAI over their first 100–150 years (Fig. 6i).

Summary and Management Implications

This study aimed to improve understanding of historical post-fire tree establishment and early cohort development in Douglas-fir/western hemlock forests of the PNW. We analyzed stand structure, ages of Douglas-fir and shade-tolerant species, and growth of Douglas-fir in the central western Cascades of Oregon to answer the following questions: (1) to what degree does the rate and duration of post-fire establishment vary among cohorts?, and in what ways is that variation influenced by (2) topography?, (3) the timing of cohort initiation?, and (4) the different pathways of cohort initiation, including variation in the severity of the cohort-initiating fire and the timing of establishment by shade-tolerant species?

Douglas-fir establishment trajectories were remarkably consistent over space and time. On average, 90% of trees established within 43.5 years of cohort initiation (Fig. 3), and establishment trajectories varied little with topography (Fig. 4), across periods of widespread fire and periods with limited burning (Fig. 5), or with the severity of the cohort-initiating fire (Fig. 6). Also, the duration of Douglas-fir establishment differed little regardless of whether shade-tolerant species established primarily along with Douglas-fir or after the Douglas-fir cohort reached canopy closure (Fig. 6d, e). These findings corroborate the findings of Freund et al. (2014), who worked in 100–300-year-old Douglas-fir/western hemlock stands that established after high-severity fire with no subsequent burning. Trajectories toward canopy closure within a few decades also have been reported following recent fires (as reviewed by Brown et al. 2013) and following timber harvest on federal land (Yang et al. 2005, Halpern and Lutz 2013).

Understanding the early development of mature-aged cohorts (Fig. 6) has important implications for the practice of thinning in plantations to accelerate development of structural complexity characteristic of older forests (Franklin and Johnson 2012), with the limitation that we have information only on trees that survived to the present. The mature age class provides a reference for stand conditions a few decades beyond the ages when thinning treatments typically occur (ca. 40–60 years in federal forests of the PNW). Natural mature-aged cohorts developed through multiple pathways leading to wide variation in total tree density and the ratio of Douglas-fir to shade-tolerant trees (Fig. 6a–c), whereas plantation management typically produces a dense, mono-specific canopy similar to natural relay floristics cohorts. Thinning younger plantations could promote a greater variety of stand structures at the mature age, including accelerating the development of a mid-canopy component of shade-tolerant trees where shade-tolerant trees are present but limited to small sizes, or decreasing stem density and increasing the growth of the remaining Douglas-fir trees in particularly dense stands. Our results suggest that thinning to a common, relatively low target density (e.g., 150 trees/ha) would be toward the low end of Douglas-fir tree densities found in natural mature-aged stands (Fig. 6; Pollock et al. 2012). A broader range of target conditions is needed to represent the diversity of development pathways evident in natural stands.

Development in cohorts that initiated following moderate-severity fire also has important implications for the practice of variable retention harvesting to promote diverse early-seral ecosystems (Franklin and Johnson 2012). In the central western Cascades of Oregon, historically moderate-severity fire commonly opened the canopy enough to permit establishment of a new Douglas-fir cohort while leaving relatively high densities (ca. 43 trees/ha) of surviving Douglas-fir trees (Fig. 6c; Tepley et al. 2013). If management objectives include the creation of early-seral habitat, understanding how long those conditions persist is key in planning the rate that new openings need to be created to maintain a target area of early-seral habitat across the landscape over time. Historical development following moderate-severity fire indicates the canopy is likely to remain open enough to permit Douglas-fir establishment for about 40 years (Fig. 6f). Relatively high abundance and diversity of early-seral forbs and shrubs are likely to persist at least through the development of tree canopy closure (Halpern and Lutz 2013).

There is growing concern that the combined effects of 20th century forest management and on-going climatic warming could increase the potential for fire-mediated conversions from forest to persistent non-forest vegetation (Collins and Roller 2013, Savage et al. 2013). However, the risk of such conversion varies widely by region and forest type. Results of this study suggest Douglas-fir/western hemlock forests are resilient to relatively wide variation in the fire regime and climatic and biotic constraints on post-fire establishment for three primary reasons. First, the ability of Douglas-fir to survive fire (e.g., due to its thick bark, self-pruning of shaded lower branches, and moderate resistance to rot if injured by fire) means seed sources tend to be available within the perimeter of most fires, and seeds are commonly dispersed to distances of about 400 m (Donato et al. 2009*a*). Some cohorts that initiated in the two periods of widespread burning (1470–1610 and 1780–1940) may have been subject to extensive and severe fires or repeated burning, but relatively rapid establishment by almost all of these cohorts (Fig. 5e, g) indicates seed-source availability was not a primary factor limiting their establishment.

Second, growth trajectories of Douglas-fir (Fig. 6g–i) support the hypothesis that it can tolerate moderate competition when young. In fact, high stand densities may even facilitate growth at very young ages (Woodruff et al. 2002). Plasticity in early growth may help Douglas-fir to establish beneath, and eventually overtop shrubs in the post-fire environment (Shatford et al. 2007). For example, repeated sampling after the Warner Creek Fire in the western Cascades of Oregon illustrates that extensive shrub cover did not impede tree regeneration (Brown et al. 2013). Tree and shrub establishment was widespread the first year, and newly established tree seedlings were abundant in subsequent samplings. By year 14, shrub cover exceeded that of tree seedlings, but numerous seedlings had emerged above the shrub canopy (Brown et al. 2013).

Finally, narrow variation in the duration of post-fire establishment in relation to topography (Fig. 4) suggests establishment in the Douglas-fir/western hemlock region may be resilient to considerable climatic variation. Even in relatively dry forests of the Willamette Valley foothills (mean annual precipitation of 127–147 cm, compared to 182 and 233 cm in the Fall Creek and Blue River study areas, respectively), Douglas-fir establishment was complete within 40 years of cohort initiation (Robbins 2004). Thus, early-seral communities may be prone to repeated burning (Agee and Huff 1987), but even under unfavorable climate, the duration of this fire-prone stage is short compared to typical fire intervals.

Our finding that Douglas-fir established primarily over a 40-year interval across a wide range of environmental conditions suggests post-fire establishment historically was a somewhat gradual process spanning several decades. Post-fire establishment in our study area was more gradual than reported in mixed-wood boreal forests of Saskatchewan or for sprouting aspen trees in the southern Rocky Mountains, where most trees established within 5–10 years following fire (Gutsell and Johnson 2002, Margolis et al. 2007), but our findings do not support the interpretation that limited regeneration within a narrow window (e.g., $<$20 years) following fire means it will take $>$100 years to re-establish forest cover (Tappeiner et al. 1997, Poage and Tappeiner 2002). In addition to the ability of Douglas-fir to establish beneath and overtop shrubs in this highly productive region (Shatford et al. 2007), the post-fire environment is prone to numerous small-scale disturbances from snag fragmentation and snagfall over 2–4 decades following fire (Brown et al. 2013), which could provide numerous opportunities for Douglas-fir establishment. The finding that the Douglas-fir trees in the cohorts initiated in both periods of widespread burning (1470–1610 and 1780–1940) established primarily over a 40-year interval following cohort initiation (Fig. 5e, g) indicates the later establishing seedlings remain an important component of the stand throughout its development.

This study illustrates that post-fire establishment in Douglas-fir/western hemlock forests of the PNW has been resilient to considerable variation in the fire regime and the post-fire environment. It also supports that the biologically-rich, early-seral stage of forest development is not a brief period of about 20 years, but relatively open canopy conditions typically persisted for about 40 years following fire. Therefore, we support suggestions of Brown et al. (2013) and Freund et al. (2014), that planting seedlings of Douglas-fir and the major shade-tolerant species following wildfire at low to mid elevations in the western Cascades may be unnecessary where management objectives focus more on ecological outcomes associated with closed canopy forests than high yield timber production (but see Collins and Roller (2013) for an alternative perspective in a drier region).

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Supplemental Material

Appendix A

Beginning in the late 1970s, several studies of tree-age distributions in Douglas-fir/western hemlock forests of the Pacific Northwest were conducted by counting tree rings on cut stumps in the field. The first of these studies was conducted in a 10-ha watershed of the central western Cascades of Oregon (Watershed 10 of the H. J. Andrews Experimental Forest, located within the Blue River study area of this study). The dominant old-growth Douglas-fir trees were found to range from 370 to 520 years in age, and the spatial distribution of tree ages did not appear to be related to variation in local site conditions or indicative of a response to fine-scale disturbances within the watershed (Franklin et al. 1979). Thus, it was suggested that the wide age range may represent protracted establishment after a single fire. This finding was so surprising compared to observations of rapid Douglas-fir regeneration after fires of the early 20th century (e.g., Hofmann 1924), that it prompted further evaluation of tree ages. Similarly wide age ranges for old-growth Douglas-fir trees were found in several additional stands (Franklin and Hemstrom 1981, Tappeiner et al. 1997, Poage and Tappeiner 2002).

Although wide age distributions for old-growth trees were found when tree ages were counted in the field, studies that employed cross-dating found a much narrower range of tree ages. For example, Winter et al. (2002) found that all 58 Douglas-fir trees present in a recently harvested 3.3-ha stand had established in a 21-year window in the early 16th century. Similarly, Yamaguchi (1993) found that 94 of 97 Douglas-fir trees sampled over an area of 10 ha near Mount St. Helens established within a 40-year window following a fire in the early 14th century. In fact, the only place where strongly protracted establishment was found near Mount St. Helens was in areas within the complete mortality zone after the 1480 eruption and inferred to be >2 km from seed sources. In these areas, Douglas-fir established gradually over >200 years. Infertile, freshly deposited, coarse tephra and very long distance from seed sources probably contributed to this long period of establishment (Yamaguchi 1993).

The differences in tree-age distributions found between field counted and cross-dated studies led us to question how much errors associated with counting tree rings in the field affect interpretations of cohort initiation. Related to this question, another study was conducted to evaluate the degree to which errors associated with dating fire scars in the field influence fire-history interpretations (e.g., due to two scars in the same year being interpreted as two fire events). In that study, Weisberg and Swanson (2001) counted fire scar dates on 60 recently cut Douglas-fir stumps in the field and then brought samples from the same stumps to the lab for sanding and cross-dating. Although the study focused primarily on how counting errors for fire scars affect fire-history interpretations, errors for pith dates were reported for 26 stumps. Eighty percent of these stumps were 300–500 years old, which corresponds to the age range of old-growth stands that have been interpreted as having initiated with protracted post-fire establishment (Franklin and Hemstrom 1981, Tappeiner et al. 1997, Poage and Tappeiner 2002).

Although it is not practical (or possible due to decay) to relocate stumps sampled in previous studies and collect samples to evaluate the counting errors, it is possible to simulate counting errors to cross-dated data to evaluate how the data likely would have been interpreted had it been counted in the field. We simulated counting errors to the cross-dated establishment dates for Douglas-fir trees in cohorts that initiated between 1470 and 1610 based on the distribution of counting errors for pith dates in the study of Weisberg and Swanson (2001). The analysis is limited to this age class because it overlaps with 80% of the pith dates evaluated by Weisberg and Swanson (2001), and previous reporting of wide age ranges have focused on old-growth stands that initiated in a similar time period. Although the time to reach establishment of 90% of the trees in a cohort averaged 41 years based on the cross-dated data, this average increases to 85–96 years after five replicates simulating counting errors.

The procedure for simulating counting errors is described below. In the distribution of counting errors for pith dates in the study of Weisberg and Swanson (2001), tree ages were mostly underestimated, but one outlier was over-estimated by 89 years (Fig. A1a). This large outlier was excluded from simulations of counting errors. For the remaining 25 trees, the proportion of errors that fall in each decade bin was calculated (Table A1). Then two uniform random variables, μ and v, were drawn to simulate counting errors assuming the probability that the error falls in each decade bin is equal to the proportion of errors in that bin and errors are uniformly distributed within each decade.

The first random variable, μ, is drawn on the interval (0, 1) to determine which decade bin the counting error falls within (Table A1). For example, a value of $\mu = 0.65$ indicates the pith date is underestimated by 21–30 years ($0.625 < \mu \leq 0.708$). Note that the probability that μ falls between 0.625 and 0.708 is 0.083, which is equal to the proportion of trees in the dataset of Weisberg and Swanson (2001) where the pith date was underestimated by 21–30 years (Table A1). The second uniform random variable, v, is drawn on the interval (0, 9) and the value is added to the minimum of the error range to determine where the error falls within that range. For example, if $\mu = 0.65$ and $v = 2$, the pith date would be underestimated by $21 + 2 = 23$ years. This procedure was repeated for each tree in the dataset to estimate what the distribution of pith dates would have been if the trees were aged by counting tree rings in the field.

The error simulation procedure is illustrated for nine replicates to the cross-dated data in Fig. 6 of Winter et al. (2002), as shown in Fig. A1b. Cross-dated pith dates all fell between 1500 and 1521, and for this analysis we assume all pith dates fall in the middle of each decade bin (i.e., 1505, 1515, or 1525). After nine replicates, we found that the range of tree ages varied between 96 and 108 years (Fig. A1c). Thus, if the counting errors of Weisberg and Swanson (2001) represent those in other studies, counting errors likely would have led to the interpretation that stands initiated with protracted establishment over about 100 years even if the trees actually established in a narrow window of a couple decades.

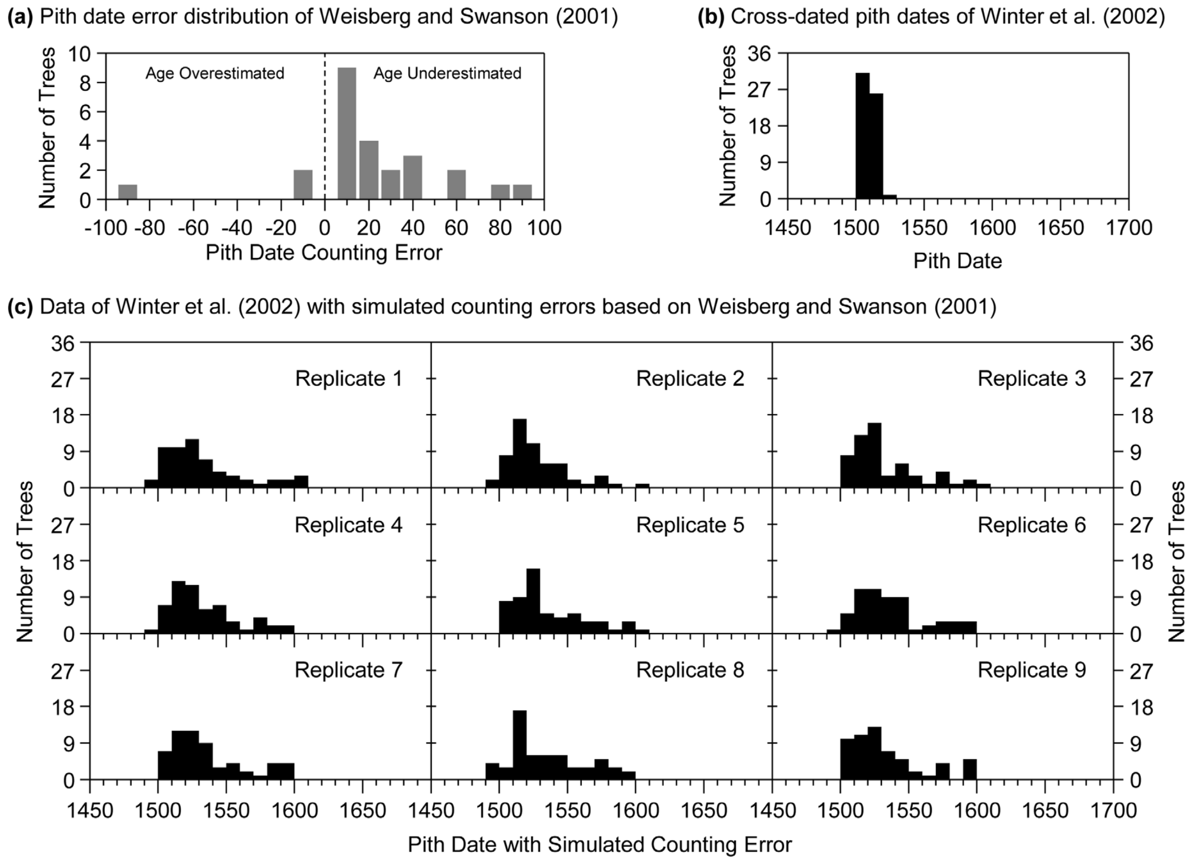

Fig. A1. Illustration of (a) the distribution of counting errors for pith dates based on Fig. 2b of Weisberg and Swanson (2001), and (b) cross-dated pith dates for 58 Douglas-fir trees in Fig. 6 of Winter et al. (2002). In (c), results of nine replicates are presented where the counting errors were simulated to the cross-dated data in (b) based on the distribution of counting errors in (a).

Table A1. The number and proportion of trees in the dataset of Weisberg and Swanson (2001) where errors on field-counted pith dates fall within each decade bin (after excluding one outlier where the age was overestimated by 89 years, see Fig. A1a). The two columns on the right provide the limits of the random variable, μ, for each decade bin (e.g., if $\mu = 0.85$, the error is in the 51–60-year bin). Note that for each bin, the range of values for μ (maximum − minimum) is equal to the proportion of trees whose counting error falls in that bin. Therefore, the probability that the simulated error falls within a given bin is equal to the proportion of counting errors in that bin.

Error range (years)				Range of values for μ	
Minimum	Maximum	No. trees	Proportion of trees	Minimum	Maximum
−10	1	2	0.083	0.000	0.083
0	0	0	0.000	0.083	0.083
1	10	9	0.375	0.083	0.458
11	20	4	0.167	0.458	0.625
21	30	2	0.083	0.625	0.708
31	40	3	0.125	0.708	0.833
41	50	0	0.000	0.833	0.833
51	60	2	0.083	0.833	0.917
61	70	0	0.000	0.917	0.917
71	80	1	0.042	0.917	0.958
81	90	1	0.042	0.958	1.000

Appendix B

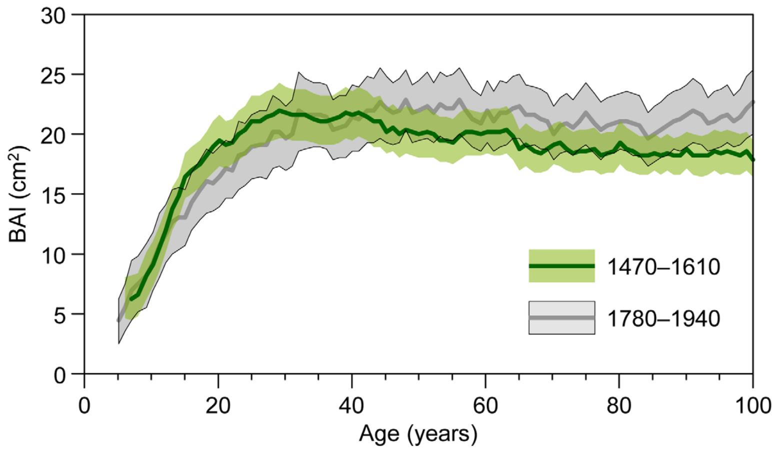

Fig. B1. Comparison of Douglas-fir basal area increment (BAI) between trees in cohorts initiated between 1470 and 1610 (n = 168 trees) and those in cohorts initiated between 1780 and 1940 (n = 138 trees). Thick lines represent the mean value at a given age for trees established in each time period. Shading represents 95% confidence intervals.