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ARTICLE

Multi-decadal establishment for single-cohort Douglas-fir forests

James A. Freund, Jerry F. Franklin, Andrew J. Larson, and James A. Lutz

Abstract: The rate at which trees regenerate following stand-replacing wildfire is an important but poorly understood process in the multi-century development of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) forests. Temporal patterns of Douglas-fir establishment reconstructed from old-growth forests (>450 year) have generated contradictory models of either rapid (<25 year) or prolonged (>100 year) periods of establishment, while patterns of tree establishment in mid-aged (100 to 350 year) forests remains largely unknown. To determine temporal patterns of Douglas-fir establishment following stand-replacing fire, increment cores were obtained from 1455 trees in 18 mature and early old-growth forests in western Washington and northwestern Oregon, USA. Each of the stands showed continuous regeneration of Douglas-fir for many decades following initiating fire. The establishment period averaged 60 years (range: 32–99 years). These results contrast both with the view of rapid (one- to two-decade) regeneration of Douglas-fir promoted in the early forestry literature and with reports of establishment periods exceeding 100 years in older (>400 year) Douglas-fir–western hemlock stands. These results have important implications for management designed to create and promote early-seral forest characteristics.

Key words: Douglas-fir, tree establishment, canopy closure, age structure, stand development, early-seral, single-cohort.

Résumé : Le taux auquel les arbres se régénèrent à la suite d'un feu sévère est un processus important, mais mal compris, du développement multiséculaire des forêts composées de douglas de Menzies (*Pseudotsuga menziesii* (Mirb.) Franco) et de pruche de l'Ouest (*Tsuga heterophylla* (Raf.) Sarg.). Le patron temporel d'établissement du douglas de Menzies reconstitué à partir de vieilles forêts (> 450 ans) a produit des modèles contradictoires de période d'établissement rapide (< 25 ans) ou prolongée (> 100 ans) alors que le patron d'établissement des arbres dans les peuplements âgés de 100 à 350 ans est peu connu. Pour déterminer le patron temporel d'établissement du douglas de Menzies à la suite d'un feu sévère, des carottes ont été prélevées sur 1455 arbres provenant de 18 forêts matures et surmatures établies dans l'ouest de l'État de Washington et dans le nord-ouest de l'Oregon, aux États-Unis. Un établissement continu de la régénération de douglas de Menzies pendant plusieurs dizaines d'années a été observé à la suite du feu à l'origine de chaque peuplement. La période moyenne d'établissement était de 60 ans (de 32 à 99 ans). Ces résultats sont différents de ceux véhiculés dans la vieille littérature forestière soit une régénération rapide (10 à 20 ans) du douglas de Menzies et de ceux mentionnés dans des rapports qui évaluent la période d'établissement à plus de 100 ans dans les vieux peuplements (> 450 ans) de douglas de Menzies et de pruche de l'Ouest. Ces résultats ont des implications importantes pour l'aménagement visant à créer et à promouvoir des caractéristiques forestières de début de succession. [Traduit par la Rédaction]

Mots-clés : douglas de Menzies, établissement d'arbres, développement des peuplements, début de succession, structure d'âge.

Introduction

Temporal patterns of tree regeneration following stand-replacement disturbances strongly influence subsequent forest development (Ashton 1976; Foster et al. 1997; Cooper-Ellis et al. 1999; Franklin et al. 2002). The initial period of tree establishment following high-severity disturbance is also significant, because it represents a stage in forest development during which trees do not exert strong competitive controls on other life forms, providing essential habitat for many early-successional species (Swanson et al. 2011). Patterns of post-disturbance tree regeneration continue to be of great interest to ecologists and managers who seek to understand ecosystem development to guide forest management and conservation of biological diversity (Franklin et al. 2002; Lindenmayer and Franklin 2002).

Post-fire tree establishment in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests is a starting point for modeling changes in structure, function, and composition over multi-century developmental sequences (Huff 1995; Franklin et al. 2002; Zenner 2005; Larson et al. 2008). Douglas-fir–western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) forests in the Pacific Northwest experience large infrequent wildfires, which typically include extensive areas of stand-replacement severity (Agee 1993). The rate and density of tree establishment after stand-replacement wildfire is hypothesized to explain multiple alternative successional pathways (Donato et al. 2012). For example, forests regenerating at high densities may undergo canopy closure more rapidly leading to an intense self-thinning phase, while stands that gradually re-establish at lower densities may not experience canopy closure and subsequent self-thinning mortality (Franklin et al. 2002; Lutz and Halpern 2006; Halpern and Lutz 2013). Knowledge of the rate and density of tree establishment in naturally regenerated forests therefore provides a basis for testing and refining conceptual models for forest succession and structural development.

Early 20th century forest researchers proposed a model of rapid and dense Douglas-fir establishment following stand-replacement wildfire (hereafter the "traditional model"). This early view of Douglas-fir cohort establishment was strongly influenced by observations of tree establishment following the 1902 Yacolt and

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1910 Cispus fires in the southern Washington Cascades, and of regenerating harvested stands in the same region (Hofmann 1924; Herring and Greene 2007). Julius Hofmann (1924), one of the earliest forest researchers investigating Douglas-fir regeneration, commented, "The main feature of interest found on the [Yacolt] burn was the good stand of young growth which almost uniformly covered the area and consisted of the same species as those which made up the burned forest." In an early synthesis paper on succession and structural development of Douglas-fir forests, Munger (1940) concluded that Douglas-fir regeneration usually occurs within a decade after the stand-initiating disturbance. The collective observations of early forest scientists clearly pointed towards a general model of rapid, dense establishment of the Douglas-fir cohort following stand-replacement disturbance.

Some modern reconstructions provide evidence that supports the traditional model of rapid and dense Douglas-fir establishment. A detailed reconstruction of Douglas-fir establishment in an old-growth stand in the southern Washington Cascades (Winter et al. 2002*a*) provides some of the most compelling evidence, with the establishment phase completed within 21 years. The traditional model of rapid establishment remains well represented in the current conceptual framing for natural Douglas-fir forest structural development: Franklin et al. (2002) describe the initial, cohort-establishment stage as lasting for around 25 years, although they do acknowledge potential for extended establishment.

Studies of old-growth (>400 years) forests beginning in the 1970s led to the development of an alternative model in which Douglas-fir establishment is protracted, lasting one to several centuries. Franklin and Hemstrom (1981) identified a >150 year period of Douglas-fir establishment in the central Oregon Cascades. Tappeiner et al. (1997) reconstructed establishment periods from several forests in coastal Oregon with establishment in 70% of the sites extending over >100 years (maximum of 364 years). A subsequent study by Poage and Tappeiner (2002) also reported a prolonged establishment period for Douglas-fir with a mean of 174 and a maximum of 430 years. Poage and Tappeiner (2002) further suggested that short periods of establishment (one to two decades) are anomalous, and that prolonged periods are most common (Poage et al. 2009).

In this study we examine the duration of Douglas-fir establishment in 18 mature (100 to 200 year) and early old-growth (200 to-300 years) stands in western Washington and northwestern Oregon that regenerated naturally following single stand-replacement wildfires. Forests included in this study are generally older than the regenerating burns studied by Hofmann (1924), Munger (1930) and Isaac (1943), but are significantly younger than the (>400 year old stands analyzed by Tappeiner et al. (1997), Poage and Tappeiner (2002), Winter et al. (2002*a*, 2002*b*). Our purpose is to expand knowledge of temporal patterns of Douglas-fir regeneration following wildfires in naturally-regenerated stands that are younger than most previously studied. We pose two questions: (1) Is the length of establishment of Douglas-fir in these mature forests supportive of the "traditional model" of rapid establishment or is it more comparable to prolonged periods observed in previous studies of old-growth? (2) How variable is the period of establishment and can it be explained by differences in local environment or current structural attributes?

Methods

Study area

Douglas-fir–western hemlock forests occur at low and middle elevations in western Washington and northwestern Oregon (Franklin and Dyrness 1988). Large, infrequent (250 to 450 years) wildfires constitute the dominant disturbance regime in the Western Hemlock zone (Agee 1993), although in some parts of the region there is increasing evidence for a more diverse fire regime (Tepley 2010), and large windstorms and volcanic eruptions can also occur (Harcombe et al. 2004; Yamaguchi 1986). Over the last millennium, large wildfires in this region have created numerous age classes of forests dominated by Douglas-fir, western hemlock, and other conifers (Franklin and Dyrness 1988; Agee 1993, 1998; Agee and Krusemark 2001). Many of these originated following a single fire event, with little evidence of subsequent disturbance of sufficient size or intensity to allow for establishment of relatively shade-intolerant Douglas-fir (Isaac 1949; Herman and Lavender 1990).

Study sites

The forests sampled were distributed between 47.95 and 44.27 N latitude along the western slope of the Cascade Range, except for one stand located in the eastern Olympic Mountains Washington (Table 1) (Fig. 1). Forests occurred on relatively moist sites and are classified by the *Tsuga heterophylla*/*Polystichum munitum*, *Tsuga heterophylla*/*Polystichum munitum*/*Oxalis oregana*, and the *Tsuga heterophylla*/*hododendron macrophyllum*/*Gaultheria shallon* plant associations within the Western Hemlock Zone (Franklin and Dyrness 1988). One site (Huckleberry) occurred in the cooler, moister Pacific Silver Fir Zone, classified under the *Abies amabilis*/*Vaccinium alaskaense* plant association (Franklin and Dyrness 1988). The climate is maritime with cool wet winters and warm dry summers (Table 1). Common tree associates of Douglas-fir include western hemlock, western redcedar (*Thuja plicata* Donn ex D. Don), western white pine (*Pinus monticola* (Dougl.), Pacific silver-fir (*Abies amabilis* (Dougl. ex. Loud) Dougl. ex Forbes), Pacific yew (*Taxus brevifolia* nutt.), noble fir (*Abies procera*), big-leaf maple (*Acer macrophyllum* Pursh), and Pacific dogwood (*Cornus nutallii* Aud.).

Site selection

Candidate sites were carefully examined and excluded if there was evidence of post-initiating disturbance (fire or wind) that could have facilitated subsequent establishment of Douglas-fir. Fine-scale disturbances (root rot, bark beetles, or wind) that affected individual trees or small clusters of trees (creating canopy gaps) were evident in most stands and were not used as criteria for rejection.

Sample sites were of two types: (*i*) early old-growth stands sampled using multiple temporary plots and (*ii*) mature stands sampled using permanent plots that were established decades before this study (http://andrewsforest.oregonstate.edu/). Sites sampled with temporary plots (n = 9 sites) were established following a review of fire-history studies (Morrison and Swanson 1990; Agee 1991; Impara 1997; Weisberg and Swanson 2003), stand age-class maps, and conversations with several ecologists familiar with the region (personal communications with Ken Bible, Rolf Gersonde, Scott Gremel, Charles Halpern, Jan Henderson, Robin Lesher, Robert Van Pelt), and extensive reconnaissance.

Nine additional sites were selected from an established network of permanent sample plots (hereafter, PNW-PSP) (Acker et al. 1998). Plots were selected from this network based on approximate age (100–200 years), dominance by Douglas-fir, and lack of evidence of disturbances post canopy closure. Forests originated from stand-replacing disturbances, varied in age, and were distributed over a broad latitudinal range (Table 1).

Several sites were located close enough to have regenerated after the same wildfire. Drift Creek, Osprey, Skynard Hill, and Cedar Flats lie within 10 km of each other in the central Lewis River Valley in the southwest Washington Cascades and evidently established after large-scale fire ca. 1800. Stands WR04, WR05, WR90, and Meditation Rock lie within 8 km of each other in the Panther Creek Division of the Wind River Experimental Forest. Although these sites may be considered pseudoreplicates (Hurlbert 1984), given the variability in fire severity and site conditions within a large wildfire it is unlikely that the two samples represent the "same" fire. Furthermore, understanding the variability created by single large-scale disturbances remains valuable (Turner et al. 1997; Larson and Franklin 2005).

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Table 1. Site characteristics for sampled stands.

SITE	Lat.	Long.	Elevation (m)	Max. stand age (year)	Douglas-fir density (%)	Douglas-fir basal area (%)	Annual precip. (mm)	July mean precip. (mm)	Jan Mean Precip (mm)	July max temp. (°C)	Jan min temp (°C)	Growing season mean precip. (mm)
Olympic National Park, Washington												
1 Sol Duc	47.95	–123.81	687	317	31	71	3622	61	483	20.3	–1.2	80.0
Cedar River Watershed, Washington												
2 Huckleberry	47.31	–121.52	799	328	16	25	2584	62	397	21.0	–2.9	74.7
Mt. Rainier National Park, Washington												
3 AX15	46.75	–121.82	1024	183	27	42	2099	44	318	22.4	–3.4	62.6
4 TB13	46.74	–121.84	1018	213	52	31	2004	43	296	22.2	–3.6	61.1
5 Ohanapecosh	46.74	–121.55	670	296	25	47	1974	35	306	23.9	–3.9	46.61
Gifford Pinchot National Forest, Washington												
6 Cedar Flats	46.11	–122.01	400	191	2	64	2972	45	455	25.2	–1.9	64.5
7 Drift Creek	46.03	–122.09	324	193	54	81	2990	46	455	24.6	–1.2	65.9
8 Osprey	46.03	–122.08	318	190	37	83	2995	46	456	24.9	–1.1	66.1
9 Skynard	46.02	–122.08	379	193	31	82	3339	51	526	24.0	–1.4	71.1
10 WR90	45.88	–121.90	715	171	33	86	2704	27	450	23.2	–2.7	43.8
11 WR05	45.84	–121.87	365	177	45	88	2506	21	399	26.9	–2.0	39.7
12 WR04	45.83	–121.87	315	168	35	91	2508	21	397	26.8	–2.0	40.1
13 Meditation Rock	45.49	–121.48	823	192	87	98	1226	22	194	22.5	–4.1	21.8
14 Goshawk	45.80	–121.97	494	114	85	98	1081	25	190	25.3	–3.7	17.4
Mt. Hood National Forest, Oregon												
15 MH123	45.31	–121.91	605	130	46	91	2259	45	325	23.2	–2.6	63.2
Willamette National Forest, Oregon												
16 Bagby	44.94	–122.17	650	297	27	66	2123	31	301	24.1	–2.4	51.7
17 Breitenbush	44.79	–121.90	760	326	32	77	1997	33	304	24.7	–3.8	45.5
18 RS26	44.27	–122.18	990	174	39	93	2130	28	288	27.5	–1.5	46.8

Note: Site numbers correspond to Fig. 1. Climate data from PRISM (Daly et al. 2002).

Field procedures for temporary plots

Sampling was conducted between June and September during 2006–2010. In each stand, six 0.2 ha circular plots were established at 100 m intervals along a linear transect. Transects were initiated from a random starting point after stand shape, boundaries, and transect azimuth were determined. Within each plot, all trees ≥5 cm dbh were identified by species, and diameters were measured 1.37 m above the base of the tree. Douglas-fir was an abundant component of the overstory in each site, indicating that Douglas-fir dominated the tree establishment phase (Table 1). Depending on Douglas-fir density in each circular plot, 6–10 live Douglas-fir were subjectively chosen for aging to represent the full range of size classes (and presumably ages). To determine that the size distribution of aged trees was representative of the larger measured population, we used a series of Kolmagorov–Smirnov (K–S) tests; all tests confirmed that there were no significant differences among cored tree diameter distributions and the remaining Douglas-fir diameter distribution.

All cores were taken at breast height (1.37 m). Although cores taken closer to the ground surface may improve the accuracy of aging, they are more difficult to obtain and more likely to include butt rot. Each core was visually inspected to determine if pith was reached. If pith was not reached and the core did not contain the majority of inner-most rings, a second core was taken. Time and labor constraints limited additional coring beyond two cores per tree. If a suitable core was not obtained after two attempts, an alternate tree of similar diameter was sampled. Cores were placed in paper straws, labeled, and stored in a waterproof container for subsequent laboratory analysis.

Field procedures for permanent plots

Based on existing diameter data for Douglas-fir, a stratified random sample was used to select trees for aging. Diameter distributions were stratified using 15 cm diameter bins, and 40%–60% of individuals per diameter bin were selected for coring. Methods for obtaining increment cores were the same as described for temporary plots.

Laboratory methods for aging increment cores

All increment cores were prepared using standard dendrochronological techniques (Stokes and Smiley 1968). All cores were mounted on grooved wooden boards and sanded three times at progressively finer grit (100, 220, and 400). Cores with narrow growth rings required additional sanding at 600 and 800 grit. Annual rings were counted with a microscope (3×); cross-dating was not attempted because it was not relevant to the study objectives. While cross-dating is essential for determining accurate pith dates for some species and growing conditions, we evaluated that it was not necessary for the Douglas-fir on moderately productive sites in the current research. A study by Weisberg and Swanson (2001) showed that for Douglas-fir samples, pith dates determined by careful laboratory ring counts on well prepared surfaces were very close to (mean difference of 1.24 years) pith dates determined by cross-dating the samples. To estimate the number of rings missing in cores that lacked a pith, we used a transparent template containing concentric circles that best fit the growth pattern present in the inner core (Applequist 1958). We examined height–growth curves for Douglas-fir in conjunction with a site productivity table (McArdle et al. 1961) to estimate age to core height. Seven to nine years were added to each site for the core height correction. The ring count, estimate of rings to pith, and estimate of age to core height were summed to obtain an estimated total age for each tree. Summed ages represent age at sample year.

Analyses

The following summary statistics were calculated for aged Douglas-fir trees at each site: age range (including 95% confidence intervals [CI]), duration of establishment for 90% of the aged trees (including 95% CI), minimum age, maximum age (as an estimate of cohort initiation), and standard error of age, to address question 1. A frequency distribution was then created for each site; 10 year age bins were used to facilitate comparison with previous studies of Douglas-fir age structure (Klopsch 1985; Stewart 1986; Huff 1995; Tepley 2010) and to assess the pace of establishment by decade.

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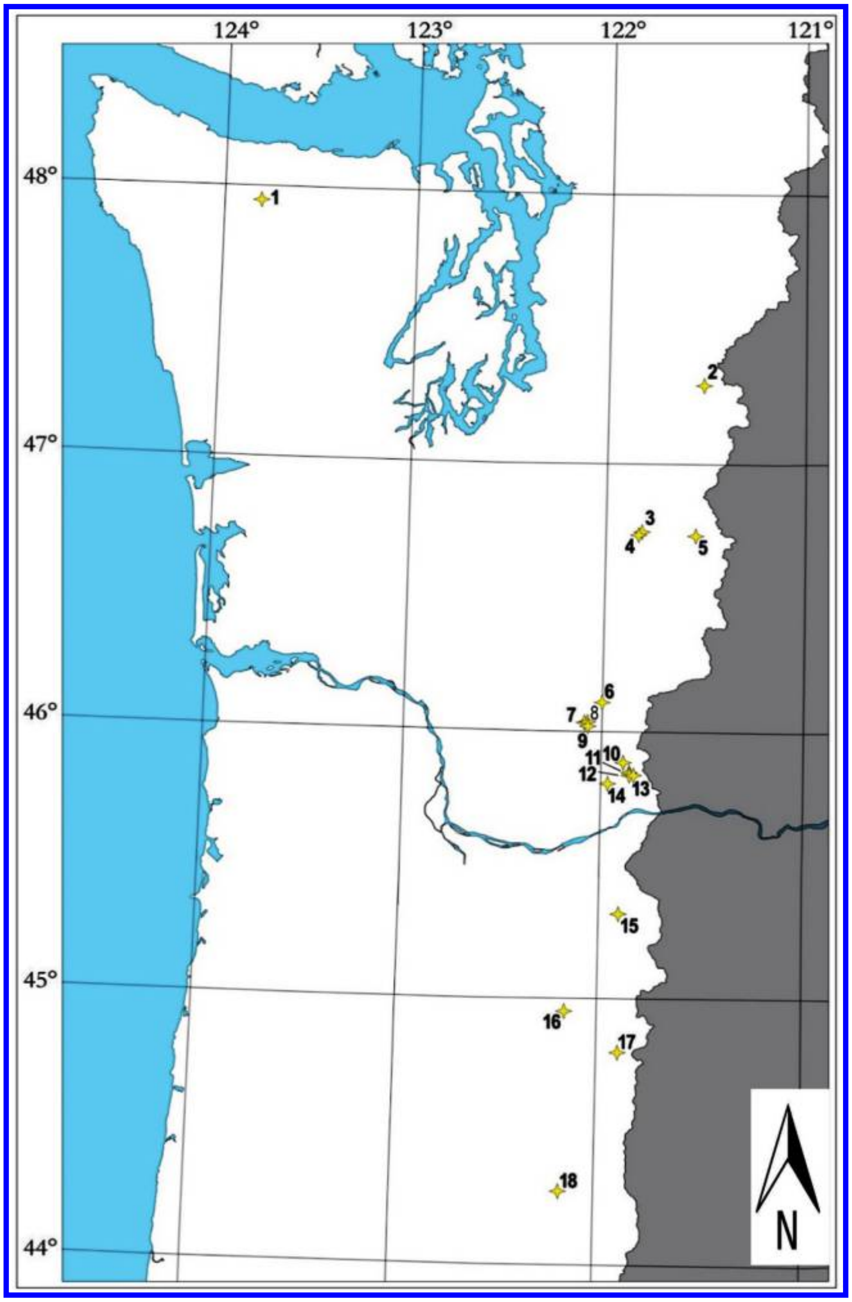
Fig. 1. Map of Washington and Oregon with study locations marked with a yellow stars. Dark grey portion represents the crest of Cascade Mountains.



Cumulative age distributions (as cumulative proportion of establishment) were developed to compare establishment patterns among sites (question 2). Although the total duration of tree establishment was of primary interest, the period representing 90% of individuals was also a useful metric for assessing the rapidity of conifer establishment.

Cumulative age distributions among sites were quantitatively compared using nonlinear regression. Data were fit to sigmoidal models using SigmaPlot Version 11.0 (Systat Software, Chicago, Illinois, USA). Parameter estimates representing time to 50% establishment and slope were evaluated to quantify inter-site variation.

Pearson correlation analyses were performed to explore whether associations existed between environmental variables and duration of establishment. Correlation matrices were created for extrinsic environmental variables of latitude, elevation, aspect, mean annual precipitation, mean July precipitation, mean January precipitation, mean growing season precipitation, maximum July temperature, and minimum January temperature. Pearson correlations were also performed on some stand variables of Douglas-fir to explore biotic controls on establishment.

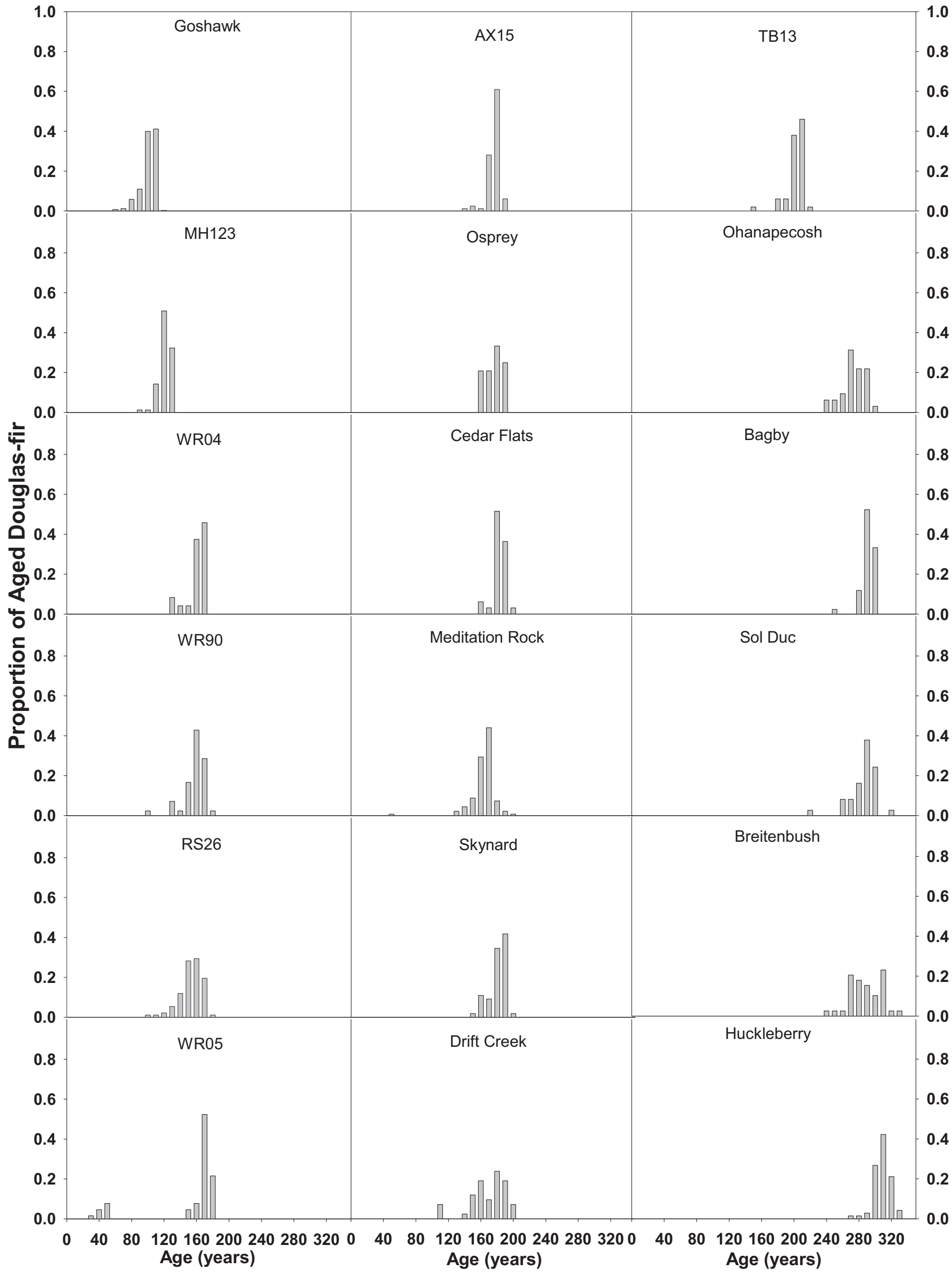
Maximum age in each stand, percentage of the Douglas-fir population aged, percentage Douglas-fir density, and percentage Douglas-fir basal area were used as biotic correlates. Pearson correlation analyses were also performed using the parameter estimates (X0, b) derived from the sigmoid regression with the same set of environmental and stand variables to assess the shape of the curve of tree establishment.

Results

Age ranges

Duration of establishment averaged 60 years (95% CI of 50–70 years) and ranged from 32 to 99 years (Fig. 2). Establishment

Fig. 2. Histograms of the distribution of Douglas-fir ages in 10 year bins. Panels are arranged from youngest to oldest sites. WRO5 has 9 trees that established in a canopy gap. Meditation Rock has one individual that established in a canopy gap following canopy closure.



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periods exceeded 75 years for only three stands (Table 2). Seventeen percent of stands established within 40 years, 40% established within 50 years, and 83% established within 75 years. Most stands achieved 90% establishment of Douglas-fir several decades sooner (mean of 35 years; 95% CI of 28–42 years) than full establishment. Duration of 90% establishment ranged from 19–65 years, with 67% of stands within 40 years and 83% of stands within 50 years. At two sites, minimum and maximum ages differed by 82 (Meditation Rock) and 115 years (WR05); summary statistics are reported including and excluding these individuals, because the trees that established later represent individuals that established in canopy gaps following forest canopy closure. Canopy gaps were visually inspected during sampling and represented areas where several Douglas-fir in early stages of decay were present.

Age distributions

Sites display broadly comparable cumulative age distributions regardless of the century when establishment began (Fig. 3). Most of the variability among cumulative age distributions is found in the 12 oldest sites (Table 2); the greatest variability in age distributions is found in 6 sites with maximum ages between 183 and 213 years (SE 0.88–3.43). Sigmoid curves were well fit to the cumulative age distributions with r^2 values in the range 0.94–0.99 (Fig. 4). Parameter estimates (X0, b) were assessed to compare the point at which each site experienced a steep increase in slope. Low values for b with corresponding low values of X0 appear to indicate rapid establishment and a shorter establishment duration. Increasing values for b with corresponding increases in X0 appear to represent a process characterized by steady and gradual estab-

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Table 2. Summary statistics for Douglas-fir ages.

Maximum age (year)	Study area	Plot type	Single-cohort establishment duration (year)	Years to 90% establishment	*n*	Mean pith correction (SD)	Douglas-fir (ha)	Mean Douglas-fir DBH (SD)	Douglas-fir basal area ($m^3 \cdot ha^{-1}$)
114	Goshawk	Permanent	60	30	411	2 (2)	414	39.5 (15.0)	58.0
130	MH123	Permanent	47	22	161	3 (1)	289	51.6 (13.2)	64.5
168	WR04	Permanent	45	32	24	4 (1)	159	33.5 (30.4)	67.0
171	WR90	Permanent	75	32	43	4 (2)	163	72.8 (20.1)	72.7
174	RS26	Permanent	75	43	89	3 (2)	302	58.7 (20.6)	91.7
177	WR05	Permanent	32	19	56	2 (2)	195	63.4 (26.6)	72.2
177	WR05*		147	135	65	—	—	—	—
183	AX15	Permanent	44	19	82	3 (2)	173	47.1 (13.9)	32.8
190	Osprey	Temporary	38	34	48	4 (3)	85	93.6 (33.4)	65.3
191	Cedar Flats	Temporary	33	19	31	4 (3)	62	98.3 (25.2)	50.0
192	Meditation Rock	Permanent	67	48	135	3 (2)	212	61.68 (19.23)	64.6
192	Meditation Rock**		149	48	136	—	—	—	—
193	Skynard Hill	Temporary	47	33	52	4 (2)	65	101.4 (26.7)	56.1
193	Drift Creek West	Temporary	88	51	42	4 (2)	87	91.9 (38.1)	67.4
213	TB13	Permanent	69	25	50	3 (2)	108	70.4 (28.5)	48.8
296	Ohanapecosh	Temporary	61	49	32	5 (3))	72	81.4 (24.7)	40.7
297	Bagby	Temporary	48	19	42	4 (2)	93	87.6 (16.0)	57.5
317	Sol Duc	Temporary	99	58	37	3 (2)	118	91.0 (31.8)	86.7
326	Breitenbush	Temporary	94	65	39	4 (2)	108	95.7 (29.3)	84.5
328	Huckleberry	Temporary	64	34	71	2 (2)	74	61.9 (12.8)	23.2
	Mean Values		**60 +/− (10.1)**	**35 +/− (7.1)**	—	—	—	—	—
	(95% CI)* **		**50–70 years**	**28–42 years**	—	—	—	—	—

*Includes 9 individuals that established in a canopy gap.

**Includes 1 individual that established in a canopy gap.

***Means and 95% CIs do not include trees establishing in gaps. Pith correction represents the mean number of years added to cores from each site with the standard deviation in parentheses. Stand data for Douglas-fir trees reported in the final three columns. DBH represents diameter at breast height.

lishment. The highest values for b and X0 appear to represent an establishment process characterized by slower more gradual establishment. Parameter estimates derived from the sigmoidal regressions did not yield any statistical association with either environmental or stand level variables ($P > 0.05$) (Table 3).

Duration of establishment did not correlate with geographic location. The two shortest establishment periods (32 and 33 years at WR04 and Cedar Flats) occurred in the southern Washington Cascades and represented different wildfires. The longest establishment periods were broadly distributed over the geographic range of sites: 88, 94, and 99 years at Drift Creek, Breitenbush, and Sol Duc, respectively (Fig. 2). In addition, the second shortest and third longest establishment periods occurred in the same river valley (several kilometers apart) presumably following the same wildfire ca. 1800 (32 years at Cedar Flats and 88 years at Drift Creek); both of these forests also represent the most productive sites (site index I; Isaac [1949]).

Pearson correlations yielded no significant statistical associations between establishment duration and elevation, latitude, aspect, maximum stand age, percent of the Douglas-fir population aged, percent Douglas-fir density, percent Douglas-fir basal area, mean annual precipitation, mean July precipitation, mean January precipitation, mean growing season precipitation, maximum July temperature, and minimum January temperature ($P > 0.05$).

Discussion

The majority of Douglas-fir forests sampled in this study established within 75 years after the initiating wildfire and always within 100 years. Duration of establishment did not differ as a function of the period during which stands established, nor did it vary with any of the environmental or stand structural variables tested in the correlation analysis. Therefore, we infer patterns of single cohort establishment following high-severity wildfire were relatively similar, at least in the stands that we examined. Moreover, we conclude that stand aspect and the regional climatic gradient covered in this study do not directly influence the pattern Douglas-fir establishment. We find it interesting that establishment periods for Douglas-fir regeneration following non-stand replacement fire in the central Oregon Cascades (Tepley 2010) were found to be nearly as long as those observed in our study of stand replacement fire. These findings bolster our interpretation of a consistent range of establishment rate and suggest that regardless of high or mixed-severity wildfire, cohorts of Douglas-fir in the western Cascades establish with a similar time course (Fig. 5).

Our study appears to provide the only significant data set on single cohort establishment patterns of Douglas-fir from mature age classes of naturally regenerated forests. A few data are available from other comparable stands, a roughly 200 year old stand at Pack Forest near Mount Rainier (Kuiper 1994) with an age range for Douglas-fir > 100 years but with 70% of the stems established within 50 years, and a roughly 200 year old stand in the western Olympic Mountains (Huff 1995), indicating complete Douglas-fir establishment within 75 years. Zenner (2005) found a 46 year age range for Douglas-fir establishment in a mature single cohort Douglas-fir stand in the southern Oregon Cascade Range. Yang et al. (2005) reconstructed early-successional conditions using aerial photo interpretation and a Chapman–Richards growth function and reported establishment periods of 40–50 years in plantations located in the western Cascades of Oregon, providing further support for our interpretation of a several decade period of early-seral forest conditions.

Comparisons with conceptual models of Douglas-fir stand establishment

Douglas-fir establishment durations in this study are not well represented by any of the previously developed conceptual models. Rates of establishment observed in mature and early old-growth stands in this study contrast with the traditional model of rapid stand establishment inferred from the observations of early research foresters, such as Munger (1940), Hofmann (1924), and Isaac (1943). However, we note that their focus was actually on establishment of sufficient Douglas-fir regeneration to ultimately produce a fully-stocked stand and not on the temporal duration of

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Fig. 3. Cumulative patterns of establishment of Douglas-fir in sites of increasing age (top to bottom panels). Black vertical lines are placed at 25 years to compare with establishment rates outlined in the Franklin et al. 2002 conceptual model. Black vertical lines are also placed at 50 years to highlight establishment rates that last twice as long as or longer than suggested by the traditional model.

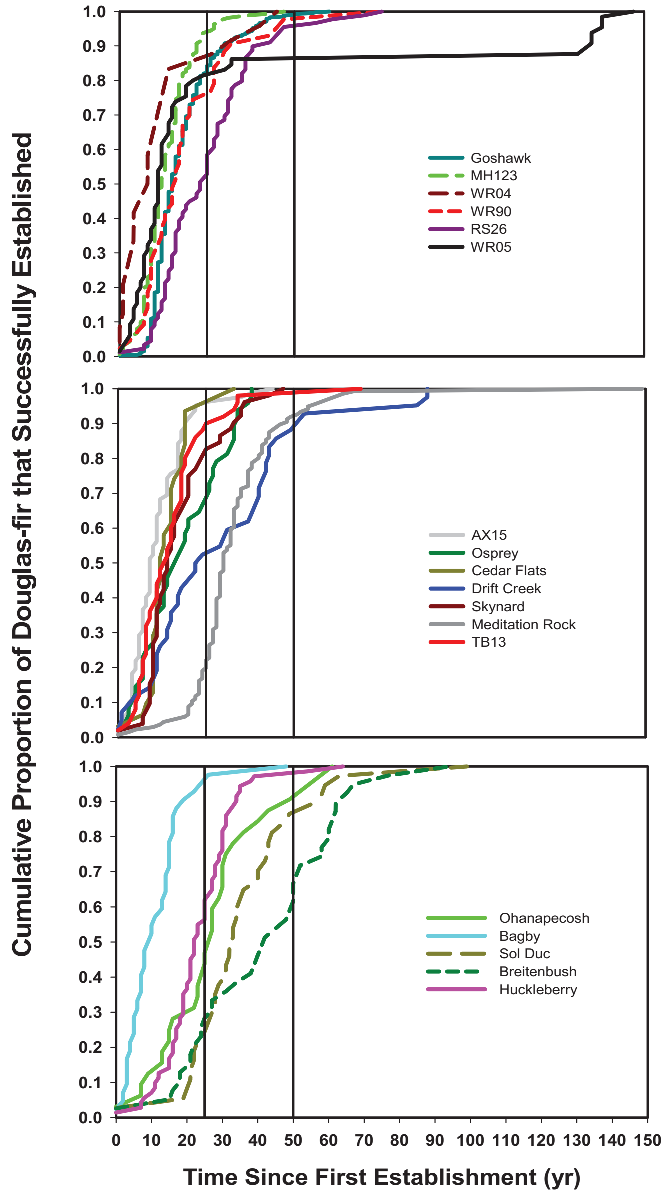


Fig. 4. Sigmoidal regression curves fit to cumulative age distributions for each sample site.

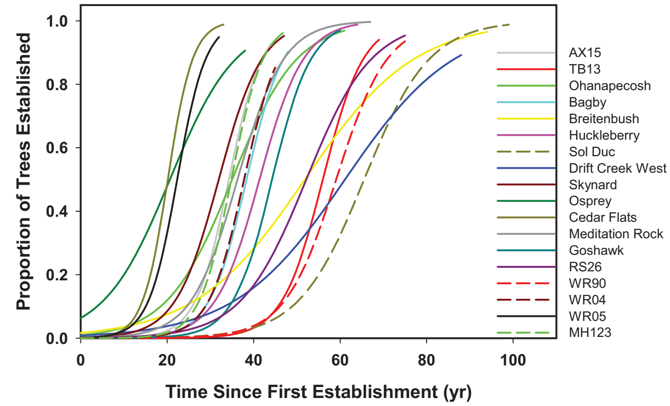


Table 3. Parameter estimates for sigmoidal regression on cumulative age distributions.

Site	Model form f = a/ (1 + exp(−(x−x0)/b)) b	x0	Adjusted R^2	*P*
Goshawk	4.51	44.29	0.97	<0.001
MH123	3.63	35.58	0.99	<0.001
WR04	4.08	37.82	0.94	<0.001
WR90	5.93	59.10	0.97	<0.001
RS26	7.55	53.18	0.98	<0.001
WR05	3.30	22.32	0.98	<0.001
AX15	3.84	34.27	0.98	<0.001
Osprey	7.66	20.63	0.97	<0.001
Cedar Flats	2.89	20.15	0.96	<0.001
Meditation Rock	5.35	36.28	0.99	<0.001
Skynard Hill	5.02	31.93	0.95	<0.001
Drift Creek	12.69	61.13	0.96	<0.001
TB13	4.70	55.99	0.98	<0.001
Ohanapecosh	7.52	35.03	0.97	<0.001
Bagby	4.30	38.36	0.97	<0.001
Sol Duc	7.57	65.56	0.97	<0.001
Breitenbush	12.67	51.85	0.98	<0.001
Huckleberry	5.10	41.35	0.99	<0.001

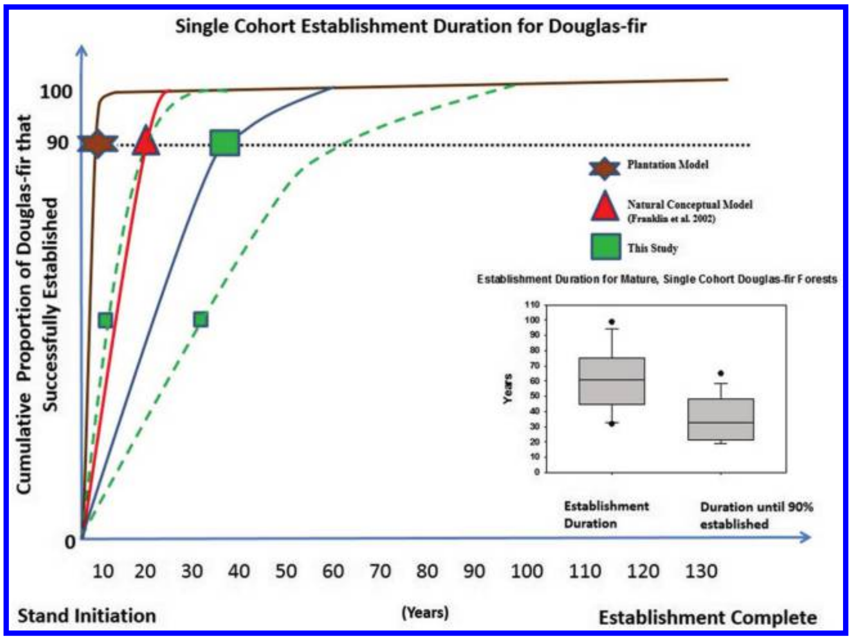
tree seedling establishment or on the rate at which forest canopies closed. This may be why their accounts of successful Douglas-fir provide no indications that regeneration may continue for many decades following a stand initiating disturbance. Therefore, rates of establishment in this study provide a useful context to compare with previous theory and observations regarding Douglas-fir establishment.

Rates of establishment in this study also contrast with descriptions of protracted, low-density establishment in older (>400 year old) forests. Douglas-fir regeneration in many older stands was interpreted as occurring over periods of more than 100 years (Hemstrom and Franklin 1982; Tappeiner et al. 1997; Poage and Tappeiner 2002). Confidence intervals (95%) for Douglas-fir establishment are between 104 and 237 years ($n = 10$) in Tappeiner et al. (1997) and Poage, and Tappeiner (2002) report 95% confidence intervals for the mean of establishment at 134–213 years ($n = 27$). The 95% confidence intervals for the mean of total establishment reported in this study (95% CI = 50–70 years, $n = 18$) clearly do not overlap with these.

Rates of establishment observed in this study contrast significantly with the model of plantation forestry. Our results suggest that persistence of open canopy conditions for several decades is common in natural forest development. In contrast, dense and uniform plantations managed for wood production are designed to achieve immediate establishment of fully-stocked stands, with canopy closure occurring within a decade or less (Smith et al. 1997).

A comparison of studies where Douglas-fir ages were used to reconstruct establishment duration indicates a complex suite of findings. In the 1970s scientists began their studies of Douglas-fir establishment by counting annual growth rings on cut stumps of Douglas-fir trees after the stands had been harvested. Their findings of age ranges spanning 1–2 centuries were inconsistent with the accepted wisdom of rapid Douglas-fir establishment and forest canopy closure, which puzzled them (Franklin and Hemstrom 1981). Subsequent studies of Douglas-fir ages in old-growth forests >400 years in Oregon also were interpreted as providing evidence of periods of establishment extending over 1 or more centuries (Stewart 1986; Tappeiner et al. 1997; Poage and Tappeiner 2002). Several hypotheses were proposed to explain these findings in-

Fig. 5. Conceptual model of single-cohort Douglas-fir establishment following high severity wildfire. The brown line represents a plantation system with synchronous establishment and rapid canopy closure (within a decade). The red line represents a developmental pathway in which establishment extends more than two decades culminating in a closed-canopy state at 25 years as suggested by Franklin et al. (2002). The solid green line represents the establishment patterns reconstructed in this study. Dashed green lines illustrate the variation in establishment duration (minimum and maximum values). The horizontal dotted line represents the time in years at which 90% of Douglas-fir have established. The box and whisker plots illustrate the variation in the duration of establishment for all trees and 90% of trees for all sites; horizontal lines represent means lower and upper boundaries representing the 25th and 75th percentiles, respectively. Whiskers represent minimum and maximum values. (See online version for colour.)



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cluding seed source limitations after the extensive fires of the late 15th and early 16th centuries, competition from hardwood shrubs and trees, and creation of opportunities for further Douglas-fir establishment by subsequent partial stand replacement disturbances. Some investigators examined the wide early growth rings in old Douglas-fir and hypothesized stand establishment to have occurred at low initial stand densities (Tappeiner et al. 1997; Poage and Tappeiner 2002). Notably, these studies were conducted in areas south and west of the study sites reported here and may reflect more frequent fire history at low elevations in the Willamette Valley and coastal ranges of Oregon than those of more northerly sites in Washington. Shorter pulses of Douglas-fir establishment were observed in two studies in Washington State, lending support for the original hypothesis of rapid forest establishment and stand closure (Yamaguchi 1986; Winter et al. 2002*a*).

Variation of study findings from old-growth forests could represent several pathways of early succession (Donato et al. 2012), or could be the result of other factors that obscure the difference between overall age structure and establishment durations. For example, subsequent disturbance including partial, stand-replacement fires may lead to multiple cohorts and periods of establishment (Tepley et al. 2013). Tepley's (2010) meticulous study of wildfire disturbances and Douglas-fir tree ages in old-growth forests in the central Cascade Range of Oregon provides strong evidence that at least some of the observed extended periods of Douglas-fir establishment represent multiple cohorts that established after partial stand-replacement fires. Another factor that could contribute to interpretations about extended periods of establishment relate to errors associated with counting rings on stumps in the field. Studies that reconstructed patterns of early development from stump counts in harvested units almost invariably involved significant errors in ring counts, which would tend to blur evidence for distinct Douglas-fir cohorts (Weisberg and Swanson 2001; Tepley 2010). When ages of cross-dated samples of old-growth Douglas-fir trees were examined in a recent study, field counts on cut stumps were conclusively found to be inaccurate and thus unsuitable for quantifying the duration of establishment (Tepley 2010). However, one study (Sensenig et al. 2013) reports that errors in counting annual rings does depend on rings per centimeter increment, and that old-growth trees consistently grew at 10 rings per centimeter.

Different study objectives, sampling procedures, and reconstruction methodologies are likely causes for some of the variability in establishment durations among multiple studies. Reconstructions of forests >500 years old require meticulous analysis that includes cross-dating (Winter et al. 2002*a*, 2002*b*; Tepley 2010), because evidence of disturbance and tree death and decay can be masked by many centuries of development. Small-scale disturbance events, which kill individual or small groups of canopy dominants, can eliminate structural features needed for accurate reconstructions of early tree establishment conditions (Gray and Spies 1997; Lutz and Halpern 2006; Kane et al. 2011) or even create entirely new cohorts. Stands that undergo gap formation created by wind, root rots, or beetles may exhibit low density recruitment of Douglas-fir. Such gap recruitment of shade-intolerant species, such as Douglas-fir, over centuries could potentially create a complex multi-modal age structure and create confusion regarding continuous establishment. Two sites included in this study (Meditation Rock, WR05) displayed recruitment of Douglas-fir, which developed in significant canopy openings after the initial cohort had closed canopy. These trees were certified as true new recruits by field observations, measurement of the snag population (data not reported) and coring, providing evidence that Douglas-fir can successfully regenerate in forests with multiple canopy gaps. Reconstructing initial periods of establishment in younger forests, as in this study, can be more accurate reconstructions of establishment than in old-growth because: (1) extensive periods of agent-based mortality, decomposition, or gap creation have not

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occurred in the forest and (2) higher quality age and ring data are more easily obtained from the smaller trees found in young and mature stages of forest development.

That said, extended (>100 year) periods of establishment can occur in Douglas-fir forests. Undoubtedly, variable rates of establishment are influenced by the extent and behavior of the initiating disturbance, presence or absence of surviving seed-bearing trees, the presence and abundance of broadleaf tree and shrub species (Franklin and Hemstrom 1981). Periods of repeated large intense wildfires might well have created areas without significant surviving Douglas-fir seed trees; such areas would initially undergo establishment of a low-density founding population, which would eventually provide a local seed source to fill in stands. Moreover, repeated wildfires occurring before an initial cohort has reached reproductive maturity may be a factor in extending establishment periods, a phenomena that has been observed in other forest systems (Larson et al. 2013). Obviously, each sere will exhibit idiosyncratic patterns, which could include such a possibility, but the probability would be low and most logically occur on very dry sites within the Western Hemlock zone (Means 1982; Tepley 2010), on very frosty sites within the Pacific Silver Fir zone (Franklin and Hemstrom 1981), on sites with multiple fires at short return intervals (Isaac and Meagher 1936; Huff 1995; Gray and Franklin 1997; Tepley 2010), and on subalpine sites (Franklin et al. 1988).

Establishment and among site variation

Cumulative patterns of establishment are generally similar in form, but the rate at which each stand established is variable (Fig. 4). Establishment rate for the majority of stands supports a general model of establishment where trees gradually but consistently establish until canopy closure occurs. The consistency with which the majority of stands follow a "steady" establishment model likely reflects a combination of availability of seed source from surviving legacy trees and competition from shrub and hardwood species (Yang et al. 2005). Some establishment rates within this data set also support alternative models. Two sites, WR05 and Cedar Flats, exhibit establishment duration and cumulative age distributions supporting a "rapid model" of tree establishment. The canopy seed bank described by Larson and Franklin (2005) could contribute to rapid and dense establishment following the stand initiating wildfire. A more "prolonged" model of establishment is also represented in this data set by the Breitenbush and Sol Duc sites,and may be the result of founding trees that become established and provide future seed source. Prolonged establishment could also occur when stands experience multiple fires within the first few decades after stand replacement events (Gray and Franklin 1997).

Establishment rates can vary even on productive sites when subjected to the same fire event, although we acknowledge that fires were not dated in this study. The second shortest and third longest durations for establishment occurred on productive sites several kilometers apart in the same river valley following what we believe was the same wildfire event. Both Cedar Flats and Drift Creek are on productive sites and Franklin et al. (2002) hypothesized that productive sites would experience canopy closure sooner than lower productivity sites. Larson et al. (2008) examined the influence of productivity on forest development and found that highly productive stands dominated by conifer species recover from disturbances more rapidly. However, the differing rates of establishment at Cedar Flats and Drift Creek support the idea that relationships between productivity and stand development, can vary greatly.

Comparison of tree establishment in Douglas-fir with other moist temperate forests

The multi-decade period of tree establishment in these Douglas-fir forests is long compared to the post-disturbance recruitment of seral tree species in other moist temperate forests. *Eucalyptus regnans* (F. Muell) forests of Australia commonly regenerate and develop closed canopies rapidly (1–5 year) following severe wildfire; by 40 years the forest is well into a thinning phase (Ashton 1976). *Quercus rubra*–*Acer rubrum* forests of central Massachusetts, as well as other forests in the northeastern United States, are dominated by angiosperms and abundantly propagate through sprouting also exhibit rapid regeneration and canopy closure following high severity wind disturbances (Cooper-Ellis et al. 1999).

Management implications

Early-seral ecosystems develop on forested sites between a stand-replacement disturbance and re-establishment of a closed forest canopy (Swanson et al. 2011). These ecosystems typically share dominance among diverse plant life forms and include individuals and groups of trees. Animal diversity is typically high and often includes species that are restricted to early-seral habitat specialists. Providing for such ecosystems is emerging as an important management goal on public lands (Franklin and Johnson 2012), but the scientific knowledge base for planning and implementing such management is limited. Specifically relevant to this study, little is known about how long such ecosystems persisted in various forest types, including those occupying the Western Hemlock Zone of the Pacific Northwest. This study provides evidence that it may not be appropriate to replant in post-wildfire landscapes where provision for earl- seral conditions is an objective.

The Douglas-fir establishment rates in naturally regenerated forests reported in this study differed dramatically from industrial plantations. Typical plantations involve intensive site preparation activities that focus primarily on planting sites at high stocking levels to achieve tree dominance and canopy closure as soon as possible (Smith et al. 1997; Curtis et al. 2007). Federal forest plantations share some characteristics of industrial plantations, however there is evidence that federal plantations can have multi-decadal establishment rates (Yang et al. 2005). The difference in timing of establishment between natural establishing stands and plantations has significant implications for many ecosystem values. Therefore, managers seeking to mimic natural process will need to consider alternatives to dense plantations. For example, when objectives necessitate mimicking natural processes, several possibilities, including reliance on natural vegetation or creating plantations that are less dense or more heterogeneous or both, may be appropriate, especially when creation of high-quality early-seral conditions is a management objective. Plantation management places a higher value on the rapid re-establishment of forest cover and generally ignores the ecological values associated with pre-canopy closure ecosystems. Policies within the National Forest Management Act of 1976 mandate that each federal forest lands have targets and strategies to replant logged over or disturbed landscapes, yet this approach may be in total opposition to stated agency goals (e.g., restoration) and management objectives, which are aimed at mimicking natural processes. These policies and associated regulations need to be addressed in specific ways to provide managers with flexibility to achieve stated goals. Ultimately, nuanced policies that recognize and provide for all successional stages are needed.

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