

Initiation of an old-growth Douglas-fir stand in the Pacific Northwest: a reconstruction from tree-ring records

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Abstract: We used tree-ring records to reconstruct the stand initiation of an old-growth Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stand in the western Cascade Range of southern Washington. All tree-ring samples were prepared and crossdated. Following a stand-replacing fire, the stand initiation period lasted from 1500 to 1540, with gradual filling-in of growing space over this period. All sampled Douglas-fir were initial colonizers, establishing (at stump-height) 1500–1521 under open conditions. A small number of the sampled western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) were also initial colonizers. Growing space filled as tree crowns widened, and by 1540, closed forest conditions had developed. At this time, Douglas-fir were spaced about 3.5 m from equivalent competitors (ca. 800 trees/ha). In the centuries following canopy closure, considerable natural thinning of the initial colonizers occurred, but the canopy never opened enough again to allow further Douglas-fir establishment. Surviving Douglas-fir developed deep crowns despite the narrow initial spacing, and without epicormic branching from the bole. Most western hemlock that were canopy trees in 1992 established after 1540, originating in the understory. This reconstruction provides an example that may be useful where management policies emphasize the development of old-growth structures.

Résumé : Nous avons utilisé des séries dendrochronologiques pour reconstituer l'initiation d'une forêt ancienne de douglas (*Pseudotsuga menziesii* (Mirb.) Franco) dans la partie ouest de la chaîne des Cascades dans le Sud de l'État de Washington. Tous les échantillons de cernes ont été préparés et synchronisés. À la suite d'un feu qui a entraîné son remplacement, la période d'initiation du peuplement s'est étendue de 1500 à 1540, avec un remplissage graduel de l'espace de croissance pendant cette période. Tous les douglas échantillonnés faisaient partie des premiers colonisateurs qui se sont établis (à hauteur de souche) entre 1500 et 1521 dans des conditions de couvert ouvert. Un petit nombre de tiges parmi les pruches de l'Ouest (*Tsuga heterophylla* (Raf.) Sarg.) échantillonnées faisaient également partie des premiers colonisateurs. L'espace de croissance s'est rempli alors que la cime des arbres prenait de l'ampleur et le couvert forestier s'est refermé aux alentours de 1540. A cette époque, les douglas étaient espacés des compétiteurs équivalents d'une distance approximative de 3,5 m (environ 800 arbres/ha). Dans les siècles qui ont suivi la fermeture du couvert, il y a eu une autoéclaircie considérable parmi les premiers colonisateurs mais le couvert ne s'est jamais suffisamment ouvert pour permettre l'établissement d'autres douglas. Malgré l'espacement initial très limité, les douglas qui ont survécu ont développé des houppiers relativement longs et sans gourmands le long du tronc. La plupart des pruches de l'Ouest qui faisaient partie du couvert en 1992 se sont établies après 1540, en se développant en sous-étage. Cette reconstitution fournit un exemple qui pourrait être utile lorsque les modalités d'aménagement mettent l'accent sur le développement de structures de forêt ancienne.

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Introduction

In the Pacific Northwest, several studies have suggested that the stand-initiation stage of existing old-growth Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests differed substantially from that of most modern young (ca. <100 years) naturally regenerated and planted Douglas-fir

stands (Franklin and Waring 1980; Franklin et al. 1981; Franklin and Hemstrom 1981; Stewart 1986; Oliver and Larson 1990; Yamaguchi 1993; Tappeiner et al. 1997). The possibility of differing early histories for old-growth compared with young stands is of particular concern for the management of young forests in this region. Decades of logging in the Pacific Northwest has transformed once exten-

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sive tracts of old-growth Douglas-fir forests to landscapes dominated by younger forests intermixed with scattered remnants of old stands (Marcot et al. 1991; Lehmkuhl and Ruggiero 1991). This conversion from old to young forests has caused widespread changes in habitats, in the abundance of many terrestrial and aquatic species (Thomas et al. 1993; FEMAT 1993), and in a variety of ecological functions such as nutrient and water cycling (Harr 1986; Harr and Coffin 1992; Jones and Grant 1996). The ecological, social, and economic consequences of this large-scale forest transformation have generated intense controversy, leading to management policies with increased emphasis on maintaining existing old-growth forests and eventually developing old-growth forests from currently young and mature forests (Thomas 1991; Thomas et al. 1993; FEMAT 1993; Aubry et al. 1999). In response to current policies, Pacific Northwest forest managers are asking if modern young forests can develop old-growth characteristics, and if so, what silvicultural interventions may be required (e.g., McComb et al. 1993; Kohm and Franklin 1997; DeBell et al. 1997; Tappeiner et al. 1997; Aubry et al. 1999). Information concerning the stand initiation of old-growth forests will help answer such questions.

Stand initiation is the period following a stand-replacing disturbance when trees and other plants colonize and expand on a relatively treeless site until available growing space is re-occupied and the establishment of new individuals becomes limited (Oliver and Larson 1990). During this period, tree growth is relatively unrestricted by shade from above or from the side, i.e., "open-growth" conditions exist. The timing and spatial patterns of tree invasion during stand initiation will leave structural imprints that persist for many decades. For example, spacing trials show that trees planted at wider initial spacings develop larger crowns and diameters, for at least several decades, than do trees planted at the same time at narrower spacings (Curtis and Reukema 1970; Reukema 1979; Smith and Reukema 1986; Oliver et al. 1986; Oliver and Larson 1990). Given the potential long-term consequences of stand initiation, knowledge of the patterns of initial tree invasion and growth in existing old-growth stands can provide a guide for managing young stands to develop old-growth structures.

The most frequently documented difference between the initiations of existing old versus young stands concerns the length of time that Douglas-fir took to colonize a site following a stand-replacing disturbance. The length of this period, herein referred to as the interval of initial establishment, is reflected in the width of the earliest peak in a distribution of ages. In modern young naturally regenerated stands, Douglas-fir commonly established over a fairly narrow interval (5–22 years; Oliver and Larson, 1990; Tappeiner et al. 1997). In contrast, tree-ring reconstructions of old-growth stands showed Douglas-fir to have very broad intervals of initial establishment (100–265 years; Franklin and Waring 1980; Franklin and Hemstrom 1981; Stewart 1986; Yamaguchi 1993; Tappeiner et al. 1997). The studies first indicating such broad intervals came as a surprise, since it had been previously assumed that colonization occurred rapidly following catastrophic fires or other stand-replacing disturbances (Munger 1940; Franklin and Waring 1980; Franklin and Hemstrom 1981). Only one previous study has

reported intervals of Douglas-fir initial establishment less than 100 years for stands meeting the definition for old-growth Douglas-fir forests (40–180 years for four stands; Yamaguchi 1993).

A second suggested difference between the stand initiations of currently old versus young stands concerns the initial spacing of Douglas-fir. Previous studies and reviews have proposed that Douglas-fir in old-growth stands established at much wider spacings than did trees in contemporary young natural or planted stands (Franklin et al. 1981; Oliver and Larson 1990; Tappeiner et al. 1997). Franklin et al. (1981) notes that the broad intervals of initial establishment reported for most reconstructed old-growth stands provide some evidence of wide initial spacing. Tappeiner et al. (1997), based on reconstructions from tree-ring records, concluded that trees in old-growth stands in the Oregon Coast Range regenerated at much wider spacings and over more prolonged intervals than did trees in nearby naturally regenerated young stands. Two reviews hypothesized wide initial spacings in old-growth stands based on the structure of the Douglas-fir trees and on inferences about how that structure might have developed (Franklin et al. 1981; Oliver and Larson 1990). Douglas-fir trees in old-growth stands are commonly 1–2 m in diameter and 50–90 m tall with very long, large, and complex crowns covering over half the length of the bole (Pike et al. 1977; Franklin et al. 1981; Massman 1982; Franklin and Spies 1991). Oliver and Larson (1990) suggested that stands containing very large old Douglas-fir may be special cases of stands that began at wide spacings. This suggestion was based on the observation that closely spaced trees have reduced diameter growth and become subject to buckling or tipping when the trees grow tall.

Franklin et al. (1981) hypothesized wide initial spacing in old-growth stands based on the contrasting crown structures of Douglas-fir in old-growth compared with young stands. In typical, closely spaced young stands, Douglas-fir generally have short crowns with structurally simple live branches confined to the upper one-third to one-quarter of the bole. Franklin et al. (1981) proposed that the long crowns of Douglas-fir in old-growth stands may have developed from establishment at wider spacings than in modern young stands, which allowed live branches to persist lower in the crown than if trees had been narrowly spaced. It was further suggested that if this inference were correct, Douglas-fir in many existing young stands may not develop crowns similar to those of Douglas-fir in existing old-growth stands. The authors also speculated that epicormic branching may be a factor important in the development of the large crowns. Discussions since the 1981 paper have led its authors to favor the epicormic branch theory over the theory of wide initial spacing to explain the development of the large and complex crowns. However, no previous study has documented the development of a Douglas-fir crown for a tree in an old-growth stand.

Although the bulk of existing evidence suggests that Douglas-fir in old-growth stands colonized at much wider spacings and over much longer time intervals than did Douglas-fir in modern young stands, none of the previous reconstructions had the express objective of addressing the stand initiation period per se. Uncertainties remain about

some details of this early phase of development for old-growth stands. For example, it is not clear whether Douglas-fir in the old-growth stands established only during an initial period with open-growth conditions or additionally in response to later canopy disturbances. Further, information is generally lacking regarding the timing of establishment for western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) during the stand initiation, the height-growth characteristics of Douglas-fir, and development of the deep Douglas-fir crowns. This last point may be of particular concern for management emphasizing the development of old-growth structures, since the large complex Douglas-fir crowns are important to many distinctive functions of old-growth forests (e.g., Pike et al. 1977; Franklin et al. 1981; Franklin and Spies 1991).

The current study used the tree-ring record (e.g., Henry and Swan 1974; Oliver and Stephens 1977; Stewart 1986; Maguire and Hann 1987; Fastie 1995) to investigate the stand initiation phase of an old-growth Douglas-fir stand, named “Yellowjacket”, in the Gifford Pinchot National Forest in the Washington Cascades. To address some of the existing uncertainties, we asked the following 4 questions: (i) what was the duration of Douglas-fir colonization following a stand-replacing disturbance, and did western hemlock successfully establish concurrently with the Douglas-fir; (ii) what was the mean initial spacing of Douglas-fir, and how does it compare with currently young stands; (iii) what was the history of early development for the large (long) Douglas-fir crowns; and (iv) was there a single standwide period of relatively open-growth conditions, and if so, how long did it persist?

Study area and forest type

This study focuses on forests dominated by Douglas-fir and western hemlock in the Western Hemlock Zone of western Washington and Oregon (Spies and Franklin 1989; Franklin and Dryness 1973). These forests are referred to herein as “Douglas-fir forests”, although western hemlock is the climax species. In this forest type, Douglas-fir acts as a long-lived, relatively shade-intolerant pioneer. Western hemlock is the primary shade-tolerant tree species. Stands up to ca. 100 years are considered to be ecologically young, and those ca. 100–200 years are considered to be ecologically mature (Franklin et al. 1981). Stands older than ca. 200 years generally share the following suite of structural features that broadly distinguish them as old-growth Douglas-fir stands (Franklin et al. 1981; Spies and Franklin 1988; Franklin and Spies 1991; Marcot et al. 1991): (i) large and old live Douglas-fir trees with typically deep crowns; (ii) shade-tolerant trees (primarily western hemlock) with a wide range of diameters, heights, and ages; (iii) large snags and downed logs; and (iv) spatial variability, i.e., “patchiness”, in structural characteristics.

Methods and rationale

Yellowjacket study site

Physical environment of study stand

The Yellowjacket study site (46°21.7'N, 121°51.5'W, 670–730 m above sea level) was established in a pre-harvest timber sale (Gifford Pinchot National Forest) in an old-

Fig. 1. Map showing the locations of the Yellowjacket study site, the DEMO sites (Butte, Paradise Hills, and Little White Salmon), and the Wind River spacing trials.



growth Douglas-fir stand in the Cascade Mountains of western Washington (Fig. 1). The stand was free of intrusive management before it was clearcut in 1992 for the timber sale. The Douglas-fir site index (m at 50 years) at Yellowjacket is 32 m, as evaluated from reconstructed height growth curves (this study). Mean annual precipitation is ca. 244 cm, with most falling November to May. Winter (January) and summer (July) temperatures range from -7 to 22°C , respectively (Gifford Pinchot National Forest 1971a; Phillips 1972). The soil is well drained, derived primarily from volcanic ash and pumice (Gifford Pinchot National Forest 1971a, 1971b). A soil pit at the base of a Douglas-fir revealed that the bulk of the roots near the bole were buried by an average of about 0.6 m of accumulated material (Winter 2000). There was abundant charcoal surrounding the roots but not above them.

Vegetation

Prior to cutting of the timber sale in 1992, Yellowjacket was a typical old-growth Douglas-fir stand for the area, as determined by comparison with data from Spies and Franklin (1991) and observation by experienced researchers. The main canopy at Yellowjacket was dominated by Douglas-fir and western hemlock. Douglas-fir were the tallest trees, ca. 65 m, with live crowns covering approximately half the total tree height. The crown forms (length and width) of Douglas-fir were fairly homogeneous across the live stand; however, the western hemlock were irregular in height and crown form. The canopy was fairly closed, with occasional small gaps. Densities of all live Douglas-fir and of live western hemlock ≥ 40 cm diameter at breast height (DBH; 1.4 m) were 14 and 73 trees/ha, respectively. Maximum diameters for these species were 190 and 146 cm, respectively (Fig. 2). Snags and logs of all decay classes were abundant. These were mostly Douglas-fir and western hemlock, but there were also few large western white pine (*Pinus monticola* Dougl. ex D. Don) snags. The understory was dominated by western hemlock, Pacific yew (*Taxus brevifolia* Nutt.), vine maple (*Acer circinatum* Pursh), Oregon grape (*Berberis nervosa* Pursh), and sword fern (*Polystichum munitum* (Kaulf.) Presl). Conifer seedlings and saplings were predominantly western hemlock; Douglas-fir regeneration was absent.

Pre-harvest fieldwork

All live Douglas-fir, all live western hemlock ca. ≥ 40 cm DBH, and all snags within a 3.3-ha study plot were tagged

Table 1. Number of trees, by category, for which stump-samples were collected, evaluated, and centre dates determined.

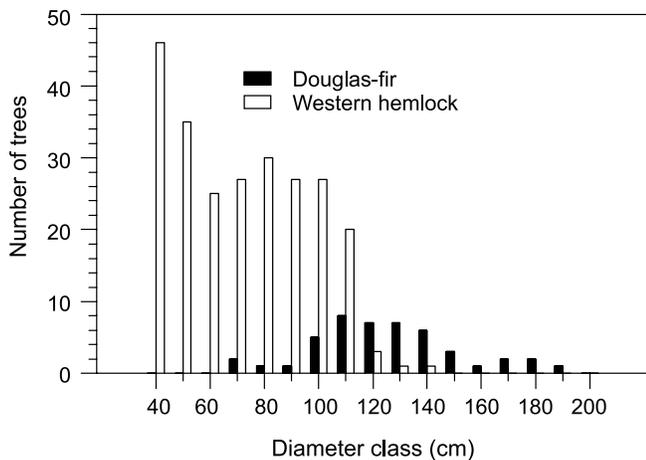
Category of tree	Present in plot	Stump-sample collected and evaluated	Exact, estimated, or missing centre date assigned			Total dates assigned
			Missing >1 cm centre: no centre date	Pith present: exact centre date determined	No pith, ≤1 cm centre missing: centre date estimated	
Douglas-fir, live in 1992	46	45 [†]	2	42	1	43
Douglas-fir snag	74	16 [†]	1	15	0	15
Western hemlock, live ca. >40 cm DBH*	254	224 [†]	52	165	7	172
Western hemlock snag	44	4 [†]	1	2	1	3
Western white pine snag	3	1 [†]	0	1	0	1
Snag, species not identified	110	0 [†]	0	0	0	0

Note: Snags were sampled only if they had a sufficient amount of sound wood.

*Twelve western hemlock slightly <40 cm DBH were sampled and evaluated.

[†]One live Douglas-fir was not sampled, because it was not felled. Thirty live western hemlocks ≥40 cm DBH were not sampled and evaluated because of post-logging conditions or because of tree rot.

Fig. 2. Diameters (DBH) of all live (in 1992) Douglas-fir ($n = 46$) and of live western hemlock ≥40 cm DBH ($n = 242$). Twelve western hemlock with diameters slightly <40 cm were sampled and evaluated (Table 1) but are not shown here. The values for the diameter classes are the bottom of each class.



and inventoried prior to the stand's harvest. The 40 cm lower limit for the western hemlock was judged sufficient to meet the study objectives. The following were recorded for each tree: species, DBH, crown class (if live), decay class (if dead), and the presence of major scars and growth anomalies. All tagged live Douglas-fir and western hemlock were main canopy trees.

Post-harvest fieldwork

After the stand was cut, several types of samples were taken from the tagged stems.

(1) Stumps

The stumps of most live (in 1992) Douglas-fir, most live western hemlock ≥40 cm DBH, and some snags were sampled for reconstructing establishment dates and diameter growth (see Table 1 for numbers of samples). For each of these stumps, a level plunge-cut was used to take a sample from a representative radius at about 0.8 m above the 1992 ground level (i.e., "stump-height"; Winter 2000). Each sample included a full radius, i.e., the wood from pith (if pres-

ent) to bark; in a few cases embedded branches were also fortuitously included. Samples taken in this way are herein referred to as "stump-samples".

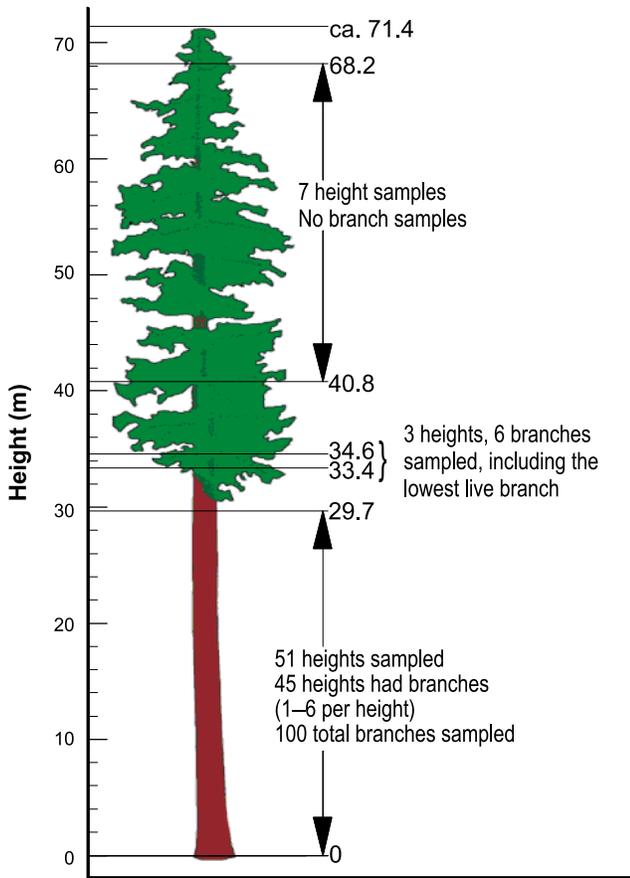
(2) Dissected Douglas-fir

Twenty dominant Douglas-fir were sampled at multiple heights (including stump-height). Each sample was cut from the bole at a measured height (relative to stump-height) and contained a full bole radius. These trees, herein referred to as the "dissected Douglas-fir" were selected as those dominant Douglas-fir that were accessible after the timber sale was felled. The selected Douglas-fir were at locations scattered throughout the stand and had been visually representative of dominant Douglas-fir in the stand, as determined from notes made prior to felling. These 20 dissected trees were sampled at 3 intensities that complemented one another for the analyses of initial spacing and crown history: intensively (1 tree), partially (10 trees), and minimally (9 trees).

Intensively dissected Douglas-fir No. 1408

For one dominant Douglas-fir, tree No. 1408 (DBH 181 cm), samples were cut from the bole at 61 heights for reconstructing the height-growth history and recession of the live crown base to the height of the 1992 crown base (Fig. 3). Wherever possible, each sample contained a full bole radius with pith, and most samples included an embedded branch. Most samples (51 heights) were taken from ≤28.3 m (above stump-height), where the bole was clear of emergent branches. 100 embedded branches were located and sampled here (from 45 of the 51 sampled heights) by splitting the large (up to 1.8 m diameter) logs along the pith. The splitting was accomplished using a hydraulic cylinder, capable of delivering up to 50 000 lb of force (1 lb = 0.454 kg), housed in a custom-designed device (Winter 2000). Between 28.3 m and the base of the 1992 live crown (33.2 m above stump-height), we sampled more lightly, sampling only at the locations of dead branches that were emergent from the bole in 1992. The large live branch at the base of the 1992 live crown was sampled as a bole wedge that included pith and bark and contained the portion of the branch that was integrated into the bole. Above this, additional cross sections were cut for reconstructing height growth.

Fig. 3. Intensively dissected Douglas-fir No. 1408: vertical structure in 1992 and sampling scheme. Heights are relative to the stand establishment surface. In the field, sampling heights were measured relative stump-heights but are shown here corrected (+1.4 m) for distance above the stand-establishment surface (see Methods).



Partially dissected trees

The boles of 10 dominant Douglas-fir were sampled at 5–11 (mean 8) measured heights as cross sections cut at bucked lengths (log lengths cut during timber harvest). These samples were for reconstructing height histories, used primarily for the analysis of initial spacing. In a few cases, embedded branches were fortuitously included.

Minimally dissected trees

The boles of 9 dominant Douglas-fir trees were sampled at 2 measured heights (stump-height and the bucked length closest to ca. 30 m) to supplement data from the partially and intensively dissected trees, for the analysis of initial spacing.

Sample preparation and cross dating

All samples were trimmed, reinforced against breakage, and finely sanded on a cross-sectional surface until cell structure was visible, according to standard dendrochronological methods (Stokes and Smiley 1968; Ferguson 1970; Fritts 1976). For samples containing branches, the prepared surfaces showed the bole rings in cross section and the branch structure in longitudinal section (Fig. 4). All samples

Fig. 4. Sample with embedded branch. This example shows a branch integrated into the bole. On the prepared surface, the bole rings are in cross section, and the embedded branch structure is in longitudinal section. The close up shows the area over which the branch was dying. X marks (is directly to the left of) the bole ring that is the latest functionally live date (LFLD) ring, dated to 1557. Y marks (is directly to the left of) the bole ring that is the earliest dead date (EDD) ring, dated to 1560. These were identified as the LFLD and EDD rings with the aid of a dissecting microscope so that cell structures could be visualized.



were examined under a binocular microscope, and each bole ring was assigned a calendar year by cross-dating samples against master ringwidth dating series, one each for Douglas-fir and western hemlock. The master series were developed from 19 Douglas-fir and 6 of the least suppressed western hemlock by measuring ringwidths with a Henson-Bannister incremental measuring machine (accuracy ±0.01 mm) and using the program COFECHA (Holmes et al. 1986) combined with visual confirmation (Stokes and Smiley 1968; Ferguson 1970; Fritts 1976; Yamaguchi 1991).

Branch rings were only dated at their convergence with crossdated bole rings.

Evaluation of individual samples

Each crossdated sample was evaluated for the following variables, wherever applicable.

(1) Centre date (Table 1)

For 225 trees whose stump-samples had pith present, an exact stump-height centre date was assigned as the calendar year of the ring surrounding the pith. For each of 9 trees whose stump-samples were missing the centre by ≤ 1 cm, a stump-height centre decade was estimated by extrapolation. For 56 trees whose stump-samples were missing >1 cm, stump-height centre dates were not assigned. For samples taken from above stump-height, centre dates at sample heights were assigned only if the pith was present.

(2) Radius at 20 years and at the beginning of each decade

For each stump-sample, we measured the distances (± 0.5 mm) from the bole pith to the outer edge of the 20th ring from the centre, the first ring in each decade, and the 1992 ring.

(3) Branch origin: normal or epicormic

A sampled branch was determined to be a normal nodal branch if it was integrated into the bole, from pith to branch death, in an orderly manner with no evidence of epicormic processes (e.g., Blum 1963; Herman 1964). For branches that were determined to be nodal, the date of the bole centre was assigned as the date of branch origin.

(4) Date(s) of branch death (Fig. 4)

Two variables were defined to describe the interval over which a branch was dying: (i) latest functionally live date (LFLD), i.e., the latest date at which the branch was producing rings and was, hence, functionally live; and (ii) earliest dead date (EDD), i.e., the earliest date at which the branch was clearly dead. In the interval between these two dates the branch was in the process of dying, i.e., not producing observable rings but not yet clearly dead. These variables were evaluated for each sample containing a branch by examining the area where the bole rings either merged with or abutted the branch (branch–bole juncture), with the aid of a dissecting microscope so that cell structure could be observed (Winter 2000). The LFLD was identified as the date of the latest bole ring that continued without interruption from the bole into the branch, where it merged with a branch ring. The EDD was identified as the date of the earliest ring that was abruptly discontinuous with the branch at the branch–bole juncture (Andrews and Gill 1939; Maguire and Hann 1987). Between the LFLD ring and the EDD ring, there were 1–14 bole rings that tapered off at the branch–bole juncture and did not enter the branch, although they were connected to the branch edge.

Analyses for the four objectives

(1) Analysis for duration of initial establishment

Stump-height centre dates were used to approximate dates of tree establishment. These dates were not corrected for the time to reach stump-height (i.e., the height of stump-samples,

ca. 0.8 m above the 1992 ground). Thus, for this study, similar to the convention followed by Cho and Boerner (1995), establishment dates are expressed as dates at stump-height. We estimate that for Yellowjacket Douglas-fir, the decade of the centre at stump-height is the same as, or immediately follows, the decade of germination. This estimate is based on (i) the distance from the Douglas-fir establishment surface to stump-height and (ii) the time it took the Douglas-fir to grow that distance. We herein refer to the Douglas-fir establishment surface as the “stand-establishment surface”. The stand establishment surface was on average ca. 0.6 m below the 1992 ground, judging from the depth of accumulated material above the Douglas-fir roots. Thus, the distance from the stand-establishment surface to stump-height was ca. 1.4 m. Data from nearby plantations show that Douglas-fir there took an average of 4 years from planting to grow from the planting surface to 1.4 m (E. Tompkins, USDA Forest Service, Cowlitz Valley Ranger District, Randle, Wash., personal communication). Backward extrapolation of reconstructed height-growth curves for Yellowjacket Douglas-fir similarly suggest that it took these Douglas-fir ca. 3–7 years to grow the 1.4 m from the stand-establishment surface to stump-height.

For western hemlock also, this study expresses establishment dates as dates at stump-height. Western hemlock likely took longer than Douglas-fir to reach stump-height, particularly those that established much later than Douglas-fir and in the understory. In addition to being slow growing, such trees could have an interval of horizontal or sinuous juvenile growth such as found by DesRochers and Gagnon (1997) for black spruce growing in the understory. In contrast, Douglas-fir growing rapidly and in the open, such as those at Yellowjacket, would not have complex and lengthy growth in the base and buried stem.

(2) Analysis for average initial spacing of Douglas-fir trees

Rationale

The approach used for the analysis of initial spacing is based on widely accepted studies showing that DBH growth of Douglas-fir trees during the early development of a Douglas-fir stand (at least for several decades) is strongly controlled by the initial spacing of these trees (Reukema 1979; Oliver et al. 1986; Oliver and Larson 1990; Tappeiner et al. 1997). However, while diameter versus age curves for Douglas-fir are characteristic of initial spacings within a uniform site, they are not characteristic across sites of different quality (Oliver et al. 1986). For a given spacing, the time at which trees reach a given diameter varies dependent on site. To compare diameter growth curves for young Douglas-fir stands on different sites, adjustment can be made for site-dependent differing growth rates by using mean dominant tree height instead of age on the horizontal axis of DBH growth curves (for further explanation see below). Accordingly, if Douglas-fir stands with different initial spacings are monitored during their early development, and their growth trends are plotted as mean DBH (or mean DBH of dominant trees; see below) versus mean dominant tree height (instead of age) the result is a family of growth curves that are ordered according to initial spacing, independent of differences in site quality. This relationship has been demon-

strated for spacing trial results (Oliver et al. 1986; Oliver and Larson 1990) and for an extensive data set from permanent plots in Douglas-fir plantations and young naturally regenerated stands having 50-year site indices from 23 to 43 m and average initial spacings from ca. 1.6 to 5 m (Wilson 1998; Wilson and Oliver 2000). This characteristic relationship was used to allow the determination of initial spacing of Douglas-fir at Yellowjacket by comparison with data from stands of known initial spacing.

As stated above, to adjust for differing growth rates on different sites and allow comparisons of DBH growth across sites, our method uses dominant tree height on the horizontal axis of DBH growth curves of young Douglas-fir stands. Many studies have similarly used dominant tree height instead of age when comparing stand structures across sites (Cremer et al. 1982; Mitchell and Cameron 1985; Oliver et al. 1986; Oliver and Larson 1990; Wilson 1998; Wilson and Oliver 2000). It must be emphasized that this usage is most appropriate for species and during times when height growth is nearly linear, such as occurs in young Douglas-fir. This usage may seem counterintuitive, requiring further explanation. Dominant height in this usage is serving as a measure of age adjusted for site quality in young Douglas-fir stands (Oliver et al. 1986; Wilson 1998; Wilson and Oliver 2000). Dominant tree height in young Douglas-fir is influenced by the combined effects of age and site quality, is not subject to the influence of shade from above, and is relatively insensitive to initial spacing except at very close spacings or at wide spacings on poor sites (Oliver and Larson 1990; Wilson 1998).

It has been shown that for a Douglas-fir that initiates in the open, initial spacing strongly influences the overall tree proportions (i.e., tree height, crown width, and stem diameter) at crown closure, regardless of the site-determined time it took a tree to reach this point in its growth (Oliver and Larson 1990). "At crown closure, widely spaced trees are taller, their crowns are larger, and their limbs and main stems have larger diameters" compared with more narrowly spaced trees (Oliver and Larson 1990, p. 206). Because of the way Douglas-fir grows, for at least several decades following crown closure, tree proportions for a given tree height will continue to be influenced by what they were at crown closure as constrained by initial spacing, irrespective of site-determined growth rates (Oliver and Larson 1990; Wilson 1998; Wilson and Oliver 2000). For example, as noted by Wilson (1998) regarding Douglas-fir, "two stands planted at the same spacing, one with a site index of 36 and the other 30, will be essentially identical in height, diameter, crown size and other measures...when the first is 50 years old and the second is 70." Five additional points were considered for this study when making comparisons of stands and inferences about initial spacing:

(1) For the determination of initial spacing, this study focuses on the dominant Douglas-fir in a stand (or largest 250 trees/ha for the spacing trials). For a stand of a given average dominant tree height, the mean DBH of all Douglas-fir will reflect initial spacing (Oliver et al. 1986); however, the mean DBH of the dominant trees will most strongly reflect initial spacing since their growth is not reduced by shade from above (Oliver and Larson 1990; Wilson 1998; Wilson and Oliver 2000). Wilson (1998) showed that the mean DBH of the largest

250 Douglas-fir/ha, for a given dominant height, is strongly and predictably influenced by the average initial spacing of all Douglas-fir. For the current study, H is used herein to denote the mean tree height for representative dominant Douglas-fir in a stand at any given time, and D is the mean DBH for the same dominant trees. The relationship between these values is referred to herein as D versus H .

- (2) In natural stands, initial colonization occurs over an interval of time. Initial spacing is used here to refer to the local spacing experienced by an initial colonizer tree at crown closure for that tree.
- (3) For a given dominant tree height, natural stands tend to have a slightly greater mean DBH than do plantations with the same initial spacing (Wilson 1998).
- (4) The mean initial spacing determined from Douglas-fir D versus H curves was taken to represent the mean initial distance between Douglas-fir trees, or between Douglas-fir and equally strong competitors (i.e., fast-growing species), but not between Douglas-fir and weaker competitors (i.e., slower-growing species such as western hemlock and western redcedar (*Thuja plicata* Donn). Wilson (1998) and Wilson and Oliver (2000) show that in mixed species stands, the initial densities of western hemlock and western redcedar have little impact on the relationship of D versus H for Douglas-fir.
- (5) Crucial to understanding the approach used here for estimating initial spacing is the knowledge that young stands differ from mature stands with respect to the influence of site quality on D versus H curves. As explained above, in young Douglas-fir stands, where height growth is nearly linear, the shape of D versus H curves is not affected by site. However in mature Douglas-fir stands the shape will be influenced by site. As stands mature, DBH growth continues but height growth slows, with the asymptotic height dependent on site. In mature stands, dominant height on the horizontal axis will no longer allow comparisons across sites. This situation in mature stands can be seen in the study by Stout and Shumway (1982) for other species. That study calculates height versus diameter curves for the mature portion of stand growth, showing the leveling off of height growth at different asymptotic values dependent on site. We suggest that to avoid confusion it is important for the reader of the current study to realize that young stands differ from mature stands with respect to the influence of site quality on the shape of the D versus H curve. For this reason, it is important that the analysis of initial spacing compares stands prior to the stage of growth when height growth slows, while DBH growth continues. In the current study, determination of initial spacing was made from stages of growth that are within the proven range of the relationship between initial spacing and mean DBH for a given dominant height. It can be seen from examination of the growth curves for the Douglas-fir spacing trials (Oliver et al. 1986) that the reported results are for stages of growth prior to the stage when height growth slows, while DBH growth continues. Wilson and Oliver (2000) prove the relationship to a height of 30 m (for a species that attains heights of 50–90 m).

Table 2. Characteristics of DEMO stands.

Location	Elevation (m)	Stand age (years)	Tree density (no./ha)*	Douglas-fir density (no./ha)*		Mean spacing between Douglas-fir (m)	Douglas-fir site index (m at 50 years)	Major (minor) overstorey species†
				Range	Mean			
Butte	975–1280	70–80	759–1781	505–1065	798	3.5	27–32	Psme (Tshe, Thpl)
Paradise Hills	850–1035	110–140	512–1005	135–223	190	7.3	26–33	Psme (Tshe, Thpl, Abam)
Little White Salmon	825–975	140–170	182–335	107–143	124	9	30	Psme (Abgr, Conu)

Note: Data are from Halpern et al. (1999) and C.B. Halpern, personal communication.

*Trees >5.0 cm DBH. Ranges are based on mean values for each of six 13-ha treatment units composed of thirty-two 0.04-ha plots each.

†Tree species codes are as follows: Abam, *Abies amabilis*; Abgr, *Abies grandis*; Conu, *Cornus nuttallii*; Psme, *Pseudotsuga menziesii*; Thpl, *Thuja plicata*; Tshe, *Tsuga heterophylla*.

Given the above, the process for estimating the mean initial spacing of Yellowjacket Douglas-fir is summarized below.

Reconstruct a *D* versus *H* curve for Yellowjacket

The Yellowjacket *D* versus *H* values used in the analysis of initial spacing were reconstructed using data from the 20 dominant dissected Douglas-fir. The reconstruction for these trees involved (Winter 2000): (i) reconstruction of height histories (height vs. date for individual trees); (ii) reconstruction of DBH histories (DBH vs. date for individual trees); (iii) compilation of individual DBH versus height values based on data collected in first two steps above; (iv) averaging of values determined in the previous step to obtain *D* versus *H* values. These steps are further described below.

The height histories for the 20 dissected trees (i above) were reconstructed using sample heights and corresponding centre dates. The sample heights (collected relative to stump-height) were corrected for the mean distance from stump-height to the stand establishment surface (1.4 m, see Analysis for duration of initial establishment in the Methods). The level of this surface was used as a reference point because the analysis was primarily concerned with the early history of the trees. Any error in this correction (ca. <0.3 m) was insignificant in relation to the magnitudes of the reconstructed heights. To reconstruct the DBH histories for the 20 dissected trees (ii above), DBHs for the beginning of each decade in the record were determined as follows: (iia) for each tree, measure (on the stump-sample) the radius to the boundary of the first ring in that decade; (iib) double that radius; and (iic) correct for bark thickness using equations derived from Johnson (1955). Note that stump-height was ca. breast height (1.4 m) relative to the stand-establishment surface. Potential errors in this approach were negligible, and any systematic errors would tend to overestimate DBH (Winter 2000). DBH histories were similarly reconstructed for 39 additional Douglas-fir that were not dissected for height growth. These were used to show whether the reconstructed DBHs for the dissected trees were similar to those for all Douglas-fir. The height and DBH values obtained as above were compiled (iii above) to represent DBH directly as a function of height. The DBH versus height values were used either as values for individual trees, or averaged (iv above) to produce *D* versus *H* values. The resulting *D* versus *H* curve would be analogous to long-term monitoring of a permanent plot, measuring DBHs (and mean

DBH) and heights (and mean height) for the dominant Douglas-fir at regular intervals through the centuries.

Compare the Yellowjacket curve with *D* versus *H* values for dominant Douglas-fir in currently young stands of known initial spacing

The average initial spacing of the Yellowjacket Douglas-fir was considered to be most similar to that of the comparison stand whose *D* versus *H* value(s) fell closest to the Yellowjacket curve of *D* versus *H*. The comparison stands were the Wind River Douglas-fir spacing trials, and 3 natural Douglas-fir stands.

The Wind River spacing trials have been ongoing since 1925 at the Wind River Experimental Forest near Carson, Wash. (Fig. 1) (elevation 400 m, Douglas-fir site index ca. 24–29 m). These trials include 6 spacings (1.2, 1.5, 1.8, 2.4, 3.0, and 3.7 m), and have been reported as average values for size classes at 3 stand ages (29, 43, 53 years). The current study used data for the largest (DBH) 250 Douglas-fir per hectare in selected spacings (Reukema 1970, 1979; Curtis and Reukema 1970). The 3 natural stands used for comparison (Butte, Paradise Hills, and Little White Salmon; Fig. 1) are dominated by Douglas-fir; are in the Gifford Pinchot National Forest; and are part of a long-term, large-scale ecological study, the Demonstration of Ecosystem Management Options (DEMO) study (Aubry et al. 1999; Halpern and Raphael 1999; Halpern et al. 1999). These stands span a range of tree ages and densities (Table 2). Butte (ca. 70 years old) has the highest tree density of the three comparison stands (ca. 800 Douglas-fir/ha, equivalent to 3.5 m spacing between Douglas-fir) and has tree structures typical of many contemporary young natural stands in the area. Little White Salmon (ca. 140 years old) has the lowest tree density (ca. 124 Douglas-fir/ha, equivalent to 9 m spacing). For these 3 stands, the Douglas-fir height and DBH data used in the current study derive from pre-treatment measurements (taken by the DEMO study) of diameter, total height, and crown class for randomly selected trees (currently unpublished data). The numbers of dominant Douglas-fir measured by that study and used in the current study were as follows: Butte, *n* = 41; Paradise Hills, *n* = 44; and Little White Salmon, *n* = 31.

(3) Analysis for early crown development of Douglas-fir

To investigate the development of large (long) crowns in Douglas-fir, the study focused on the development of crown

length (tree top minus crown base). The crown length of a tree changes by the combined effects of tree height growth and recession of the crown base, i.e., retraction of the base above the ground as the lower branches die. For the intensively dissected tree No. 1408, height growth and recession of the crown base were reconstructed by examining graphs of data from all samples for this tree (Winter 2000). The graphed variables were centre dates, LFLDs, EDDs, and sample heights. Visual examination of these graphed data was used to determine, for a series of selected dates, the heights to the tree's top, to the "crown base 1" (definition follows) and to the "crown base 2" (definition follows). For a given date, crown base 1 is the base of the functionally live crown, defined as the height of the lowest branch that was functionally live at that date (i.e., the LFLD for the branch was at or later than the selected date). This definition placed crown base 1 at the abrupt base of a functionally live crown consisting mostly of functionally live branches. For a given date, crown base 2 is the base of the zone of dying branches, defined as the height of the lowest branch that was not yet dead (i.e., the EDD for the branch was later than the selected date). This definition places crown base 2 at the base of a zone of dying branches below crown base 1. Between crown base 1 and crown base 2, no sampled branches were functionally live; below crown base 2, all sampled branches were dead. The purpose of defining the two crown bases is to show the zone of dying branches at the base of a receding crown, such as has been observed in other studies (e.g., Andrews and Gill 1939; Maguire and Hann 1987; Kershaw et al. 1990).

Branch histories for other Douglas-fir trees

The intensive reconstruction for tree 1408 was supplemented with branch data from an additional 12 Douglas-fir trees for which a total of 28 embedded branches were fortuitously included in stump-samples or in samples from partially dissected trees.

(4) Analysis for duration of open growth conditions

Two lines of evidence were used in this study to identify whether a tree began its life in relatively open conditions or beneath a closed canopy (Lorimer et al. 1988; Lorimer and Frelich 1989):

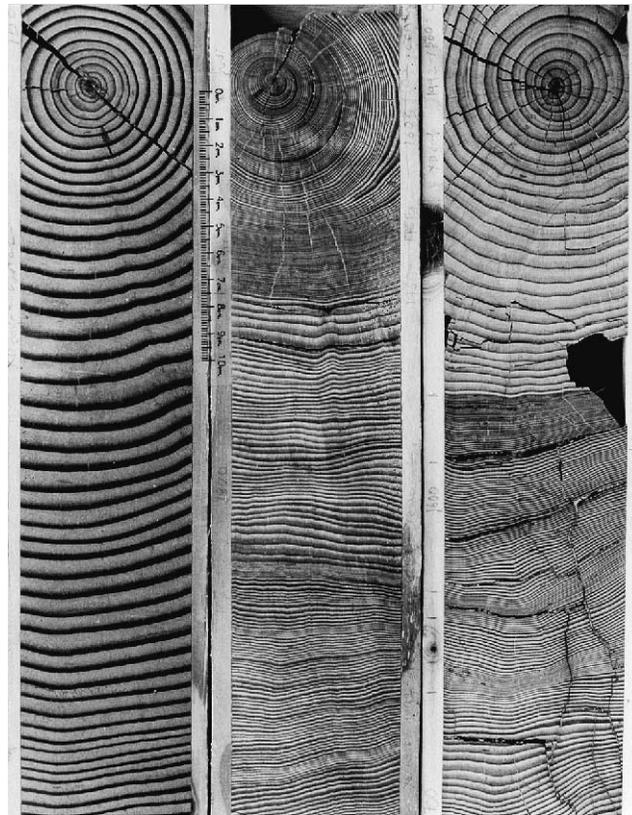
Juvenile radial growth rates

Radial growth rates of saplings growing beneath closed canopies are generally lower than radial growth rates of saplings growing in canopy openings on the same or a similar site (Canham 1985; Lorimer et al. 1988). On this basis, for the current study a scatterplot of juvenile radial growth rate (represented by the stump-height radius at 20 years, inside bark) versus establishment decade at stump-height (represented by the stump-height centre decade) for Douglas-fir and western hemlock was examined for evidence of a standwide transition from open to closed canopy conditions.

Long-term ringwidth patterns (Fig. 5)

Two types of long-term radial ringwidth patterns low on the bole (i.e., near breast height) have been interpreted as deriving from (i) tree establishment in relatively open conditions or (ii) tree establishment beneath a closed canopy of trees or shrubs (Lorimer 1985; Lorimer et al. 1988; Lorimer and Frelich 1989; Canham 1985, 1990; Fastie 1995). In an

Fig. 5. Samples with open and closed ringwidth patterns at stump-height. The leftmost sample is Douglas-fir and illustrates the open ringwidth pattern (centre date 1504). The middle sample is western hemlock and has a closed ringwidth pattern (centre date 1603). The sample on the right is a western hemlock with an open ringwidth pattern (centre date 1510). The ruler is in centimetres.



"open" ringwidth pattern, early ringwidths are wide, and there is a ringwidth peak, the highest in the life of the tree, attained within the first few decades from the pith. Subsequent to the peak, ringwidth declines gradually or abruptly. In a "closed" ringwidth pattern the early ringwidths are narrow, and there is no early ringwidth peak. The narrow ringwidths continue for many years to decades. Various "other" patterns may occur that are due to establishment under conditions other than those described above. For use in the current study, the ringwidth pattern of each stump-sample with a centre date (233 trees) was classified as open, closed, or other (Winter 2000).

Availability of study data

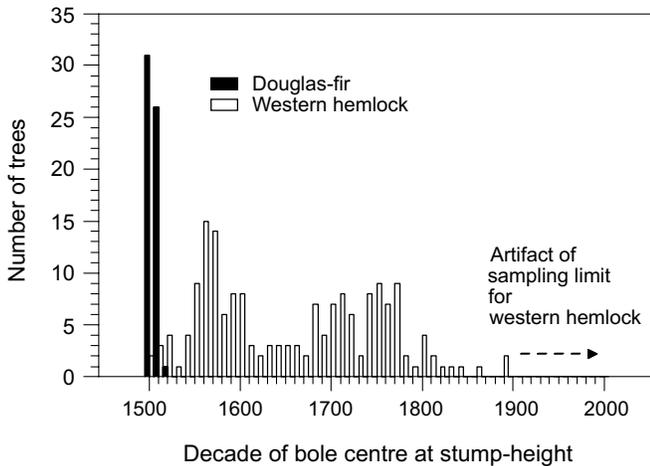
This study generated a large set of data that has been placed in the Forest Science Data Bank managed jointly by Oregon State University and the USDA Forest Service Pacific Northwest Research Station.

Results

Duration of initial establishment

The stump-height centre dates of Douglas-fir ranged from 1500 to 1521 ($n = 58$), while those of western hemlock ranged from 1508 to 1897 ($n = 175$), and the date of one

Fig. 6. Establishment history for all Douglas-fir ($n = 58$) and western hemlock (≥ 40 cm DBH, $n = 175$) with stump-height centre dates, whether live or dead in 1992 (see Table 1 for numbers of trees with stump-height centre dates). The decreasing numbers of establishment dates after ca. 1850 is an artifact of the 40 cm minimum DBH limit for sampling of western hemlock.



western white pine centre was 1507 (Fig. 6). The stump-height centres of all shade-intolerant trees (58 Douglas-fir, 1 western white pine), and 10 of the shade-tolerant trees (western hemlock) pre-dated 1540. The stump-height centres of most western hemlock (165) post-dated 1540. The decreasing numbers of establishment dates after ca. 1850 is an artifact of the 40 cm minimum DBH limit for sampling of western hemlock.

Initial spacing of Douglas-fir

Height, DBH, and D versus H histories for dissected Yellowjacket Douglas-fir

The mean height of the 20 dissected Douglas-fir increased rapidly and continuously until ca. 1550 to 1570 and more slowly after this (Fig. 7). By ca. 1600 the mean rate of height growth had slowed considerably, yet over the ensuing centuries significant additional height accrued (Fig. 7). These trees appear to have been dominant throughout their lives, as indicated by the finding that none had abrupt increases in height growth suggestive of release from a suppressed state. For each of the 9 minimally dissected trees, the single upper height versus date value fell close to the curves for the more intensively dissected trees.

For the 20 dissected Douglas-fir, the mean DBH increased rapidly until ca. 1540, after which this mean shifted to a slower but positive continuing rate (Fig. 8). This pattern is very similar in shape and magnitude to the pattern of mean DBH growth for all sampled Douglas-fir ($n = 59$) (Fig. 8). Examination of individual DBH curves for all Douglas-fir indicates that none of the dissected trees attained their dominant 1992 DBH status by transition from a suppressed state (not shown).

The curve of D versus H for the dissected trees (Fig. 9) shows a gradual increase in D until an H of about 45 m (attained in ca. 1600), soon after which D began to rise more steeply (Fig. 9). The sharp post-1600 rise reflects the sub-

Fig. 7. Reconstructed tree heights for the dissected Yellowjacket Douglas-fir ($n = 1$ intensively, 10 partially, and 9 minimally dissected trees; see Methods), used to construct the D versus H values, and the individual DBH versus height values (Figs. 9 and 10). Heights are shown relative to the stand-establishment surface, which was estimated to be 1.4 m below stump-height (see Methods). The uppermost sampled height for each tree is not the full 1992 height. The means were computed for dates with reconstructed DBHs (see Fig. 8) and were used as H values for the stand at those dates.

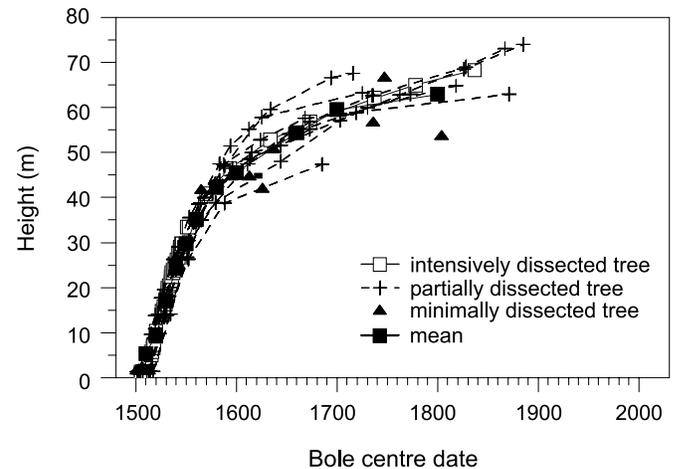
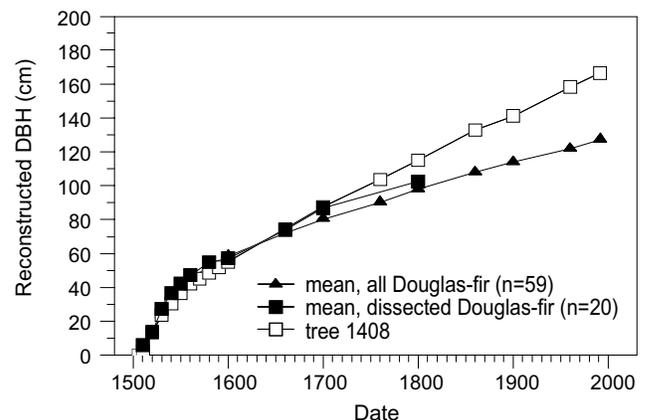


Fig. 8. Yellowjacket reconstructed mean DBHs at dates for the dissected Douglas-fir ($n = 20$) and for all Douglas-fir ($n = 59$), and reconstructed individual DBHs at dates for the intensively dissected tree 1408. The DBHs were reconstructed for every decade present in the samples, but only selected dates are shown for simplification. The DBH means for the dissected Douglas-fir are those used to construct the D versus H values (Fig. 9; see Methods) and are not shown for dates past 1800, because corresponding mean heights were not available past 1800 (see Fig. 7). The means for all Douglas-fir include the dissected trees.

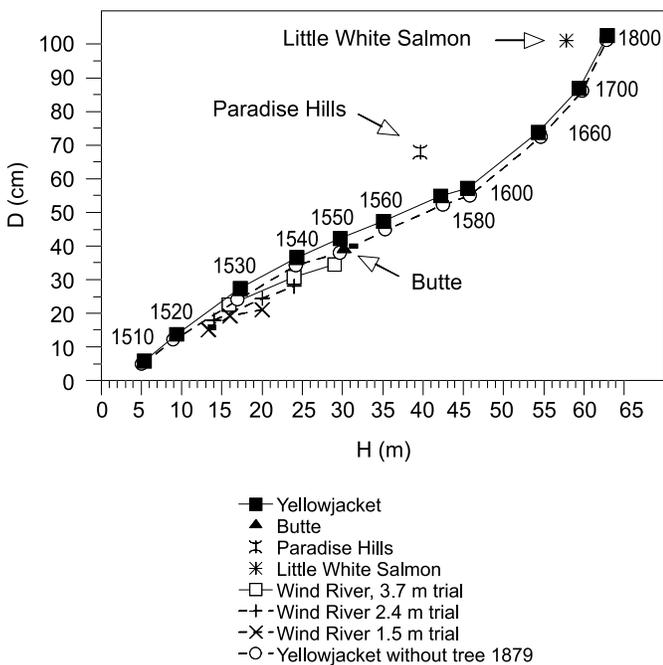


stantial slowing of height growth in the late 1500s (Fig. 7), while DBH growth continued (Fig. 8).

Comparison of Yellowjacket to natural stands and spacing trials

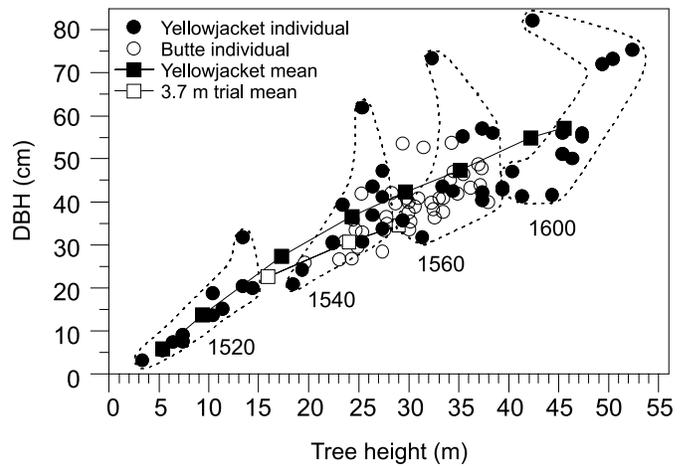
The D versus H value for dominant Douglas-fir at Butte (ca. 3.5-m spacing; Table 2) fell close to the Yellowjacket

Fig. 9. *D* versus *H* curves and values for dominant Douglas-fir at Yellowjacket, natural stands in the DEMO study (Butte, Paradise Hills, and Little White Salmon), and the Wind River spacing trials. *H* is the mean measured tree height for representative dominant (or largest 250 trees/ha for the spacing trials) Douglas-fir at any given time, and *D* is the mean DBH for the same dominant trees. *H* on the horizontal axis here is serving as a measure of age adjusted for site quality for young stands (prior to the slowing of height growth), thus adjusting for differing growth rates on different sites and allowing comparisons of DBH growth across sites for young stands (see Methods). Each point represents a *D* versus *H* value at a point in time for dominant Douglas-fir in a stand, although time is not otherwise a critical variable for the analysis. The annotated dates are for the Yellowjacket curves. The Yellowjacket curves are for the 20 dissected Douglas-fir, or for these trees with one extreme tree (No. 1879) removed from the means (see Fig. 10). The data for the Wind River spacing trials are from Reukema (1970, 1979) and Curtis and Reukema (1970). The data for Butte, Paradise Hills, and Little White Salmon derive from pre-treatment measurements taken as part of the DEMO study (currently unpublished data made available by that study).



curve of *D* versus *H* (Fig. 9). In contrast, the *D* versus *H* values for dominant Douglas-fir at Paradise Hills (ca. 7.3-m spacing) and Little White Salmon (ca. 9-m spacing) fell considerably above the Yellowjacket curve. The Little White Salmon value was above that portion of the Yellowjacket curve where *H* had slowed substantially, while *D* continued. The similarity of Butte dominant Douglas-fir to Yellowjacket dominant Douglas-fir in their youth is even more apparent in a comparison of DBH vs. height values for individual trees (Fig. 10). The values for Butte trees closely overlap with values for the Yellowjacket dissected Douglas-fir in 1540 to 1560, except for one Yellowjacket tree whose DBH vs. height values were much higher than for other trees (Fig. 10). With this atypical tree omitted, the *D* versus *H*

Fig. 10. DBH versus tree height for individual and average dominant Douglas-fir trees at Yellowjacket and Butte. For an explanation of the use of tree height on the horizontal axis, see Fig. 9 and Methods. The Yellowjacket values are for the dissected Douglas-fir at the four annotated dates. For each of those dates, the corresponding Yellowjacket values are encircled by the broken lines. All reconstructed dates were examined, but only these are shown to reduce confusion. The Yellowjacket high outlier at all 4 dates is a single tree (No. 1879). The Butte values are for dominant Douglas-fir at a single stand age (ca. 70 years). The average curves for Yellowjacket and the Wind River are the same as shown in Fig. 9. Data sources are given in the caption for Fig. 9.



value for Yellowjacket Douglas-fir in 1550 was remarkably close to the *D* versus *H* for Butte Douglas-fir (Fig. 9).

The comparison with the spacing trials was made with the knowledge that plantation stands tend to have slightly lower average DBHs for a given dominant tree height than do natural stands with comparable initial spacing. The curve of *D* versus *H* for the Wind River 3.7 m spacing trial (the widest spacing tested in the Wind River trials) fell close to but somewhat below the *D* versus *H* curve for Yellowjacket in 1530–1550 (Fig. 9).

Development of long Douglas-fir crowns

Crown length development for Douglas-fir No. 1408

This tree was representative of other Douglas-fir at Yellowjacket. For example, its height history was close to the average history for the dissected trees (Fig. 7). Its DBH history was close to the average history for all Douglas-fir until ca. 1660 and close to the average history for the dissected trees until ca. 1700, after which it diverged somewhat from these means (Fig. 8). Within the stand, the crown forms of Douglas-fir (length and width), were fairly homogeneous, and for tree 1408 the 1992 crown form and size (Fig. 3) were fairly typical of Douglas-fir for the stand. The reconstructed crown history for tree No. 1408 shows the following (Figs. 11a and 11b). Tree No. 1408 germinated in ca. 1500 (stump-height centre date was 1505). The young tree increased in height, while the base of the functionally live crown (crown base 1) remained at the ground level until 1525. In 1525 the functionally live crown was 13.1 m long. Shortly after 1525 and 1530, respectively, crown base 1 and

Fig. 11. Crown development for Douglas-fir 1408. (a) Raw data for all branches: bole centre date, LFLD (latest functionally live date), and EDD (earliest dead date). See Fig. 3 for sampling scheme. Heights are shown relative to the stand-establishment surface (see Fig. 3 and the Methods for explanation). (b) Summary of raw data shown in the top graph (see Methods for summary process), displaying for each of a series of dates the tree's reconstructed height (top) and the heights to the reconstructed crown bases (crown base 1 and crown base 2). Crown base 1 is the base of the functionally live crown at a date. Crown base 2 is the base of a lower zone of dying branches just below the functionally live crown. The lines are linear interpolations between adjacent data points. The long line between the data points at 1630 (height of 29.7 m) and 1992 (height of 34.6 m, the 1992 live crown base) shows the dramatic increase in branch longevity over this short height interval. The drawn trees are only approximate schematic representations as an aid to interpreting the graph.

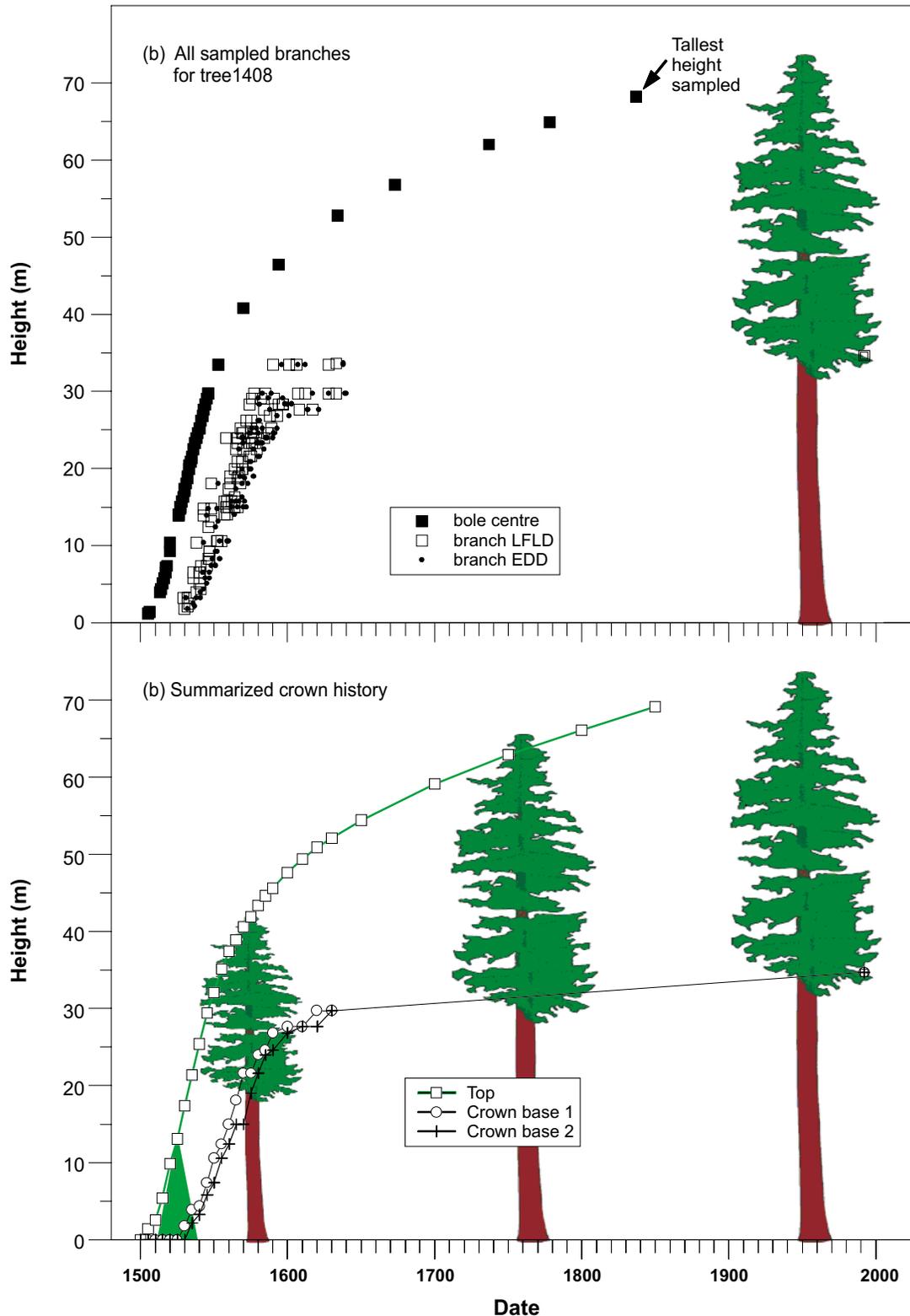
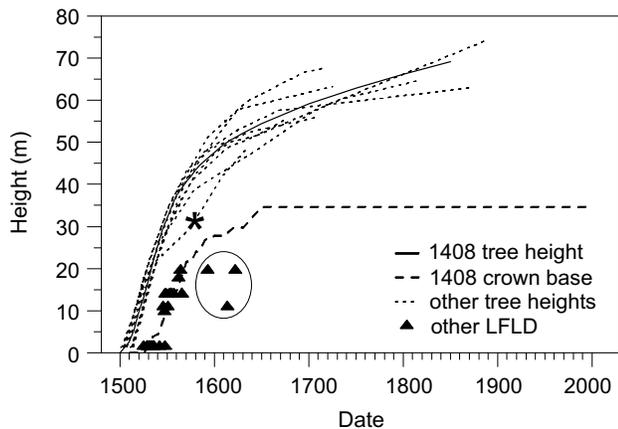


Fig. 12. Crown history for tree No. 1408 compared with limited crown data for other dominant Douglas-fir at Yellowjacket. Heights are shown relative to the stand-establishment surface (see Fig. 3 and Methods for explanation). The crown history for tree No. 1408 is as shown and described in Fig. 11. For 12 other dominant Douglas-fir, branch heights and corresponding LFLDs (latest functionally live dates) are shown for 28 branches. Height histories were reconstructed for 8 of these other trees. One of these trees, tree No. 1187, was unusual for its reduced height growth in the mid-1500s (star), late LFLDs (circled points) relative to branches at corresponding heights in other trees, a massive injury to its bole in 1560, and a long double top in 1992. For this tree, only heights and DBHs prior to the injury are included in the analysis for initial spacing and in the dominant heights shown in Fig. 7.

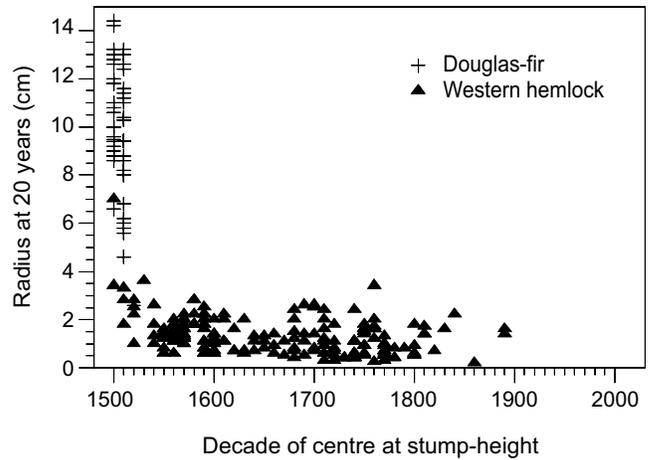


the base of the zone of dying branches (crown base 2), began to recede, marking the beginning and completion of the tree's crown closure (Oliver and Larson 1990). The subsequent histories of these two crown bases are similar but with a distance of 0–6.6 m (mean 1.5 m) between them for any given date. Following crown closure and throughout the remaining life of the tree, the rate of recession for these crown bases was less than the rate of height growth; hence, the crown lengthened. The lengthening became particularly pronounced following ca. 1600, when the recession of the crown bases abruptly slowed, and following 1630, when the recession stopped while tree height growth continued. By 1630 the functionally live crown was 22.4 m long, i.e., 1.7 times its length at the beginning of crown closure in 1525. By 1992 it was 36.8 m long, i.e., 2.8 times its length at the beginning of crown closure. The lifelong lengthening of the crown was accomplished with no observed epicormic branching from the bole. All embedded branches sampled in the closely sampled portion of the bole (i.e., to 29.7 m; Fig. 3) were normal, nodal branches. There was not enough information to evaluate the mode of branch origin for the short interval of the bole (from 29.7 to 34.6 m; Fig. 3) that was sampled only at the location of dead emergent (in 1992) branches.

Histories for 28 branches from 12 additional Douglas-fir

For 11 of the 12 additional trees, the early development of crown length appears to have been similar to that reconstructed for tree No. 1408, as suggested by LFLDs and reconstructed height histories for these other Douglas-fir (Fig. 12). For 25 branches from these 11 trees, the branch

Fig. 13. Juvenile radial growth rate (represented by radius at 20 years, stump-height and inside bark) versus decade of establishment at stump-height (represented by decade of centre at stump-height) for trees with stump-height centre dates (Table 1): $n = 58$ Douglas-fir, $n = 172$ western hemlock (3 western hemlock with centres were missing data for radii at 20 years).



height versus LFLDs fell on or fairly close to the crown base 1 recession curve (which was based on LFLDs) for tree No. 1408. Seven of these 11 trees had been dissected for height growth, and their height histories were similar to that of tree No. 1408. One of the 12 additional trees (tree No. 1187) showed a different pattern. This tree had reduced height growth in the middle to late 1500s. For 3 branches from this tree (No. 1187), the LFLDs were considerably later than were LFLDs for branches of other trees at corresponding heights, suggesting that this tree had developed a much longer crown by ca. 1600 than did the other trees.

Duration of open growth conditions

Juvenile radial growth rate (stump-height radius at 20 years, inside bark) (Fig. 13)

The 57 Douglas-fir that established before 1520 had relatively high juvenile radial growth rates (4.6–14.4 cm/20 years, mean 10.1). The final Douglas-fir established in 1521 and had a substantially reduced juvenile growth rate (2.6 cm/20 years). For the western hemlock, a shift in juvenile radial growth rates occurred in ca. 1540. The juvenile radial growth rates of the 10 western hemlock establishing prior to 1540 (1.0–7.0 cm/20 years, mean 3.04) were generally higher than for 162 western hemlock establishing after 1540 (0.2–3.4 cm/20 years, mean 1.27). None of the western hemlock establishing prior to 1540 had juvenile radial growth rates <1.0 cm/20 years, whereas 35% of the trees establishing after 1540 had juvenile growth rates <1.0 cm/20 years.

Long-term ringwidth patterns at stump-height (Fig. 5, Table 3)

Among the 68 Douglas-fir and western hemlock that established prior to 1540, 59 had open ringwidth patterns, 4 had closed ringwidth patterns, and 5 had other patterns. All of the open patterns were for trees that established prior to the cessation of Douglas-fir establishment in ca. 1521. Among the 165 western hemlock that established after 1540,

Table 3. Number of trees with open, closed, or other ring-width patterns.

Pattern	Established pre-1521		Established 1521–1539		Established 1540+	
	Douglas-fir	Western hemlock	Douglas-fir	Western hemlock	Douglas-fir	Western hemlock
Open	57	2	0	0	0	0
Closed	0	1	1	2	0	146
Other	0	3	0	2	0	19

Note: Period of establishment is based on stump-height centre dates.

none had open patterns, 146 had closed patterns, and 19 had other patterns.

Discussion

The results of the Yellowjacket reconstruction differ from previous findings that Douglas-fir in old-growth stands colonized over a prolonged interval and at wide initial spacings (Franklin and Waring 1980; Franklin and Hemstrom 1981; Stewart 1986; Yamaguchi 1993; Tappeiner et al. 1997). In contrast, the stand-initiation phase at Yellowjacket was similar to that observed for typical modern young natural Douglas-fir stands in the Pacific Northwest. This result suggests that old-growth stands have developed from multiple pathways.

Yellowjacket stand initiation

The study produced the following conclusions for the four study objectives concerning the stand initiation at Yellowjacket.

(1) Duration of initial establishment

The narrow range of stump-height establishment dates (1500–1521) for the Douglas-fir and one western white pine suggests that shade-intolerant trees successfully colonized the site over two decades following a stand-replacing disturbance in the late 1400s (Fig. 6). A small number (10) of the sampled western hemlock established concurrently with the Douglas-fir. The abundance of charcoal surrounding Douglas-fir roots strongly suggests that the initiating disturbance was fire. Although the establishment dates are not corrected for the time to reach stump-height, we expect that the length of the interval of initial establishment at stump-height for Douglas-fir should be similar to the length of this interval at the stand-establishment surface in these rapidly growing open-grown trees. The short interval of initial establishment found for Yellowjacket Douglas-fir is similar to the 5- to 22-year intervals of initial establishment reported for currently young, naturally regenerated, Douglas-fir stands (Oliver and Larson 1990; Tappeiner et al. 1997) and is in marked contrast to the prolonged intervals of initial establishment (100–265 years) reported in most previous reconstructions of old-growth Douglas-fir stands (Franklin and Waring 1980; Franklin and Hemstrom 1981; Stewart 1986; Yamaguchi 1993; Tappeiner et al. 1997). This contrast between the findings for Yellowjacket compared with other old-growth stands cannot be explained by differences in plot size, since the previous reconstructions of old-growth stands sampled areas ranging from 0.8 to 18 ha, and even the

smallest plot (0.8 ha) had a prolonged interval (100 years) of initial Douglas-fir establishment (Stewart 1986).

(2) Initial spacing of Douglas-fir

Among the comparison stands, the *D* versus *H* value for Butte and the *D* versus *H* curve for the widest spacing tested at Wind River (3.7 m) fell closest to the Yellowjacket curve (Fig. 9). The mean initial spacing of Douglas-fir at Butte would have been no wider, and likely narrower, than its value at 70 years: 3.5 m (Table 2). The comparisons for Paradise Hills, and particularly Little White Salmon, may be somewhat complicated, because these stands may be near or past the point where height growth has slowed. Regardless of the uncertainties involved in the comparisons with these latter two stands, it is clear that the Butte value and the curve for the widest Wind River trial fall close to the Yellowjacket curve. In evaluating the relative positions of values for these two stands compared with the Yellowjacket curve, and making inferences about initial spacing, there are a few considerations to take into account. First, it should be considered that plantations differ slightly from natural stands with respect to their *D* versus *H* values. It has been shown (Wilson 1998) that the average DBHs of dominant Douglas-fir (largest 250 per hectare in this case) for a given dominant height and initial spacing tend to be slightly greater in natural stands than in plantations. A second consideration is that if there was a systematic error in the Yellowjacket DBH reconstructions, it would have been to overestimate rather than underestimate DBHs (Winter 2000). The final consideration is that with the atypical tree No. 1879 omitted from the Yellowjacket curve, the *D* versus *H* value for Butte fell directly on the Yellowjacket curve (Fig. 9).

Given the comparisons and considerations, we conclude that Douglas-fir at Yellowjacket had a mean initial spacing similar to that of Douglas-fir at Butte, i.e., in the neighborhood of 3.5 m. Although this estimate is based on *D* versus *H* of dominant Douglas-fir, it is interpreted to be the initial spacing for all Douglas-fir, since Wilson (1998) showed that the initial spacing of all Douglas-fir influences the *D* versus *H* curves of dominant Douglas-fir. Also in accordance with previous work, 3.5 m represents the mean initial distance between Douglas-fir trees, or between Douglas-fir and equally strong competitors, but not between Douglas-fir and weaker competitors (Wilson 1998). Thus, the inferred mean initial spacing for Yellowjacket Douglas-fir may have occurred within any of a variety of early scenarios with respect to composition and total stand density; nevertheless, Butte provides an example of one such possibility. It appears that the dominant Douglas-fir in this typical natural young stand are starting out on a path similar to the early history of domi-

nant Douglas-fir at Yellowjacket, with individual DBH vs. height values remarkably similar to the youth of Yellowjacket dominant Douglas-fir (Fig. 10).

The inferred initial spacing of 3.5 m for Douglas-fir at Yellowjacket falls within the range of mean initial spacings occurring in modern naturally regenerated young Douglas-fir stands in the region (ca. 1.6–4.5 m; Wilson 1998). The initial spacing for Yellowjacket Douglas-fir is also consistent with the quickness with which Douglas-fir colonized the Yellowjacket site (Fig. 6) and the forest closed (Fig. 13). This finding contrasts with the study by Tappeiner et al. (1997), which concluded that Douglas-fir in old-growth stands in the Oregon Coast Range established at much wider spacings and over much longer time periods than did nearby currently young stands that regenerated naturally after logging.

(3) *Crown development of Douglas-fir*

Franklin et al. (1981) suggested that the large, long crowns of Douglas-fir in old-growth stands may have developed as a consequence of wide initial spacing and (or) epicormic branching. However, despite an initial spacing that was not unusually wide relative to modern young Douglas-fir stands, the Douglas-fir at Yellowjacket were readily observed to have deep crowns typical of old-growth stands in the region. Thus, wide initial spacing is apparently not a necessary condition for development of deep old-growth Douglas-fir crowns. The intensive crown reconstruction of tree No. 1408 (Fig. 11) is not necessary for this conclusion. However the measurement of this representative Douglas-fir gives weight to the visual observation of “deep” Douglas-fir crowns, and the reconstructed history provides a detailed example of one possibility for crown lengthening in the absence of wide initial spacing, and without epicormic branching from the bole.

The intensive crown reconstruction of tree No. 1408 reveals pronounced crown lengthening following crown closure for this tree, showing the timing and dimensions for how the crown lengthened because of the combined effects of tree height growth and recession of the crown base. Although it is not clear what factors were involved in the pronounced crown lengthening after crown closure, epicormic branching from the bole did not play a significant role. All embedded branches that were evaluated for mode of branch origin below the 1992 crown base were normal, nodal branches. An additional reason for suspecting that epicormic branching did not contribute significantly to the lengthening is that in 1992, the sizes of lower branches appeared consistent with their relative position in the canopy, given an assumption of non-epicormic origins. This latter observation was true in general for dominant Douglas-fir at Yellowjacket in 1992.

The suggestion that the long crowns of other Douglas-fir in the stand likely developed by histories similar to that of tree No. 1408 is supported by the 28 branches analyzed for 12 other Douglas-fir. This suggestion is also supported by the very average DBH and height growth of tree No. 1408 for the first couple of hundred years of its life, which is consistent with an average initial spacing, leading to average crown development during that time at least. The DBH history did diverge somewhat from the mean for all Douglas-fir after about 1660, and from the mean for the dissected trees

after about 1700. However, by 1660 the crown of tree No. 1408 had already lengthened considerably, and the recession of the crown base had slowed or even stabilized. Further crown lengthening was due largely to height growth, which was very close to the mean for the dissected trees throughout its life. Regardless of whether details of the history of crown development for tree No. 1408 were average for the stand, the fact remains that other Douglas-fir in the stand had typically deep old-growth crowns despite the relatively narrow initial spacing.

(4) *Duration of open growth conditions*

The juvenile radial growth rates and the ringwidth patterns at stump-height show that relatively open conditions existed prior to 1521 and that closed forest conditions existed after 1540, with gradual filling in of growing space between these times. The rapidity with which the trees colonized the site and grew to closed forest conditions is consistent with the narrow spacing inferred for Douglas-fir. The results show that by about 1540, trees standwide had developed closed crowns, and the forest as a whole had closed. The stand-initiation period had ended, and the forest remained closed until it was clearcut in 1992. Although considerable thinning of the initial colonizers occurred over the centuries, the stand never opened up enough after 1540 to allow further Douglas-fir establishment.

Multiple pathways for the development of old-growth stands

Yellowjacket is just one site. By chance, its early history may represent an exception rather than a common occurrence for old-growth stands. Nonetheless, the fact remains that this stand initiated quickly and at close spacing but developed typical old-growth structures. In marked contrast, previous reconstructions have suggested that other old-growth stands started out very slowly and at low density. The ecological causes of these contrasting initiations are not clear but may be related to regional gradients in climate, environmental conditions, and disturbance characteristics across the large geographic area covered by the various studies (i.e., Coastal Range of Oregon, Cascades of Oregon, and southern Washington; Spies and Franklin 1991). Regardless of the ecological causes, the strong contrasts between the stand initiation for Yellowjacket versus other previously reconstructed old-growth Douglas-fir stands shows that typical old-growth structures can develop by multiple pathways. The likelihood of different developmental pathways for old-growth stands has been suggested previously based on the variability in overall old-growth structure across the large geographic area where these forests are found (Spies and Franklin 1991). Differences between Yellowjacket and past reconstructions provide empirical evidence for varied pathways. It is also possible that there is a range of early histories that do not support the eventual development of typical old-growth structure, for example, early histories where initial spacing is too narrow or where there is little size differentiation (Wilson 1998).

Management implications

Knowledge about initial histories of old-growth forests is of considerable importance to forest managers faced with

policies that emphasize maintenance and development of old-growth stands in the Pacific Northwest. In pursuing these policies, managers must ask whether current young stands are likely to develop old-growth structures or whether silvicultural treatments might be required (e.g., Halpern and Raphael 1999; Aubry et al. 1999; Thomas 1997; Kohm and Franklin 1997; DeBell et al. 1997; Tappeiner et al. 1997; McComb et al. 1993). The past offers the only time-tested guide to answering such questions. It was for reasons such as these that Tappeiner et al. (1997) also reconstructed old-growth stands in the Oregon Coast Range, concluding that the trees in these stands established and grew at much lower densities compared with trees in modern young stands and suggesting that young stands may need to be aggressively thinned to enable them to develop into stands with old-growth characteristics.

The results of the current study suggest caution about applying thinning on a widespread basis. Natural young stands that are not overly dense and that are developing strong differentiation of tree sizes may require only time to develop old-growth structures, with no intrusive management required. Although it is not clear where the overly dense boundary lies, the Yellowjacket reconstruction suggests that currently young stands with dominant Douglas-fir DBH and height structures similar to Butte are likely starting on a developmental pathway similar to the early history of Yellowjacket dominants. This leaves little reason to doubt that some young stands like Butte can develop old-growth characteristics, although others may not. In some cases, intervention may be considered because a stand is very dense or to speed the development of greater size variability and complexity, but the gains of such intervention should be weighed carefully against the ecological costs of silvicultural interventions.

Spies and Franklin (1991) have suggested that "... management of old growth in western Oregon and Washington should be sensitive to the regional diversity of old-growth conditions." The current study suggests that management should also be sensitive to the diversity of pathways that lead to old-growth conditions. Variability in the pathways to old-growth structures, as well as variability in the endpoints themselves, may be important in maintaining diversity in habitat and ecosystem functions at many scales (spatial and temporal) across the landscape. For example, very different ecological characteristics would be expected for prolonged versus short stand initiations, particularly when considered at the scale of multiple forests across the landscape (e.g., Franklin et al. 1989) or for a stand with a single Douglas-fir cohort versus multiple cohorts. It would be unwise to apply simple generalizations as to how current old forests developed, or how the current young forests will develop, and risky to implement a simple management prescription at the landscape scale. Rather, as Kohm and Franklin (1997) have suggested, we need an "array of tools and ideas" as to how these forests develop and an appreciation of their complexity. Where the objective is to maintain and develop old-growth structures, many approaches are being suggested, and the "menu" of ideas is continually growing (e.g., Halpern and Raphael 1999; Aubry et al. 1999; Thomas 1997; Kohm and Franklin 1997; DeBell et al. 1997; Tappeiner et al. 1997; McComb et al. 1993). The current

study, together with the reconstruction of canopy disturbances for Yellowjacket (Winter 2000; Winter et al. 2002), provides the most detailed currently available "real-time" (as opposed to chronosequence) history for the entire lifetime of an old-growth Douglas-fir stand.

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References

- Andrews, S.R., and Gill, L.S. 1939. Determining the time branches on living trees have been dead. *J. For.* **37**: 930–935.
- Aubry, K.B., Amaranthus, M.P., Halpern, C.B., White, J.D., Woodard, B.L., Peterson, C.E., Lagoudakis, C.A., and Horton, A.J. 1999. Evaluating the effects of varying levels and patterns of green-tree retention: experimental design of the DEMO study. *Northwest Sci.* **73**(Spec. Issue): 12–26.
- Blum, B.M. 1963. Excessive exposure stimulates epicormic branching in young northern hardwoods. *U.S. For. Serv. Res. Note NE-9*.
- Canham, C.D. 1985. Suppression and release during canopy recruitment in *Acer saccharum*. *Bull. Torrey Bot. Club*, **112**: 134–145.
- Canham, C.D. 1990. Suppression and release during canopy recruitment in *Fagus grandifolia*. *Bull. Torrey Bot. Club*, **117**: 1–7.
- Cho, D., and Boerner, R.E.J. 1995. Dendrochronological analysis of the canopy history of two Ohio old-growth forests. *Vegetatio*, **120**: 173–183.
- Cremer, K.W., Borough, C.J., McKinnell, F.H., and Carter, P.R. 1982. Effects of stocking and thinning on wind damage in plantations. *N.Z. J. For. Sci.* **12**: 244–268.
- Curtis, R.O., and Reukema, D.L. 1970. Crown development and site estimates in a Douglas-fir plantation spacing test. *For. Sci.* **16**: 287–301.
- DeBell, D.S., Curtis, R.O., Harrington, C.A. and Tappeiner, J.C. 1997. Shaping stand development through silvicultural practices. *In Creating a forestry for the 21st century. Edited by K.A. Kohm and J.F. Franklin.* Island Press, Washington, D.C. pp. 141–149.
- DesRochers, A., and Gagnon, R. 1997. Is ring count at ground level a good estimation of black spruce age? *Can. J. For. Res.* **27**: 1263–1267.
- Fastie, C.L. 1995. Causes and ecosystem consequences of multiple pathways of primary succession at Glacier Bay, Alaska. *Ecology*, **76**: 1899–1916.
- Ferguson, C.W. 1970. Concepts and techniques of dendrochronology. *In Scientific methods in medieval archaeology. Edited by R. Berger.* University of California Press, Los Angeles, Calif. pp. 183–200.
- Forest Ecosystem Management Assessment Team (FEMAT). 1993. Forest ecosystem management: an ecological, economic, and social assessment. Joint publication of the United States Depart-

- ment of Agriculture, Forest Service; United States Department of Commerce, National Oceanic and Atmospheric Administration and National Marine Fisheries Service; United States Department of the Interior, Bureau of Land Management, Fish and Wildlife Service, and National Park Service; and United States Environmental Protection Agency, Washington, D.C.
- Franklin, J.F., and Dyrness, C.T. 1973. Natural vegetation of Oregon and Washington. USDA For. Serv. Gen. Tech. Rep. PNW-8.
- Franklin, J.F., and Hemstrom, M.A. 1981. Aspects of succession in the coniferous forests of the Pacific Northwest. *In* Forest succession: concepts and applications. Edited by D. West, D. Botkin, and H. Shuggart. Springer-Verlag, New York. pp. 212–229.
- Franklin, J.F., and Spies, T.A. 1991. Composition, function, and structure of old-growth Douglas-fir forests. *In* Wildlife and vegetation of unmanaged Douglas-fir forests. Edited by L.F. Ruggiero, K.B. Aubry, A.B. Carey, and M.H. Huff. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-285. pp. 71–80.
- Franklin, J.F., and Waring, R.H. 1980. Distinctive features of the Northwestern coniferous forest: development, structure, and function. *In* Forests: Fresh Perspectives from Ecosystem Analysis. Proceedings of the 40th Annual Biological Colloquium, Corvallis, Oreg. Edited by R.H. Waring. Oregon State University Press, Corvallis, Oreg. pp. 59–86.
- Franklin, J.F., Cromack, K., Jr., Denison, W., McKee, A., Maser, C., Sedell, J., Swanson, F., and Juday, G. 1981. Ecological characteristics of old-growth Douglas-fir forests. USDA For. Serv. Gen. Tech. Rep. PNW-118.
- Franklin, J.F., Perry, D.A., Schowalter, T.D., Harmon, M.E., McKee, A., and Spies, T.A. 1989. Importance of ecological diversity in maintaining long-term site productivity. *In* Maintaining the long-term productivity of Pacific Northwest forest ecosystems. Edited by D.A. Perry, R. Meurisse, B. Thomas, R. Miller, J. Boyle, J. Means, C.R. Perry, and R.F. Powers. Timber Press, Inc., Portland, Oreg. pp. 82–97.
- Fritts, H.C. 1976. Tree rings and climate. Academic Press, New York.
- Gifford Pinchot National Forest. 1971a. Soil resource inventory. USDA Forest Service, Pacific Northwest Region.
- Gifford Pinchot National Forest. 1971b. Soil resource atlas of maps and interpretive tables. USDA Forest Service, Pacific Northwest Region.
- Halpern, C.B., and Raphael, M.G. 1999. Preface. Special issue on retention harvests in Northwest forest ecosystems: the Demonstration of Ecosystem Management Options (DEMO) study. *Northwest Sci.* **73**(Spec. Issue): 1–2.
- Halpern, C.B., Evans, S.A., Nelson, C.R., McKenzie, D., Liguori, D.A., Hibbs, D.E., and Halaj, M.G. 1999. Response of forest vegetation to varying levels and patterns of green-tree retention: an overview of a long-term experiment. *Northwest Sci.* **73**(Spec. Issue): 27–44.
- Harr, R.D. 1986. Effects of clearcutting on rain-on-snow runoff in western Oregon: a new look at old studies. *Water Resour. Res.* **22**: 1095–1100.
- Harr, R.D., and Coffin, B.A. 1992. Influence of timber harvest on rain-on-snow runoff: a mechanism for cumulative watershed effects. *In* Interdisciplinary approaches in hydrology and hydrogeology. Edited by M.E. Jones and A. Laenen. American Institute of Hydrology, Washington, D.C. pp. 455–469.
- Henry, J.D., and Swan, J.M.A. 1974. Reconstructing forest history from live and dead plant material — an approach to the study of forest succession in southwest New Hampshire. *Ecology*, **55**: 772–783.
- Herman, F.R. 1964. Epicormic branching of Sitka spruce. U.S. For. Serv. Res. Pap. PNW-18.
- Holmes, R.L., Adams, R.K., and Fritts, H.C. 1986. Quality control of crossdating and measuring: a user's manual for program COFECHA. *In* Tree-ring chronologies of western North America: California, eastern Oregon and northern Great Basin. Laboratory of Tree-Ring Research, University of Arizona, Tucson, Ariz. pp. 41–49.
- Johnson, F.A. 1955. Estimating past diameters of Douglas-fir trees. USDA For. Serv. Pac. Northwest For. Range Exp. Stn. Res. Note 112.
- Jones, J.A., and Grant, G.E. 1996. Peak flow responses to clear-cutting and roads in small and large basins, western Cascades, Oregon. *Water Resour. Res.* **32**: 959–974.
- Kershaw, J.A., Maguire, D.A., and Hann, D.W. 1990. Longevity and duration of radial growth in Douglas-fir branches. *Can. J. For. Res.* **20**: 1690–1695.
- Khom, K.A., and Franklin, J.F. 1997. Introduction. *In* Creating a forestry for the 21st century. Edited by K.A. Kohm and J.F. Franklin. Island Press, Washington, D.C. pp. 1–5.
- Lehmkuhl, J.F., and Ruggiero, L.F. 1991. Forest fragmentation in the Pacific Northwest and its potential effects on wildlife. *In* Wildlife and vegetation of unmanaged Douglas-fir forests. Edited by L.F. Ruggiero, K.B. Aubry, A.B. Carey, and M.H. Huff. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-285. pp. 35–46.
- Lorimer, C.G. 1985. Methodological considerations in the analysis of forest disturbance history. *Can. J. For. Res.* **15**: 200–213.
- Lorimer, C.G., and Frelich, L.E. 1989. A methodology for estimating canopy disturbance frequency and intensity in dense temperate forests. *Can. J. For. Res.* **19**: 651–663.
- Lorimer, C.G., Frelich, L.E., and Nordheim, E.V. 1988. Estimating gap origin probabilities for canopy trees. *Ecology*, **69**: 778–785.
- Maguire, D.A., and Hann, D.W. 1987. A stem dissection technique for dating branch mortality and reconstructing past crown recession. *For. Sci.* **33**: 858–871.
- Marcot, B.G., Holthausen, R.S., Teply, J. and Carrier, W.D. 1991. Old-growth inventories: status, definitions, and visions for the future. *In* Wildlife and vegetation of unmanaged Douglas-fir forests. Edited by L.F. Ruggiero, K.B. Aubry, A.B. Carey, and M.H. Huff. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-285. pp. 47–60.
- Massman, W.J. 1982. Foliage distribution in old-growth coniferous tree canopies. *Can. J. For. Res.* **12**: 10–17.
- McComb, W.C., Spies, T.A., and Emmingham, W.H. 1993. Douglas-fir forests: managing for timber and mature-forest habitat. *J. For.* **91**: 31–42.
- Mitchell, K.J., and Cameron, I.R. 1985. Managed stand yield tables for coastal Douglas-fir: initial density and precommercial thinning. B.C. Ministry of Forests, Victoria, B.C. Land Manage. Rep. 31.
- Munger, T.T. 1940. The cycle from Douglas-fir to hemlock. *Ecology*, **21**: 451–459.
- Oliver, C.D., and Larson, B.C. 1990. Forest stand dynamics. McGraw-Hill, Inc., New York.
- Oliver, C.D., and Stephens, E.P. 1977. Reconstruction of a mixed-species forest in central New England. *Ecology*, **58**: 562–572.
- Oliver, C.D., Michalec, W., DuVall, L., Wierman, C.A., and Oswald, H. 1986. Silvicultural costs of growing Douglas-fir of various spacings, sites, and wood qualities. *In* Douglas-fir: stand management for the future. Edited by C.D. Oliver, D.P. Hanley, and J.A. Johnson. College of Forest Resources, University of Washington, Seattle, Wash. Inst. For. Resour. Contrib. 55. pp. 123–141.
- Phillips, E.L. 1972. The climates of Washington. *In* Climates of the States. Vol. II. National Oceanographic and Atmospheric Administration, Water Information Center, Washington, D.C.

- Pike, L.H., Rydell, R.A., and Denison, W.C. 1977. A 400-year-old Douglas fir tree and its epiphytes: biomass, surface area, and their distributions, 1977. *Can. J. For. Res.* **7**: 680–699.
- Reukema, D.L. 1970. Forty-year development of Douglas-fir stands planted at various spacings. USDA For. Serv. Res. Pap. PNW-100.
- Reukema, D.L. 1979. Fifty-year development of Douglas-fir stands planted at various spacings. USDA For. Serv. Res. Pap. PNW-253.
- Smith, J.H.G., and Reukema, D.L. 1986. Effects of plantation and juvenile spacing on tree and stand development. *In Douglas-fir: stand management for the future. Edited by C.D. Oliver, D.P. Hanley, and J.A. Johnson.* College of Forest Resources, University of Washington, Seattle, Wash. Inst. For. Resour. Contrib. 55. pp. 239–245.
- Spies, T.A., and Franklin, J.F. 1988. Old growth and forest dynamics in the Douglas-fir region of Western Oregon and Washington. *Nat. Areas J.* **8**: 190–201.
- Spies, T.A., and Franklin, J.F. 1989. Gap characteristics and vegetation response in coniferous forests of the Pacific Northwest. *Ecology*, **70**: 543–545.
- Spies, T.A., and Franklin, J.F. 1991. The structure of natural young, mature, and old-growth Douglas-fir forests in Oregon and Washington. *In Wildlife and vegetation of unmanaged Douglas-fir forests. Edited by L.F. Ruggiero, K.B. Aubry, A.B. Carey, and M.H. Huff.* USDA For. Serv. Gen. Tech. Rep. PNW-GTR-285. pp. 91–109.
- Stewart, G.H. 1986. Population dynamics of a montane conifer forest, western Cascade Range, Oregon, USA. *Ecology*, **67**: 534–544.
- Stokes, M.A., and Smiley, T.L. 1968. An introduction to tree-ring dating. University of Chicago Press, Chicago, Ill.
- Stout, B.B., and Shumway, D.L. 1982. Site quality estimation using height and diameter. *For. Sci.* **28**: 639–645.
- Tappeiner, J.C., Huffman, D., Marshall, D., Spies, T.A., and Bailey, J.D. 1997. Density, ages, and growth rates in old-growth and young-growth forests in coastal Oregon. *Can. J. For. Res.* **27**: 638–648.
- Thomas, J.W. 1991. Research on wildlife in old-growth forests: setting the stage. *In Wildlife and vegetation of unmanaged Douglas-fir forests. Edited by L.F. Ruggiero, K.B. Aubry, A.B. Carey, and M.H. Huff.* USDA For. Serv. Gen. Tech. Rep. PNW-GTR-285. pp. 1–4.
- Thomas, J.W. 1997. Foreword. *In Creating a forestry for the 21st century. Edited by K.A. Kohm and J.F. Franklin.* Island Press, Washington, D.C. pp. ix–xii.
- Thomas, J.W., Raphael, M.G., Anthony, R.G., Forsman, E.D., Reeves, H., Sedell, J.R., and Solis, D.M. 1993. Viability assessments and management considerations for species associated with late-successional and old-growth forests of the Pacific Northwest. The report of the scientific analysis team. USDA Forest Service, Portland, Oreg.
- Wilson, J.S. 1998. Wind stability of naturally regenerated and planted Douglas-fir stands in coastal Washington, Oregon, and British Columbia. Ph.D. dissertation, University of Washington, Seattle, Wash.
- Wilson, J.S., and Oliver, C.D. 2000. Stability and density management in Douglas-fir plantations. *Can. J. For. Res.* **30**: 910–920.
- Winter, L.E. 2000. Five centuries of structural development in an old-growth Douglas-fir stand in the Pacific Northwest: a reconstruction from tree-ring records. Ph.D. dissertation, University of Washington, Seattle, Wash.
- Winter, L.E., Brubaker, L.B., Franklin, J.F., Miller, E.A., and DeWitt, D.Q. 2002. Canopy disturbances over the five-century lifetime of an old-growth Douglas-fir stand in the Pacific Northwest. *Can. J. For. Res.* **32**: 1057–1070.
- Yamaguchi, D.K. 1991. A simple method for cross-dating increment cores from living trees. *Can. J. For. Res.* **21**: 414–416.
- Yamaguchi, D.K. 1993. Forest history, Mount St. Helens. *Res. Explor.* **9**: 294–325.