FIVE CENTURIES OF STRUCTURAL DEVELOPMENT
IN AN OLD-GROWTH DOUGLAS-FIR STAND
IN THE PACIFIC NORTHWEST:
A RECONSTRUCTION FROM TREE-RING RECORDS

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This is to certify that I have examined this copy of a doctoral dissertation by

Linda Ellen Winter

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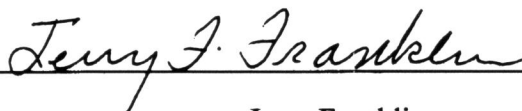examining committee have been made.

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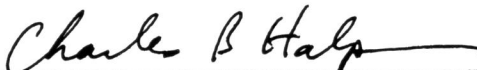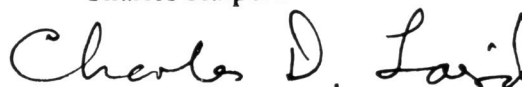
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ABSTRACT

FIVE CENTURIES OF STRUCTURAL DEVELOPMENT IN
AN OLD-GROWTH DOUGLAS-FIR STAND IN THE PACIFIC NORTHWEST:
A RECONSTRUCTION FROM TREE-RING RECORDS

By Linda Ellen Winter

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Tree-ring records were used to reconstruct the history of an old-growth Douglas-fir stand in the western Cascade Range of southern Washington. Prior to a scheduled harvest, a 3.3 ha plot was inventoried and mapped. After felling in 1992, samples were collected from stumps of all mapped trees, and from multiple additional heights of a subset of these trees. One tree was intensively dissected to locate and extract embedded branches. Data taken from crossdated samples were used to reconstruct a history that focused on stand initiation and canopy disturbances, but also included diameter, height and crown development.

All sampled Douglas-fir were initial colonizers, establishing 1500-1521 under open conditions following a stand-replacing fire. A minor component of sampled western hemlock were also initial colonizers. Growing space filled as tree crowns widened, and by 1540 closed canopy conditions had developed. At this time, Douglas-fir were spaced about 3.5 m from equivalent competitors (ca. 800 trees/hectare).

In the centuries following canopy closure, considerable natural thinning of the initial colonizers occurred. Although the canopy never opened enough to allow further Douglas-fir establishment, at least three disturbances thinned the canopy across areas large enough to reliably reconstruct, each affecting areas ≥ 0.8 ha. Surviving Douglas-fir increased in stature and developed long crowns despite the narrow initial spacing, and without

epicormic branching. Most western hemlock that were canopy trees in 1992 established after 1540, originating in the understory where they grew slowly for years to decades before ascending to the canopy through multiple abrupt increases in growth.

This reconstruction provides a case history, extending across centuries, that may be useful where management policies emphasize the development of old-growth structures. The quick establishment at close spacing by Douglas-fir in the study stand is similar to establishment patterns for typical young stands in the region, and is very different from the prolonged establishment at wide spacings found for Douglas-fir in other reconstructed old-growth stands. Such differences show that old-growth structures can develop by multiple pathways, and that intrusive management may not be required to allow many typical young stands to develop old-growth structures.

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CHAPTER 1

INTRODUCTION

Decades of logging in the Pacific Northwest has transformed once extensive tracts of old-growth Douglas-fir (*Pseudotsuga menziesii*) 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 and developing old-growth ecosystems across the current and future landscapes of the Pacific Northwest (Thomas 1991, Thomas et al. 1993, FEMAT 1993, Aubry et al. 1999). Since ecological function is a direct consequence of forest structure, and forest structure is a feature that can be manipulated by management, these policy changes focus on management of the structural characteristics of the forest (e.g. Franklin et al. 1981, Franklin and Spies 1991).

In view of the increased emphasis on old-growth ecosystems, our limited knowledge about how old-growth structures developed over the centuries has been of concern. In particular, little information exists about 1) tree recruitment and growth during the stand initiation phase, and 2) tree responses to minor disturbances. This shortcoming makes it difficult to develop management plans that will insure the development of old-growth characteristics from young stands (e.g. Tappeiner et al. 1997). Our uncertainties arise in part because most conceptual models of the development of old-growth forests derive from chronosequences (progressively older modern stands assumed to represent developmental sequences of single stands in time). However, stands of a chronosequence cannot be controlled for differences in stand histories, such as differences in early establishment or in subsequent minor disturbance (e.g. Franklin 1989, Pickett 1989, Spies

and Franklin 1991, Fastie 1995). The current study addresses some of these uncertainties by using tree-ring records to reconstruct a detailed history of the structural development over the entire life of an old-growth Douglas-fir stand (e.g. Henry and Swan 1974, Oliver and Stephens 1977, Stewart 1986a, Maguire and Hann 1987, Fastie 1995), with particular focus on 1) stand initiation, and 2) canopy disturbances (i.e. disturbance less severe than a stand-replacing disturbance). This reconstructed history will be of considerable value to the management of old-growth Douglas-fir forests.

STUDY AREA AND FOREST TYPE

This study focuses on forests dominated by Douglas-fir and western hemlock (*Tsuga heterophylla*) in the *Tsuga heterophylla* 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 true climax species. Old forests of this type are the primary example of old-growth ecosystems in western Oregon and Washington.

Prior to Euro-American settlement, the widespread dominance of Douglas-fir in this region was largely due to immense but infrequent wildfires (Agee 1991). In this forest type, Douglas-fir acts as a long-lived, relatively shade-intolerant pioneer that does not generally establish naturally within closed stands except on very dry sites or in gaps larger than 750 to 1000 m² (Franklin and Dyrness, 1973, Spies and Franklin 1989, Spies et al. 1990). Western hemlock is the primary shade-tolerant species, although it may also act as a pioneer species. Stands up to ca. 100 years are considered to be ecologically young, and those ca. 100 to 200 years are considered to be ecologically mature (Franklin et al. 1981). Stands older than ca. 200 years generally share a suite of structural features that broadly distinguish them as old-growth Douglas-fir (Franklin et al. 1981, Spies and Franklin 1988, Franklin and Spies 1991, Marcot et al. 1991). These features include:

1. *Live old-growth Douglas-fir trees.* These trees are commonly 50 to 90 m tall and 1 to 2 m in dbh (diameter at breast height), with very long, large, and complex crowns extending from the top of the tree to 20 to 40 m above the ground. Branches are

generally irregularly distributed, and include large and complex branch structures where multiple large-diameter branches merge together close to the bole. These trees generally colonized centuries ago following catastrophic disturbance, then grew to their massive sizes and complex structures while other trees died and more shade-tolerant trees became established. Collectively, these Douglas-fir can constitute a major portion of the total biomass of a stand even though they may be greatly outnumbered by the shade-tolerant trees. The large old Douglas-fir trees give old-growth forests much of their character, from the canopy to the forest floor.

2. *Shade tolerant trees (primarily western hemlock) with a wide range of diameters, heights, and ages.* The presence of these trees contributes to a deep, multilayered canopy.

3. *Large snags and downed logs (i.e. 'coarse woody debris').*

4. *Spatial variability, i.e. "patchiness", in structural characteristics.* Patchiness is a stand-scale structural feature created by variations in the spatial distribution of the individual characteristics described above. The spatial patchiness of these forests is not regularly cited in lists of old-growth features, but is commonly noted by researchers who work in these forests (J.F. Franklin personal communication, personal observation).

Old-growth structures are important for a variety of production, habitat, material cycling, and material retention functions in forests and streams (e.g. Pike et al. 1977, Maser et al. 1979, Thomas et al. 1979, Franklin et al. 1981, Maser et al., 1988, Carey et al. 1991, Corn and Bury 1991, Ruggiero et al. 1991). For example, the large live Douglas-fir and western hemlock trees represent a huge surface area where many community and ecosystem processes occur. These trees host a large community of epiphytes (including nitrogen fixers), vertebrates, invertebrates, and bacteria (e.g. Pike et al. 1977, Franklin et al. 1981, Carey et al. 1991, Corn and Bury 1991). They also moderate the environment by influencing the cycling of nutrients, water, air and light. A comparable, but little understood, influence exits below ground where large root systems affect the physical,

chemical, and biotic properties of the soil. In addition, these trees contribute to the forest floor as they continuously shed their needles, branches, bark, and roots, and after death provide large snags and logs that continue to influence ecosystem processes, potentially for centuries.

For this study, I conducted an extensive search using aerial photographs, old-growth inventory maps (Morrison et al. 1991), forest service timber sale information, and ground reconnaissance to locate a suitable old-growth Douglas-fir stand that was a pre-harvest timber sale. This allowed collection of data prior to and after the trees were cut, but did not require old-growth trees to be cut for the express purpose of the study. Placement of the study in a pre-harvest sale allowed assessment of the characteristics of the old-growth stand in a way that would not be possible had the study been placed in a clearcut. For example, patchiness within the stand would be very difficult to evaluate after the trees were cut. The site chosen for the study ("Yellowjacket", lat. 46°21.7'N, long. 121°51.5'W, elev. 670 to 730 m) is in the Yellowjacket Creek drainage in the Gifford Pinchot National Forest, on the western slope of the Washington Cascade Range (Figure 1, Figure 2).

ORGANIZATION OF THE DISSERTATION.

Chapter 2 presents the reconstruction of the stand initiation of Yellowjacket. Chapter 3 presents the reconstruction of the history of canopy disturbances over the life of Yellowjacket. Appendices A-D present more detailed descriptions of some aspects of the sampling and reconstruction techniques used in this study.

AVAILABILITY OF STUDY DATA

This study generated a large set of data that will be placed in the Forest Science Data Bank managed jointly by Oregon State University and the USDA Forest Service Pacific Northwest Research Station.
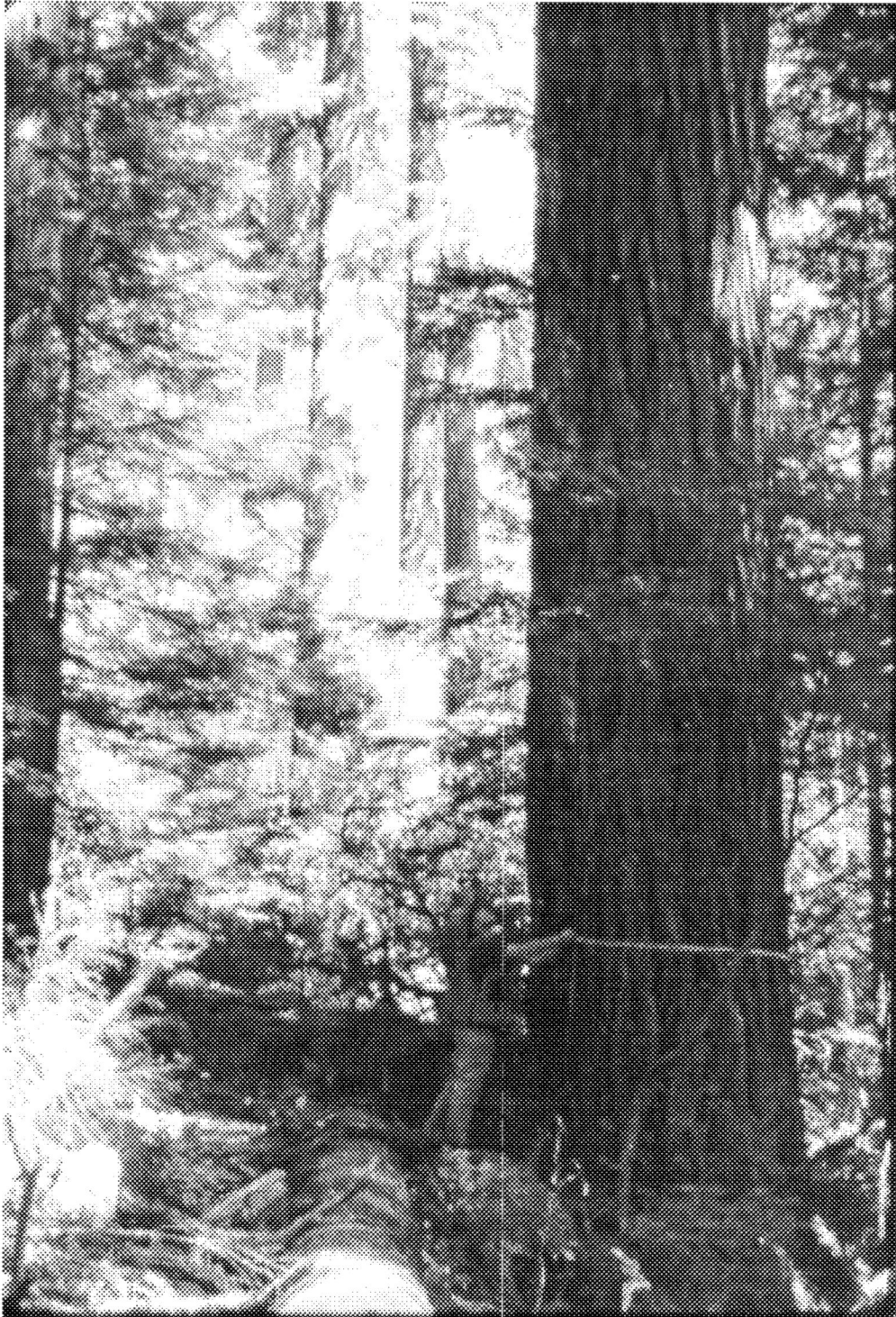
Figure 1. General view of the forest at Yellowjacket.

The old-growth Douglas-fir forest at Yellowjacket in 1992, prior to its cutting. Linda Winter is preparing to measure the dbh of a live Douglas-fir tree. The understory trees are western hemlock.

CHAPTER 2
STAND INITIATION FOLLOWING A CATASTROPHIC DISTURBANCE

INTRODUCTION

In the Pacific Northwest, several studies have suggested that the stand initiation stage of existing old-growth Douglas-fir forests differed substantially from that of most modern young (< ca. 100 years) naturally regenerated and planted Douglas-fir stands in the region (Franklin and Waring 1980, Franklin et al. 1981, Franklin and Hemstrom 1981, Stewart 1986a, Oliver and Larson 1990, Yamaguchi 1993, Tappeiner et al. 1997). The possibility of differing early histories for old-growth compared to young stands is of particular concern in this region where management policies have been shifting toward increased emphasis on maintaining and developing old-growth forests. 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 will 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 (Oliver, 1990). The timing and spatial patterns of tree invasion during stand initiation will leave structural imprints that persist for many decades (Oliver and Larson 1990). 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 an age distribution. In modern young stands, Douglas-fir commonly establish over a fairly narrow interval (5 to 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 to 265 years; Franklin and Waring 1980, Franklin and Hemstrom 1981, Stewart 1986a, 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). Various hypotheses have been offered to explain these prolonged intervals of initial establishment including multiple disturbances, lack of seed source following an extensive fire, and competition from shrubs or hardwood trees (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 (40 to 180 years for 4 stands; Yamaguchi 1993).

A second suggested difference between the stand initiations of currently old versus young stands concerns the initial densities 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 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 young stands. Two reviews hypothesized wide initial spacings in old-growth stands based on the structure of the Douglas-fir trees, and 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 to 2 m in diameter, and 50 to 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 tree grows tall.

Franklin et al. (1981) hypothesized wide initial spacing in old-growth stands based on the contrasting crown structures of old-growth Douglas-fir versus Douglas-fir in 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-fourth of the bole. Franklin et al. (1981) proposed that the long crowns of old-growth Douglas-fir 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 existing old-growth trees. 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 (J.F. Franklin personal communication). However, no previous study has documented the development of an old-growth Douglas-fir crown.

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 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 1986a, Maguire and Hann 1987, Fastie 1995) to investigate the stand initiation phase of an old-growth Douglas-fir stand in the Gifford Pinchot National Forest in the Washington Cascades. To address some of the existing uncertainties, I asked the following questions:

1. What was the duration of Douglas-fir colonization following a stand-replacing disturbance?

2. Did western hemlock successfully establish concurrently with Douglas-fir?

3. What was the initial spacing of Douglas-fir and how does it compare with currently young stands?

4. What was the history of early development for the large (long) Douglas-fir crowns?

5. Was there a single standwide period of relatively open growth conditions and, if so, how long did it persist?

This study is the first part in a two-part reconstruction of Yellowjacket's history, and will complement the second part of the study, i.e. the reconstruction of the history of canopy disturbances.

METHODS AND RATIONALE

Yellowjacket study site

Physical environment of study stand. The Yellowjacket study site was established in a pre-harvest old-growth Douglas-fir timber-sale in the Cascade Mountains of western Washington (Gifford Pinchot National Forest, Figure 2). Yellowjacket was on an east-facing slope (35%), 30 to 90 m above Yellowjacket Creek at lat. 46°21.7'N, long. 121°51.5'W, elev. 670 to 730 m. The Douglas-fir site index (m at 50 years), evaluated from neighboring plantations on similar sites, is 36 to 39 m (E. Tompkins, personal communication). Mean annual precipitation is ca. 244 cm, with most falling November to May; January mean minimum and mean maximum temperatures are -7 and 0° C, respectively; July mean minimum and mean maximum temperatures are 9 and 22° C, respectively (Gifford Pinchot National Forest 1971 a, Phillips, 1972). The soil is well drained, derived primarily from volcanic ash and pumice; bedrock consists of hard andesites and andesitic breccias (Gifford Pinchot National Forest 1971 a,b). A soil pit at the base of a Douglas-fir revealed that the bulk of the roots near the bole were buried by about half a meter of accumulated material (Appendix B). There was abundant charcoal surrounding the roots, but not above them.

Vegetation. Yellowjacket was in a forest type denoted as "Douglas-fir forest" (as described in Chapter 1) in the *Tsuga heterophylla* Zone (Franklin and Dryness 1973). The stand was free of intrusive management before it was clearcut in 1992. The main canopy was dominated by Douglas-fir and western hemlock, with a minor presence (< 10% of canopy trees) of western redcedar (*Thuja plicata*). A few large western white pine (*Pinus monticola*) snags indicated that this species also was at one time a minor component of the canopy. Douglas-fir were the tallest trees, ca. 65 m, with live crowns covering half the total tree height. The canopy was irregular in height and fairly closed, with occasional small gaps. Densities of all live Douglas-fir and of live western hemlock ≥ 40 cm dbh (i.e. diameter at breast height; 1.4 m) were 14 and 73 trees/ha, respectively. Maximum diameters for these species were 190 and 146 cm, respectively (Figure 3). The minimum

dbh for Douglas-fir was 75 cm. Snags of all decay classes were abundant (ca. 70 snags/ha), and many were > 50 cm in diameter and > 5 m tall. Logs of all decay classes were also numerous. In most areas the understory was dominated by western hemlock, pacific yew (*Taxus brevifolia*), vine maple (*Acer circinatum*), Oregon grape (*Berberis nervosa*) and sword fern (*Polystichum munitum*). Devil's club (*Oplopanax horridum*) or salal (*Gaultheria shallon*) were common in wet and dry microsites, respectively. Conifer seedlings and saplings were predominantly western hemlock; Douglas-fir regeneration was absent.

Yellowjacket met the standards for old-growth forests set in 1986 by the Old-Growth Definition Task Group (Marcot et al., 1991), with the exception of a slightly lower density of live old-growth Douglas-fir trees (> 81 cm dbh or > 200 years old) than the standards (≥ 20 trees/ha). However, recently fallen Douglas-fir would bring Yellowjacket to ≥ 20 trees/ha in the near past. An additional check on the old-growth status of Yellowjacket is provided by a comparison with data from Franklin and Spies (1991). The Yellowjacket densities of live trees > 100 cm dbh (Douglas-fir > 100 cm dbh, 13 trees/ha; all species > 100 cm dbh, 28 trees/ha) were similar to those in old-growth Douglas-fir stands of a moderate moisture-class in Washington (Douglas-fir > 100 cm dbh, mean 15 trees/ha; all species > 100 cm dbh, mean 22 trees/ha; Franklin and Spies 1991).

Pre-harvest field work

All live Douglas-fir, all live western hemlock ≥ ca. 40 cm dbh, and all snags within a 3.3 hectare study plot were tagged prior to the stand's harvest. The 40 cm lower limit for the western hemlock was judged sufficient to meet the study objectives within the time constraints. 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, although the western hemlock varied considerably with respect to their height within the deep canopy.

Post-harvest field work

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", Appendix B). Each sample included a full radius, i.e. the wood from pith (if present) 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 (measured relative to the stump surface) and contained a full bole radius. These trees, herein referred to as the "dissected Douglas-fir", were at locations scattered throughout much of the sand and were visually representative of dominant Douglas-fir in the stand. These 20 dissected trees were sampled at 3 intensities: intensively (1 tree), partially (10 trees) and minimally (9 trees). The differing sampling intensities complemented one another for the analyses of initial spacing and crown history. The uppermost sample position for each tree was not the full 1992 height because of damage to tops during felling. .

   a. *Intensively dissected Douglas-fir #1408.* For one dominant Douglas-fir, tree 1408, samples were cut from the bole at 61 heights for reconstructing the height history and recession of the live crown base to the height of the 1992 crown base (Figure 4, Appendix A). 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 (relative to the stump surface) 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 logs along the pith (Appendix A).

The only live branch that was sampled was at the base of the 1992 crown (33.2 m above the stump surface). This branch was sampled as a bole wedge including pith and bark and containing the portion of the branch that was integrated into the bole. Above this, cross-sections were cut for reconstructing height growth, but no branches were sampled.

b. *Partially dissected trees.* The boles of 10 dominant Douglas-fir were sampled at 5 to 11 (average of 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. Four western hemlock trees were similarly partially dissected.

c. *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, crossdating, and measurement of ringwidths

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 (Figure 5, 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 (arranged to intersect the branch pith, (Figure 6). For a subset of branches, a few slices per branch were cut in multiple orientations and prepared to provide a check on the repeatability of identifying the timing of branch death. All samples were examined under a binocular microscope, and each bole ring was assigned a calendar year by crossdating 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 samples, 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 not dated (not required) except at their convergence with crossdated bole rings. Ringwidths of 52 samples (30 Douglas-fir, 22 western hemlock) were measured with a Henson–Bannister Incremental Measuring Machine (accuracy ± 0.01 mm). Twenty-five of the measured series, those without intervals of suppression, were used to develop the master dating series.

Evaluation of individual samples

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

1. *Center date.* Stump-samples were assigned exact (n=225), estimated (n=9), or missing (n=56) center dates depending on whether the pith was present, missing by ≤ 1 cm, or missing by > 1 cm (Table 1). An exact center date is the calendar year of the innermost ring of the bole. An estimated center date is the estimated decade of the center (e.g., 1880, 1890 etc.). Center dates were assigned to those samples taken from above stump-height only if an exact date was available.

2. *Radius at 20 years and at the beginning of each decade.* For each stump-sample, numerous radii were measured using a ruler and magnification. These radii were the distances (± 0.5 mm) from the bole pith to the outer edge of: the 20th ring from the center, the first ring in each decade, and the 1992 ring. For a subset of samples, radii were measured for alternate decades. For the dissected trees, radii were not measured (not required) for samples above the stump.

3. *Growth-changes.* Measured only for stump-samples, these are changes in ringwidth that were abrupt (achieved within ≤ 3 years) and sustained (i.e. ringwidths prior to and following the change had to each be relatively constant for ≥ ca. 10 years) (Chapter 3). A growth-change was designated as either a "growth-increase" or "growth-decrease". The growth-change date was assigned as the date of the earliest ring of the growth-change. Growth-changes were used in the evaluation of ringwidth patterns as discussed later.

4. *Date of branch origin*. In a sample containing a branch, the date of the bole center was assigned as the date of branch origin.

5. *Date(s) of branch death* (Figure 6). Several studies have shown that branch death is often a gradual process. Branches in the lower portion of a receding crown may experience a period of low vigor prior to dying, during which they may not produce growth rings and may be sparsely foliated (Andrews and Gill 1939, Maguire and Hann 1987, Kershaw et al. 1990). It is typical for Douglas-fir to have many sparsely foliated branches near the crown base (Maguire and Hann 1987). Based on these observations, 2 variables were defined to describe the interval over which a branch was dying: 1) *Latest Functionally Live Date (LFLD)*, i.e. the latest date at which the branch was producing rings and was hence functionally live, and 2) *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 (see Appendix C).

Analysis for duration of initial establishment

Stump-height center dates were used to approximate dates of tree establishment. I estimated that Douglas-fir took 2 to 5 years to reach stump-height, western hemlock that established with Douglas-fir took 6 to 8 years, and western hemlock that established later likely took longer. This estimate is based on the average height of stump-samples above the 1992 ground (ca. 0.8 m) and the depth of accumulated material above the Douglas-fir roots (about half a meter, Appendix B), combined with height growth from this study (Figure 9, Figure 26) and data from nearby plantations on similar sites,

Analysis for average initial spacing of Douglas-fir trees.

Rationale. The approach used for the analysis is based on the demonstration that dbh growth in the youth of a Douglas-fir stand is strongly controlled by initial spacing (Reukema, 1979, Oliver et al 1986, Oliver and Larson 1990). However, while diameter-vs-age curves are characteristic of initial spacings within a uniform site, they are not characteristic across sites of different quality (Oliver et al. 1986). Plotting average dbh growth, instead, as a function of dominant tree height results in a growth curve that is characteristic of that stands initial spacing, and is relatively independent of site quality (Reukema, 1979; Oliver et al 1986, Smith and Reukema 1986, Oliver and Larson 1990, Wilson 1998). $Height_{Dom}$ is used to denote the average measured tree height for representative dominant Douglas-fir at any given time (as used in Oliver et al. 1986, Wilson 1998). Dbh_{avg} is the average of the diameter at breast height for the subject trees. The relationship between these values will be referred to as $Dbh_{avg}\text{-}vs\text{-}Height_{Dom}$.

The fact that Dbh_{avg}-vs-$Height_{Dom}$ is dependent on initial spacing has been demonstrated for spacing trial results (Oliver et al. 1986, Oliver and Larson 1990), and for an extensive dataset from permanent plots in plantations and naturally regenerated stands (Wilson 1998). When stands of differing initial spacing are plotted in this manner, a family of curves is generated that are conspicuously ordered according to initial spacing. This characteristic relationship was used to allow the determination of initial spacing of Douglas-fir at Yellojacket by comparison to data from stands of known initial spacing.

Several additional points were also considered in making comparisons used in this study:

1. The Dbh_{avg}-vs-$Height_{Dom}$ comparisons focus on the dominant Douglas-fir for each stand (or largest 250 trees/hectare for the spacing trials). This class of trees will most strongly reflect initial spacing since their height and diameter growth are not reduced by shade from above (Oliver and Larson 1990, Wilson 1998). Wilson (1998) showed that the average dbh of the largest 250 Douglas-fir per hectare, at a given average height, is strongly and predictably influenced by the average initial spacing of all Douglas-fir.

2. Determination of initial spacing was made from stages of growth only within the proven range of the relationship between height growth and dbh growth. As stands age, eventually height growth will uncouple from dbh growth because height growth slows substantially while dbh growth continues (Oliver and Larson, 1990). After this point, the relationship between dbh-vs-height and initial spacing has not been tested. The spacing trial results are for stands whose height and dbh growth have not uncoupled, as can be seen from examination of their Dbh_{avg}-vs-$Height_{Dom}$ curves (Oliver et al. 1986).

3. At a given $Height_{Dom}$, natural stands tend to have a slightly greater average dbh than do plantations with the same initial spacing (Wilson 1998). This difference is apparently related to the greater differentiation of tree diameters that occurs in natural stands compared to plantations.

4. The average initial spacing determined from Douglas-fir Dbh_{avg}-vs-$Height_{Dom}$ curves was taken to represent the average initial distance between Douglas-fir trees, or between Douglas-fir and equally strong competitors (i.e. fast-growing species such as western white pine, red alder, bigleaf maple or grand fir), but not between Douglas-fir and weaker competitors (i.e. slower-growing species such as western hemlock and western redcedar). Wilson (1998) showed that in mixed species stands, the initial densities of western hemlock and western redcedar have little impact on the relationship of Dbh_{avg}-vs-$Height_{Dom}$ for Douglas-fir. However, it is possible that stronger competitors (i.e. western white pine, red alder and bigleaf maple) would have greater impact on Douglas-fir development; such species were not tested by Wilson (1998).

5. Since results have not been reported for trials of Douglas-fir spacings > ca. 5 m (Oliver et al. 1986, Smith and Reukema 1986), the question arises whether there is an upper spacing limit for the influence of initial spacing on diameter growth. Smith and Reukema (1986) addressed this question and concluded that diameter growth should

continue to increase with increased initial spacing up to very wide spacings (at least to 9 m).

6. There is no single point in time when the initial spacing of a natural stand as a whole can be defined because initial colonization may occur over an interval of time. Initial spacing is used here to refer to the local spacing experienced by a tree when it comes into direct competition with adjacent neighbors, and its crown begins to recede and its diameter growth slows.

Given the above, the process for estimating the average initial spacing of Yellowjacket Douglas-fir is summarized by the following steps:

1. Construct a graph of Dbh_{avg}-vs-$Height_{Dom}$ values from the reconstructed histories of Yellowjacket dominant Douglas-fir.

2. Compare the reconstructed curve for Yellowjacket to Dbh_{avg}-vs-$Height_{Dom}$ values for Douglas-fir in currently young stands. The average initial spacing of the Yellowjacket Douglas-fir was considered to be most similar to the initial spacing of the comparison stand whose Dbh_{avg}-vs-$Height_{Dom}$ value(s) fell closest to the Yellowjacket curve.

The implementation of these steps is described below.

Step 1: Reconstruction of Dbh_{avg}-vs-$Height_{Dom}$. The Yellowjacket Dbh_{avg}-vs-$Height_{Dom}$ values used in the analysis of initial spacing were reconstructed using data from the 20 dominant dissected Douglas-fir (1 intensively, 10 partially, and 9 minimally dissected trees). The reconstruction for these trees involved 4 steps: a) reconstruction of individual trees height-vs-date histories; b) reconstruction of individual trees dbh-vs-date histories; c) compilation of individual dbh-vs-height values based on data collected in steps a & b above; d) averaging of values determined in c to obtain Dbh_{avg}-vs-$Height_{Dom}$ values

a. *Reconstruction of height histories (individual tree height at date).* Height histories were reconstructed for the 11 partially and intensively dissected Douglas-fir using center dates and corresponding sample heights. The measured sample heights were corrected for average stump-height (ca. 0.8 m) plus the approximate depth of

accumulated material above the 1500 ground (ca. half a meter, Appendix B) to give the height of the sample above the estimated 1500 ground level. This level was used 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. For each of the 9 minimally dissected Douglas-fir, a single upper (above stump-height) height-at-date value was similarly reconstructed.

b. *Reconstruction of dbh histories (individual tree dbh at date).* Dbh histories were reconstructed for the 20 dissected Douglas-fir and for 39 additional Douglas-fir that were not dissected. The latter were used to show whether the reconstructed dbhs for the dissected Douglas-fir were similar to those for all Douglas-fir. For each of these 59 trees, dbhs for the beginning of each decade in the record were calculated by doubling the corresponding stump-height radii (inside bark) and correcting for bark thickness using equations derived from Johnson (1955). An evaluation of the sources of potential error in this technique indicated negligible errors, and that any systematic errors would tend to overestimate dbh (see Appendix B).

c. *Compilation of reconstructed individual dbh-vs-height for the 20 dissected Douglas-fir.* The height and dbh values reconstructed for each tree in a & b are parametrically related, with date as the parameter (Hill & Linker, 1938). To represent dbh directly as a function of height, the height and dbh for a given tree at identical dates are selected and plotted on a graph with height and dbh as the independent and dependent axis, respectively. By design, date information is no longer present as an axis of this graph, but has been retained as a label whose only purpose is to annotate the source of the individual points.

Due to the nature of the sampling, dbh was readily available for all decade boundaries, but height was only known at the center dates of the individual height samples for a particular tree. Height values to correspond with the exact date of a particular dbh were obtained by interpolating between sampled heights. For each of the 11 intensively and partially dissected trees, height was interpolated for a given

dbh date only if the reconstructed height history had sufficient points near that date to assure accurate interpolation. For each of the 9 minimally dissected trees, a height was estimated only for the dbh date closest to the date for the one reconstructed height. The accuracy of this one-point estimate was enhanced using curves from the more closely dissected trees as examples. The maximum height error in this procedure is estimated to be ± 0.5 m for the intensively and partially dissected trees, and ± 1.0 m for the minimally dissected trees.

d. *Determining Dbh_{avg}-vs-$Height_{Dom}$.* For a particular date, the individual dbh values that had associated heights were averaged to obtain Dbh_{avg}. The associated individual height values were averaged to obtain the corresponding $Height_{Dom}$. These averages were then plotted, as described above, to yield a single point on a graph of Dbh_{avg}-vs-$Height_{Dom}$. This process was repeated for other dates to create a growth curve representing average values throughout the life of the stand. The resulting graph would be analogous to long-term monitoring of a permanent plot, measuring average dbh and average height for the dominant Douglas-fir at regular intervals through the centuries.

Step 2: Comparison to stands of known initial spacing. The average initial spacing for Yellowjacket was determined by comparison with the Wind River spacing trials and with 3 natural stands:

The Wind River spacing trials have been ongoing since 1925 at the Wind River Experimental Forest near Carson Washington (Figure 2) (elevation 400 m, Douglas-fir site index ca. 24 to 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, taken from Reukema (1970, 1979) and Curtis and Reukema (1970).

The 3 natural stands used for comparison (Butte, Paradise Hills, and Little White Salmon) 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 et al. 1999). These stands span a range of tree ages and densities (Table 2). Butte, ca. 70 years old, has tree structures typical of many contemporary young natural stands in the area, and has the highest tree density of the 3 comparison stands (ca. 800 Douglas-fir/ha, equivalent to 3.5 m spacing). 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 as part of the DEMO study (currently unpublished data). Diameter, crown class and total height were measured for 40 trees per species in each of six 13-ha treatment units at each site (yielding a total of 240 trees per species per site). Trees within each treatment unit were selected as a conditional random sample, with the condition that both the smallest and the largest tree in the sample were within 5% to 10% of either extreme of a diameter distribution determined from a large random sample. The selected trees were also chosen to adequately reflect the vertical structure of the stand. The numbers of dominant Douglas-firs measured and used in the current study were: Butte n = 41, Paradise Hills n = 44; Little White Salmon, n = 31).

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 #1408, height growth and recession of the crown base were reconstructed by graphing data from all samples for this tree. The graphed variables were: center dates, LFLDs (branch Latest Functionally Live Dates), EDDs (branch Earliest Dead Dates), and sample heights. For a series of selected dates, the heights to the tree's top, and to the crown base (CB1 and CB2, defined below) were determined from the graphed data as follows:

1. *Top of tree 1408.* The height of the tree's top for a selected date between 1505 (center date at stump-height) and 1837 (center date of uppermost sample) was interpolated (± 0.5 m) from the graph of sample heights-vs-center dates. The 1992 height was estimated by extrapolation from the uppermost sample at 68.2 m (center date of 1837). The germination date was estimated to be 5 years less than the stump-height center date.

2. *Base of the functionally live crown for tree 1408: (CB1; Crown Base 1).* CB1 for a given date was defined as the height of the lowest branch that was functionally live at that date (i.e. the Latest Functionally Live Date for the branch was at or later than the selected date). This definition placed CB1 at the abrupt base of a functionally live crown consisting of all, or almost all, live branches. This method of determining the lower extent of the live crown was found to produce results consistent with measures used in other studies of Douglas-fir crowns (Maguire and Hann 1987). For the earliest period in the reconstruction, 1500 to 1525, the height of CB1 was determined by extrapolation because of the 1.8 m gap in sampling between the lowest sampled branch and the 1500 ground. LFLDs were extrapolated (5 years) to estimate the latest date for which ground level branches were functionally live. Because this date was determined to be 1525, the CB1 height was set to 0 for dates from 1500 to 1525.

3. *Base of the zone of dying branches for tree 1408 (CB2; Crown base 2).* CB2 for a given date was defined as the height of the lowest branch that was not yet dead (i.e. the Earliest Dead Date for the branch was later than the selected date). This definition places CB2 at the base of a zone of dying branches below CB1. Between CB1 and CB2 no branches were functionally live; below CB2, all sampled branches were dead. For the earliest period in the reconstruction, 1500 to 1530, the height of CB2 was determined by extrapolation because of the 1.8 m gap in sampling between the lowest sampled branch and the 1500 ground. EDDs were extrapolated (5 years) to estimate the latest date for which ground level branches were finished dying. Because this date was determined to be 1530, the CB2 height was set to 0 for dates from 1500 to 1530.

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 that had a total of 28 embedded branches fortuitously included in stump-samples or in samples from partially-dissected trees.

<center>*Analysis for initial open growth conditions.*</center>

Two lines of evidence can be used to identify whether a tree at an early age was growing in relatively open conditions or beneath a closed canopy: 1) juvenile radial growth rates and 2) long-term ringwidth patterns (Lorimer et al. 1988, Lorimer and Frelich 1989). This evidence was used to reconstruct the presence and duration of open-growth conditions.

1. *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). A scatterplot of juvenile radial growth rate (represented by the radius at 20 years) versus establishment date (represented by center date at stump-height) for Douglas-fir and western hemlock was examined for evidence of a standwide transition from open to closed canopy conditions.

2. *Long-term ringwidth patterns* (Figure 7). Two types of long-term ringwidth patterns low on the bole (i.e. near breast height) have been interpreted as deriving from 1) tree establishment in relatively open conditions or 2) tree establishment beneath a closed canopy of trees or shrubs (Lorimer 1985, Lorimer et al. 1988, Lorimer and Frelich 1989, Canham 1985 and 1990, Fastie 1995). An "open" pattern is characterized by 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, usually by a combination of gradual and abrupt decreases in growth rate. In a "closed" pattern there is no early peak in radial growth rate, but instead there is low early growth followed after years or decades by an abrupt increase in ringwidth. "Other" patterns may occur that are due to establishment under conditions other than those described above (i.e. establishment in open but dense conditions).

All stump-samples with center dates (233 trees) were evaluated for whether the ringwidth pattern of each was open, closed, or other. To classify the ringwidth pattern, the following questions were asked: 1) Was the early growth rate (radius at 20 years) clearly the highest in the life of the tree? 2) Was there a clear ringwidth peak in the first few decades? 3) Was the first growth-change in the life of the tree a growth-increase or a growth-decrease? If the answers to questions 1 and 2 were yes, and the first growth-change was a decrease, the ringwidth pattern was classified as open. If the answers to 1 and 2 were no and the first growth-change was an increase, it was classified as closed. Otherwise, it was classified as other. The direction of the first growth-change was the single most objective discriminator between the pattern types. Whereas the answers to questions 1 and 2 required examination of the radii for all decades over the life of the tree, the answer to question 3 was decided by a single variable.

RESULTS

Duration of initial establishment

The stump-height center dates of Douglas-fir ranged from 1500 to 1521 (57 exact, 1 estimated), while western hemlock ranged from 1508 to 1897 (167 exact, 8 estimated), and the date of one western white pine was 1507 (exact) (Figure 8; Table 1). The centers 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 centers of most western hemlock (165) post-dated 1540, with dates falling in broad interval of higher establishment (1540-1610, 1680-1779) and lower establishment (1610-1679, 1780+). The decreasing numbers after the 1780+ peak is an artifact of the 40 cm minimum dbh limit for sampling of western hemlock.

Initial spacing of Douglas-fir

Height, dbh, and Dbh$_{avg}$-vs-Height$_{Dom}$ histories for Yellowjacket Douglas-fir. The average height of the 20 dissected Douglas-fir increased rapidly and continuously until ca. 1550 to 1570, and more slowly after this (Figure 9). By ca. 1600 the average rate of height growth had slowed considerably, yet over the ensuing centuries significant additional height accrued (Figure 9). Twenty-seven percent of the average height in 1800 was attained in the second and third centuries of growth. No tree had abrupt increases in height growth suggestive of release from a suppressed state, indicating that these trees were dominant throughout their lives. One tree did have an abrupt decrease in height growth in the mid 1500s (Figure 14, tree 1187), coincident with a massive injury to its bole. For this tree, only heights prior to the injury are included in the analysis for initial spacing. For each of the 9 minimally dissected trees, the single upper height-at-date value fell close to the curves for the more closely dissected trees.

For the 20 dissected Douglas-fir, the average dbh increased rapidly until ca. 1540, when the dbh growth rate transitioned to a slower rate (Figure 10). This pattern is very similar in shape and magnitude to the pattern of average dbh growth for all sampled Douglas-fir (n = 59) (Figure 10). 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 Dbh$_{avg}$-vs-Height$_{Dom}$ for the dissected trees shows a gradual increase in dbh until a height of about 45 m (attained in ca. 1600), soon after which dbh began to rise more steeply (Figure 11). The sharp post-1600 rise reflects the uncoupling of dbh growth from height growth, i.e. height growth in the late 1500s slowed considerably (Figure 9) while the dbh growth continued at approximately the same rate (Figure 10).

Comparison of Yellowjacket to natural stands and spacing trials. The Dbh$_{avg}$-vs-Height$_{Dom}$ value for dominant Douglas-fir at Butte (800 Douglas-fir/ha, ca 3.5 m spacing, Table 2) was closer to the Yellowjacket curve of Dbh$_{avg}$-vs-Height$_{Dom}$ than were values for Paradise Hills (190 Douglas-fir/ha, ca. 7.3 m spacing) or Little White Salmon (124

Douglas-fir/ha, ca 9 m spacing) (Figure 11). For example, the Dbh_{avg} and $Height_{Dom}$ for Douglas-fir at Butte (38.8 cm, 30.2 m, respectively) were close to the corresponding values for Douglas-fir at Yellowjacket in 1550 (42.3 cm, 29.7 m, respectively). In contrast, the Dbh_{avg}-vs-$Height_{Dom}$ values for dominant Douglas-fir at Paradise Hills and Little White Salmon fell considerably above the Yellowjacket curve. The Little White Salmon value was above that portion of the Yellowjacket curve where Dbh_{avg} had uncoupled from $Height_{Dom}$.

The similarity of Butte Douglas-fir to Yellowjacket Douglas-fir in their youth is even more apparent in a comparison of dbh-vs-height values for individual trees (Figure 12). 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 (Figure 12). Although the height growth for this tree was not unusual, until the late 1500s its dbh at any date was far above all other Douglas-fir in the stand. With this atypical tree omitted, the Dbh_{avg} and $Height_{Dom}$ for Yellowjacket Douglas-fir in 1550 were 38 cm and 29.7 m, respectively, remarkably close to the Dbh_{avg} and $Height_{Dom}$ for Butte Douglas-fir (38.8 cm and 30.2 m, Fig. 11).

The comparison with the spacing trials was made with the knowledge that plantation stands tend to have slightly lower average diameters at a given dominant height than do natural stands with comparable initial spacing. The curve of Dbh_{avg}-vs-$Height_{Dom}$ 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 Dbh_{avg}-vs-$Height_{Dom}$ curve for Yellowjacket in 1530-1550 (Figure 11). For example, the $Height_{Dom}$ for Yellowjacket in 1540 was very close to the $Height_{Dom}$ for the 3.7 m spacing trial at 43 years: 24.3 and 24 m respectively. The corresponding average dbhs at these heights were 36.6 and 30.7 cm. The curves for the other spacings (3.0, 2.4, 1.8, 1.5 and 1.2 m) at Wind River fell below the 3.7 m spacing curve.

Development of long Douglas-fir crowns

Crown length development for Douglas-fir #1408. This tree was representative of other dominant Douglas-fir at Yellowjacket. For example, its 1992 crown form (Figure 4) was visually similar to the crowns of dominant Douglas-fir in the stand; its dbh history was close to the average history for all Douglas-fir until ca. 1660, after which it diverged somewhat from the average (Figure 10); and its height history was close to the average history for the dissected trees (Figure 9). The reconstructed crown history for tree 1408 can be roughly divided into 3 intervals (Figure 13 a,b):

1. *1500 to 1525. Before crown closure.* Tree 1408 germinated ca. 1500. Its height increased slowly until about 1510, then rapidly throughout the remainder of this interval. The base of the functionally live crown (CB1) remained at the ground level until 1525; at this time, it was 13.1 m long.

2. *1525 to 1630. Crown closure to start of stabilization (29.7 m, Figure 4).* CB1 and CB2, bracketing the zone of dying branches, began to recede (rise above the ground) shortly after 1525 and 1530, respectively, marking the beginning and completion of the tree's crown closure (Oliver and Larson, 1990). From these dates until ca. 1600, CB1 and CB2 each receded somewhat more slowly than the rate of continuing tree height growth, with an offset (0 to 6.6 m, avg 1.5 m) between these two bases for any given date. In ca. 1600 the recession of CB1 and CB2 abruptly slowed. By 1630 the tree was ca. 130 years old and 52.1 m tall with both CB1 and CB2 at 29.7 m. At this time the functionally live crown was 22.4 m long with no zone of low-vigor branches. The functionally live crown had lengthened to 1.7 times what it was at the beginning of crown closure in 1525. This lengthening was accomplished with no observed epicormic branching from the bole, as all branches at and below 29.7 m were normal, nodal branches. That is, they were integrated with the bole, from pith to branch death, in an orderly manner with no evidence of epicormic processes.

3. *1630 to 1992. Stabilization of crown base.* During this interval CB1 and CB2 further receded to 34.6 m (their 1992 height) and stabilized at that height while tree height

continued to slowly increase to 71.4 m (1992 tree height). Thus between 1630 and 1992, the functionally live crown further lengthened, from 22.4 m in 1630 to 36.8 m in 1992, 2.8 times its length at crown closure.

Branch histories for other Douglas-fir. A total of 28 embedded branches were analyzed for 12 additional Douglas-fir trees. Although these trees had too few sampled branches to reliably reconstruct their crown-base histories, a graph for the sampled branches showing branch-heights-vs-LFLDs (latest functionally live dates), combined with the tree-height histories, can be used to suggest the early crown lengths for these trees in relationship to the crown history of tree 1408 (Figure 14). Eight of these trees had been dissected for height growth. All but one showed height growth similar to that for tree 1408; the exception (tree 1187) had reduced height growth in the mid to late 1500s. For 25 branches from 11 trees, the branch-heights-vs-LFLDs fell on or fairly close to the CB1 recession curve for tree 1408 in ca. 1500 to 1600, suggesting these trees and 1408 had similar early histories of crown-base recession and development of crown length. For 3 branches from one tree (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. This tree was also exceptional in that it had a massive injury to its bole in 1560 and a long double top in 1992; it may have lost its top when it was injured in 1560.

Duration of open growth conditions.

Juvenile radial growth rate. The 57 Douglas-fir that established before 1520 had relatively high juvenile radial growth rates of 4.6 to 14.4 cm/20-years (avg 10.1, Figure 15). The final Douglas-fir established in 1521 and had a substantially reduced juvenile growth rate of 2.6 cm/20-years. For the western hemlock, a shift in juvenile radial growth rates occurred in ca. 1540 (Figure 15). The rates for the 10 western hemlock establishing prior to 1540 (1.0 to 7.0, avg 3.04 cm/20-years) were generally higher than for 162 western hemlock establishing after 1540 (0.2 to 3.4, avg 1.27 cm/20-years). Juvenile growth rates for 3 additional western hemlock established after 1540 could not be

evaluated. The most apparent difference between the two groups of western hemlock was that none of the trees establishing prior to 1540 had juvenile radial growth rates < 1.0 cm/20-years, whereas 35% of the trees establishing after 1540 had rates < 1.0 cm/20-years.

Long-term ringwidth patterns at stump-height. 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 (Figure 16, Table 3). All of the open patterns were for trees that established prior to the cessation of Douglas-fir establishment in ca. 1521 (Table 3). Among the 165 western hemlock that established after 1540, none had open patterns, 146 had closed patterns, and 19 had other patterns (Table 3).

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 1986a, Yamaguchi 1993, Tappeiner et al. 1997). However, 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, with important implications for the management of Douglas-fir stands in the Pacific Northwest.

Yellowjacket stand initiation

Duration of initial establishment. The narrow range of establishment dates (1500 to 1521) for the Douglas-fir and western white pine suggests that shade-intolerant trees successfully colonized the site over two decades following a stand-replacing disturbance in the late 1400s (Figure 8). The abundance of charcoal surrounding Douglas-fir roots strongly suggests this disturbance was fire. This short colonization period 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 to 265 years) reported in most previous reconstructions of old-growth Douglas-fir stands (Franklin and Waring 1980, Franklin and Hemstrom 1981, Stewart 1986a, Yamaguchi 1993; Tappeiner et al. 1997).

The previous old-growth reconstructions sampled areas ranging from 0.8 to 18 ha; the plot size at Yellowjacket was 3.3 ha. The question arises whether the very different lengths of initial establishment intervals for Yellowjacket compared to these other reconstructions is simply a matter of scale. Among the previous studies, even the smallest plot (0.8 ha) had a 100 years interval of initial Douglas-fir establishment (Stewart 1986a), and one 10-ha plot, with an initial establishment interval of 265 years, had similar age distributions for separate habitat segments within the plot (Franklin and Waring 1980, Franklin and Hemstrom 1981). For these two studies, sampling area alone does not explain the wider intervals of initial establishment compared to Yellowjacket, although it may be a factor for some of the other reconstructions.

Initial spacing. Determination of initial spacing of the Yellowjacket Douglas-fir relied on the Dbh_{avg}-vs-$Height_{Dom}$ curve reconstructed from the dissected trees. These trees were visually representative of dominant Douglas-fir in 1992, and they appear to have been dominant throughout their lives, as shown by both their dbh and height histories. Thus the curve reconstructed from these trees was taken to represent the growth of dominant Douglas-fir throughout the life of the stand. I determined that the average initial spacing of the Yellowjacket Douglas-fir was most similar to the average initial spacing of the comparison stand whose Dbh_{avg}-vs-$Height_{Dom}$ value(s) fell closest to the reconstructed Yellowjacket curve.

Among the natural stands, the Dbh_{avg}-vs-$Height_{Dom}$ value for Butte fell closer to the Yellowjacket curve than did the values for Paradise Hills or Little White Salmon (Figure 11). The comparisons for Paradise Hills, and particularly Little White Salmon, may be somewhat complicated by the uncoupling of dbh growth from height growth. The Little White Salmon value clearly lies above that portion of the Yellowjacket curve where dbh

and height growth have uncoupled. The age of Paradise Hills (ca. 110 years) in comparison to the age of Yellowjacket (ca. 75 years), when they were of similar height, suggests that it may also have entered this phase of growth. Reliable inferences from comparisons with these sites is problematic, and is further compounded by the fact that only one data point is available from each of these sites. To my knowledge, no previous studies have provided Dbh_{avg}-vs-$Height_{Dom}$ curves for Douglas-fir forests, showing the timing and shape of the uncoupling for a stand. Until this uncoupling is more thoroughly explored, it is reasonable to use this study's example to project an expected curve where data is sparse, particularly among stands with relatively similar site indexes. When this is done, it is estimated that if curves were available for Paradise Hills and Little White Salmon they would lie further above the Yellowjacket curve than the Butte value lies below the curve, although the extent of this difference can not be determined precisely.

Regardless of the uncertainties involved in the comparison with Little White Salmon and Paradise Hills, it is clear that the Butte value is very close to the Yellowjacket curve, and that the stand is young enough that dbh and height growth are still strongly coupled. This supports the conclusion that Douglas-fir at Yellowjacket and Butte experienced similar average initial spacings. An estimate for the initial spacing of Douglas-fir at Butte is provided by the density of Douglas-fir at Butte at ca. 70 years: 798 trees per hectare (Table 2), equivalent to ca. 3.5 m spacing between Douglas-fir trees. The average initial spacing of Douglas-fir at Butte would have been no wider, and likely narrower, than this value at 70 years. Thus, the comparison between Butte and Yellowjacket shows an average initial spacing of 3.5 m or less for Douglas-fir at Yellowjacket.

The Wind River spacing trials, consisting of plantations with planned initial spacings, provide a different type of comparison for Yellowjacket. The data points for the widest spacing tested (3.7 m) fell slightly below the curve for Yellowjacket in the interval 1530 to 1550 (Figure 11). The Butte value fell between these 2 curves. At first glance the comparisons of Yellowjacket with Wind River and Butte suggest that Douglas-fir at Yellowjacket and Butte experienced an average initial spacing greater than 3.7 m. Although this result appears to differ slightly from the results of the Butte comparison

alone, it may simply reflect the fact that dbhs for a given height and spacing tend to be greater in natural stands than in plantations (Wilson 1998). So, if the natural Yellowjacket stand started at an average spacing in the neighborhood of 3.5 to 4.0 m, it would be expected to have a higher Dbh_{avg}-vs-$Height_{Dom}$ curve than a plantation with the same initial spacing, which is consistent with the observations. An additional consideration is that if there was a systematic error in the Yellowjacket dbh reconstructions, it would have been to overestimate rather than underestimate dbhs (see Methods), and hence the real Dbh_{avg}-vs-$Height_{Dom}$ curve would pass even closer to the values for Butte and the 3.7 m spacing trial. With the atypical tree #1879 omitted from the Yellowjacket curve, the Dbh_{avg}-vs-$Height_{Dom}$ value for Butte fell directly on the Yellowjacket curve (Figure 11).

From these comparisons, I conclude that Douglas-fir at Yellowjacket had an average initial spacing in the neighborhood of 3.5 m. However, this does not reveal the initial composition and total density for all trees at Yellowjacket in its youth. The simplest interpretation of the results is that the early composition at Yellowjacket was similar to that at Butte (Table 2), mostly Douglas-fir mixed with a minor component of a weaker competitor (i.e. western hemlock or western redcedar). If this interpretation is correct, the inferred initial spacing at Yellowjacket would be the average initial distance between Douglas-fir trees (see Methods) and the initial density of Douglas-fir trees would have been close to 800 tph (trees per hectare). The total stand density would be even higher, depending on the number of western hemlock and redcedars present. This possibility could not be distinguished from more complex situations with a high proportion of trees of another fast growing species, in which case the inferred initial spacing might be the distance between Douglas-fir and the nearest equally strong competitor (i.e. fast-growing species such as western white pine, red alder, bigleaf maple or grand fir; see Methods). Although the inferred initial spacing for Yellowjacket Douglas-fir may thus have occurred within any of a variety of early scenarios with respect to composition and total stand density, Butte provides an example of one such possibility. It appears that the dominant Douglas-fir in this typical young stand are starting out on a path similar to the

early history of dominant Douglas-fir at Yellowjacket, with individual dbh-vs-height values remarkably similar to the youth of Yellowjacket dominant Douglas-fir (Figure 12).

In naturally regenerated young Douglas-fir stands in the region, average initial densities of Douglas-fir range from 500 to 4000 tph (equivalent to 4.5 to 1.6 m average spacing between Douglas-fir), with stand densities being fairly evenly distributed except for the highest densities (> ca. 3000 tph) which are less frequent (Wilson 1998). Thus it appears that the inferred initial spacing for Yellowjacket Douglas-fir (regardless of whether this is the distance to other Douglas-fir trees or to equally fast-growing competitors) falls near the wide end, but is not atypical, of the range of initial spacings for Douglas-fir in modern young naturally regenerated stands. This finding is consistent with the quickness with which Douglas-fir colonized the Yellowjacket site (Figure 8) and the forest closed (Figure 15). 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 currently young stands that regenerated naturally after logging. The comparison young stands in that study had densities of 223 to 600 trees/ha (equivalent of 4.1 to 6.7 m spacing) at 50 to 70 years, all less dense than Butte.

Crown development. Franklin et al. (1981) suggested that the large, long crowns of old-growth Douglas-fir trees may have developed as a consequence of wide initial spacing and/or epicormic branching. It is clear that wide initial spacing could lead to the development of long crowns; in general, Douglas-fir stands begun at wider initial spacing have longer and larger crowns in their early years than do stands of the same age but with narrower initial spacings (Curtis and Reukema 1970, Oliver and Larson 1990). However, the dominant Douglas-fir at Yellowjacket have deep old-growth crowns despite an initial spacing that was not unusually wide relative to modern young Douglas-fir stands. Apparently, wide initial spacing is not a necessary condition for development of large, deep old-growth Douglas-fir crowns.

The intensive reconstruction of tree 1408 (Figure 13) provides an example of crown lengthening in the absence of wide initial spacing, and without epicormic branching from the bole. At the beginning of crown closure for this tree (ca. 1525), the functionally live crown was 13.1 m long; initial spacing was probably an important factor in the development of this length at crown closure (Oliver and Larson 1990). However, after crown closure, the crown continued to lengthen; by 1630 the functionally live crown was 1.7 times the length it was at crown closure, and by 1992 it was 2.8 times the length it was at crown closure. Overall, it is not clear what factors were involved in the pronounced crown lengthening after crown closure, but it was found that epicormic branching from the bole did not play a significant role. For at least the first 130 years of the tree's life (i.e. until 1630) the lengthening of the crown was accomplished without any epicormic branching from the bole, as evidenced by the finding that all sampled branches at and below the 1630 crown base at 29.7 m were normal, nodal branches.

It is possible that sometime after 1630, the base of the live crown receded above 34.6 m (its 1992 height) and then later dropped back down to this final height via epicormic sprouting. However, based on the continually slowing rate of crown base recession in the decades prior to 1630, I concluded that if epicormic branching from the bole did occur at this height, its overall contribution to the lifelong lengthening of the crown was small (Figure 13). 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.

Suggestions for other factors that may have contributed to the lengthening of the crown include minor disturbances with associated damage to or mortality of neighbors, and differentiation in tree heights. For example, if the minor disturbance(s) that occurred in the late 1500s (Chapter 3) killed or damaged neighbors of tree 1408, the increased space and light might have resulted in the abrupt slowing of crown recession in ca. 1600. As another example, if tree 1408 grew progressively taller than its neighbors in the 1500s,

the recession of its crown base might have been similar to its neighbors, while its top increasingly outdistanced the neighbors' tops. This would be consistent with the result that from 1525 to 1630, the crown base receded more slowly than tree height increased, and the crown thus lengthened.

Duration of open growth conditions, and synthesis for stand initiation. The juvenile radial growth rates and the ringwidth patterns show that relatively open conditions existed prior to 1521 and closed forest conditions existed after 1540, with gradual filling in of growing space between these times. This result, combined with the history of establishment, the Douglas-fir dbh histories, and the crown history for tree 1408, is consistent with a single and distinct stand initiation stage for Yellowjacket that lasted about 40 years. A synthesis of this reconstructed stage follows.

From ca. 1500 to 1521, when growth conditions were relatively open, the shade-intolerant Douglas-fir and western white pine trees established, and had high radial growth rates and open ringwidth patterns. Two western hemlock establishing during this interval also had open ringwidth patterns. Between ca. 1521 and 1540 conditions had become too crowded to allow further successful establishment by shade-intolerant species, yet were still open enough that the western hemlock establishing during this interval had relatively high juvenile radial growth rates (compared to those establishing after 1540), but did not exhibit open ringwidth patterns (Figure 15, Table 3). Between 1521 and 1540, the trees were large enough that crowns of adjacent trees were close. The slowing of Douglas-fir dbh growth in ca. 1540 (Figure 10) is typical of the dbh growth pattern associated with the onset of inter-tree competition and crown closure (Oliver and Larson 1990, DuVall 1983). The findings that ground-level branches of tree 1408 began dying between 1525 and 1530, and were dead after 1530, is consistent with these interpretations.

By about 1540, trees standwide had developed closed crowns and the forest as a whole had closed, as shown by the plotwide shift to lower juvenile radial growth rates for western hemlock establishing after 1540 (Figure 15). The stand initiation period had

ended, and the forest remained closed until it was clearcut in 1992. 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, and might also indicate that the initial disturbance was relatively small or not intense, such that seed sources were very near, and conditions were favorable for germination and growth. After 1540 western hemlock continued to successfully establish (Figure 8), but now beneath a closed canopy (Figure 15, Figure 16, Table 3).

Many trees died in the decades and centuries that followed the stand initiation. Based on the initial spacing found, I estimate that there were at least ca. 800 trees/ha at the end of the stand initiation period, yet in 1992 only 55 (17/ha) of the initial colonizers remained alive (46 live Douglas-fir, 14/ha; 9 western hemlock, 3/ha). The 231 (70/ha) snags (table 1) and many fallen trees present in 1992 were from the trees that died recently enough and were large enough to leave evidence of their presence. Many others likely died so long ago and at such a size that they left no record. 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, synchronous pulses of western hemlock establishment, or high juvenile growth rates or open ringwidth patterns for western hemlock (Figure 8, Figure 15, Table 3, Chapter 3).

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 started out fast and dense yet was still capable of developing 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. Perhaps causes were in part 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 genetic potential of Douglas-fir for longevity and large size may allow for versatility in the development of old-growth Douglas-fir structure from a wide range of initial conditions. Conversely, it is also possible that there is a range of early histories that do not support the development of typical old-growth structure. For example, Wilson (1998) suggests that Douglas-fir trees in young stands that are very dense, that have little size differentiation, and that occur in areas of high wind may not develop the stability and resiliency to attain an old age and large size. 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.

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. While current old-growth structures, and the pathways leading to them, are not necessarily the best or the only models to guide management, they "provide a reference point for current and future conditions and an opportunity for understanding processes that lead to the development and maintenance of the current late successional ecosystem (FEMAT 1993)." It was for these reasons 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, and suggesting that natural 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 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 in order 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 timber silvicultural interventions (e.g. ground disturbance, unintended consequences for understory communities or other components of forest ecosystems).

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 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 (see also Chapter 3). 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. Using this knowledge and awareness, management strategies could be tailored to meet the particular conditions of locality, prior stand history, objectives and ownership. 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 (Chapter 3), provides the most detailed currently available "real time" (as opposed to chronosequence) history for the entire lifetime of an old-growth Douglas-fir stand. This study serves as an example of the natural processes that led to the successful development of a late successional ecosystem.
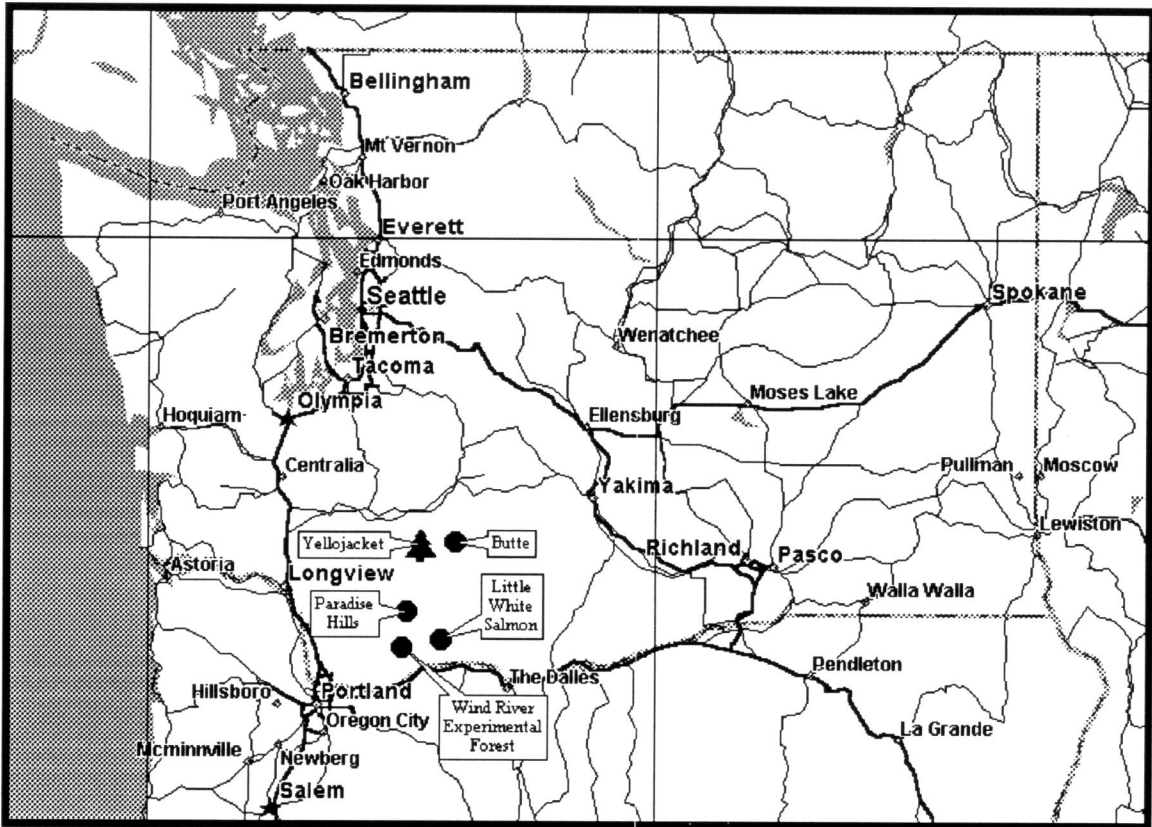
Figure 2. Location map.

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.
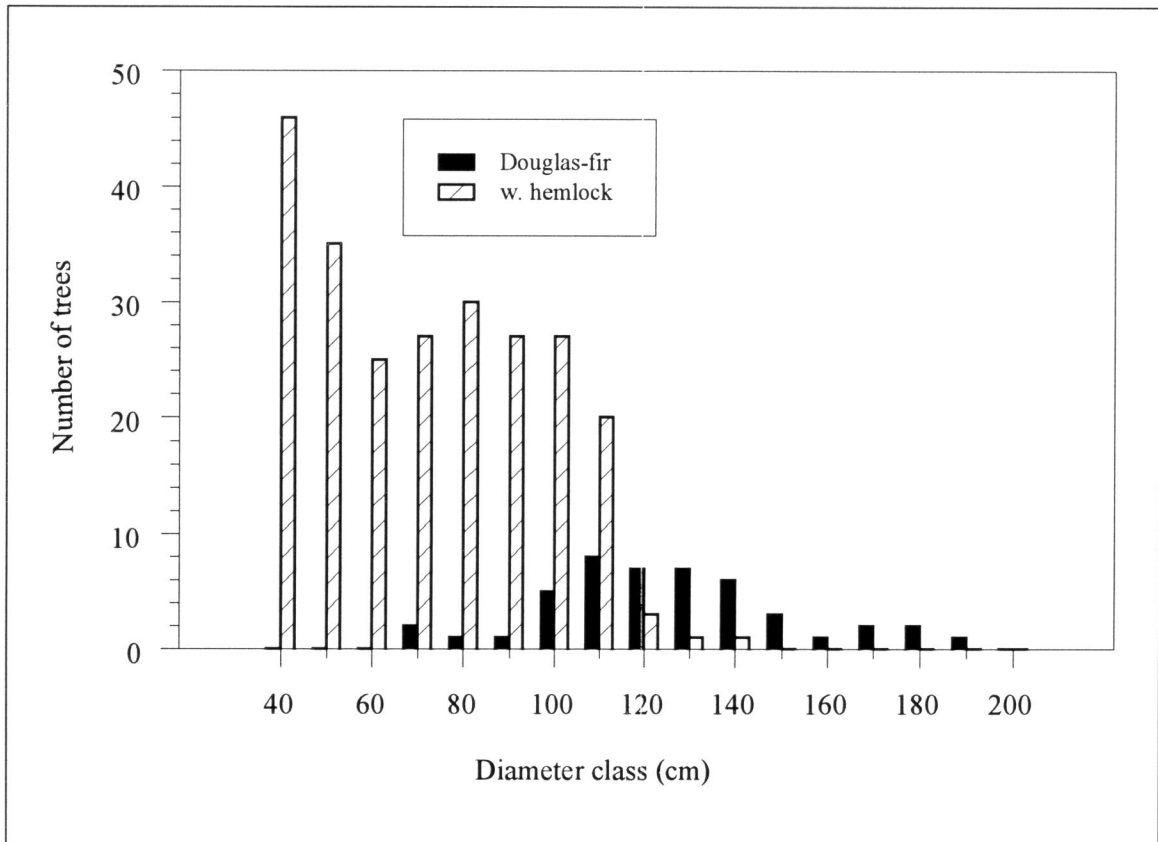
Figure 3. Diameters in 1992.

Diameters (dbh) of all Douglas-fir (n = 46) and western hemlock (≥ 40 cm dbh; n = 242)) alive in 1992. 12 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.
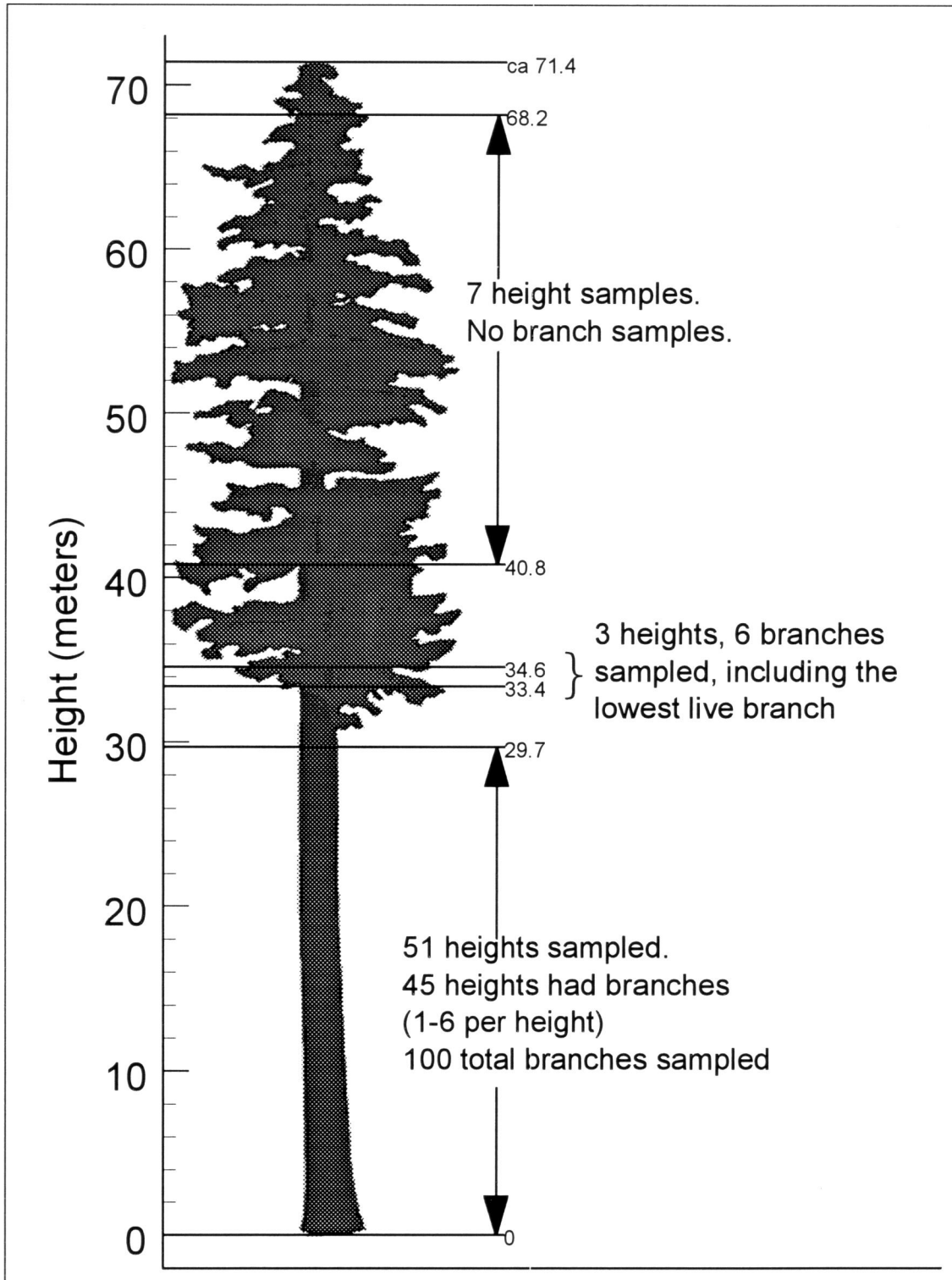
Figure 4. Intensively dissected Douglas-fir 1408.

Vertical structure in 1992 and sampling zones. Heights are relative to estimated lovel of the ground surface of the early 1500s.
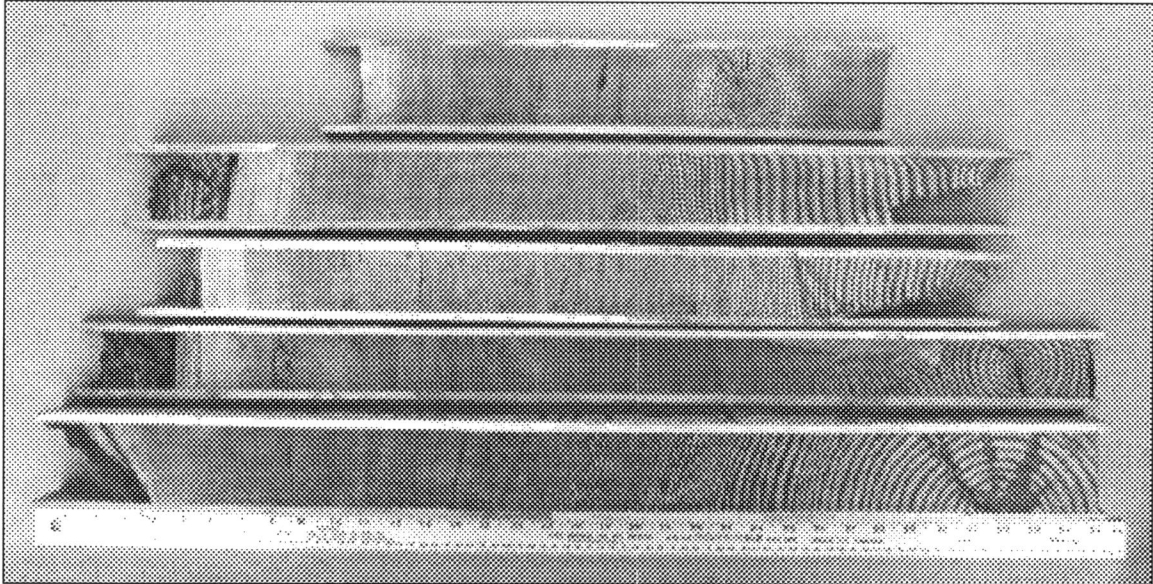
Figure 5. Examples of prepared Douglas-fir stump-samples.

After being cut from the stumps, the samples were trimmed, braced with wood strips glued to the sides, finely sanded on a cross-sectional surface and crossdated. Four of the examples shown here have centers with pith (from the smallest to largest radius, exact center-dates = 1511, 1507, 1501, 1514). The longest sample is missing the center by an estimated 2 rings (inner ring = 1503; estimated center decade = 1500).
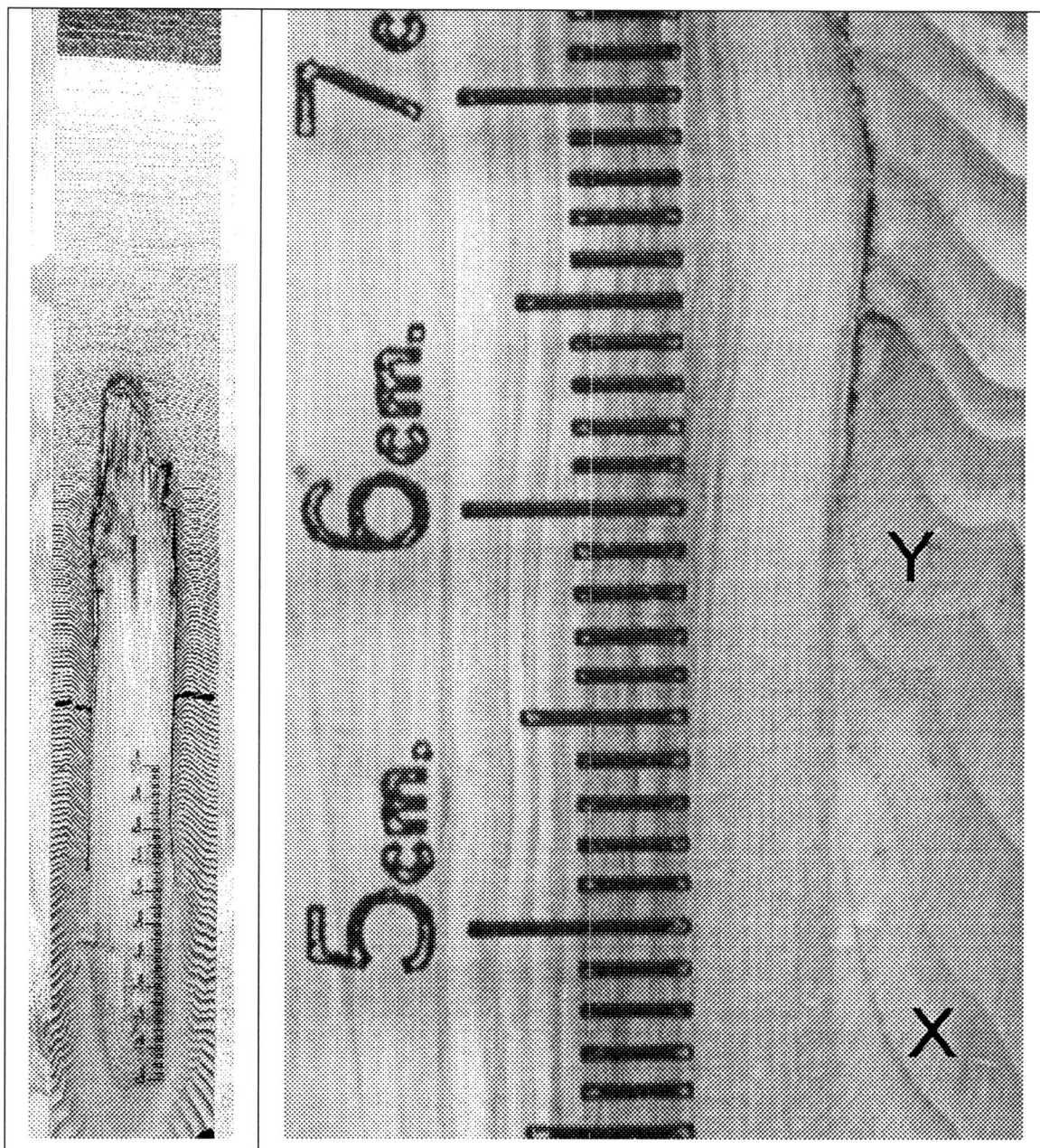
Figure 6. Sample with embedded branch.

This shows where the branch is integrated into the bole. The close up shows the area over which the branch was dying. X marks the Latest Functionally Live Date (LFLD) ring, dated to 1557. Y marks 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 observed.
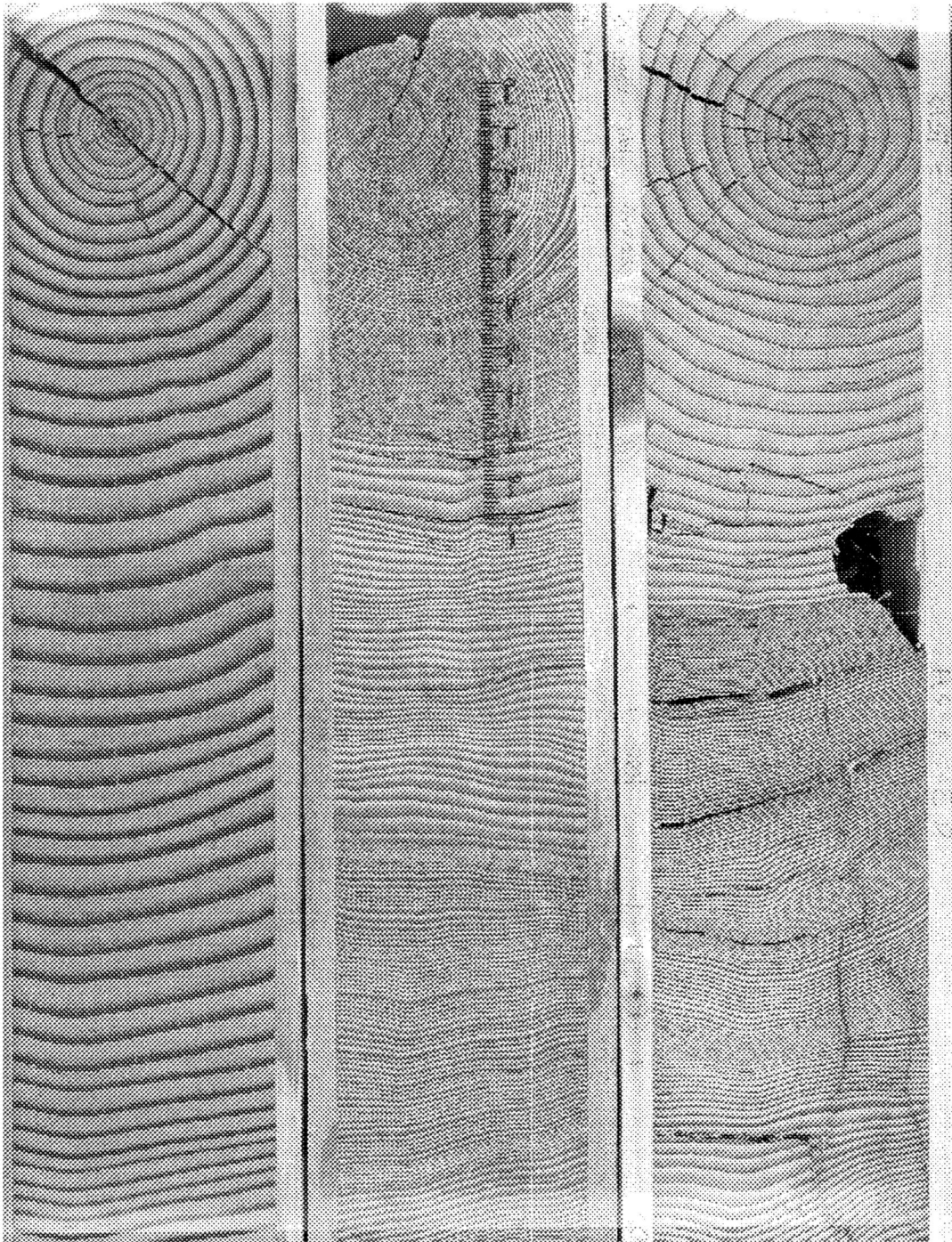
Figure 7. Samples with open and closed ringwidth patterns.

The leftmost sample is Douglas-fir and illustrates the open ringwidth pattern (center date = 1504). The middle sample is western hemlock and has a closed ringwidth pattern (center date = 1603). The sample on the right is a western hemlock with an open ringwidth pattern (center date = 1510).
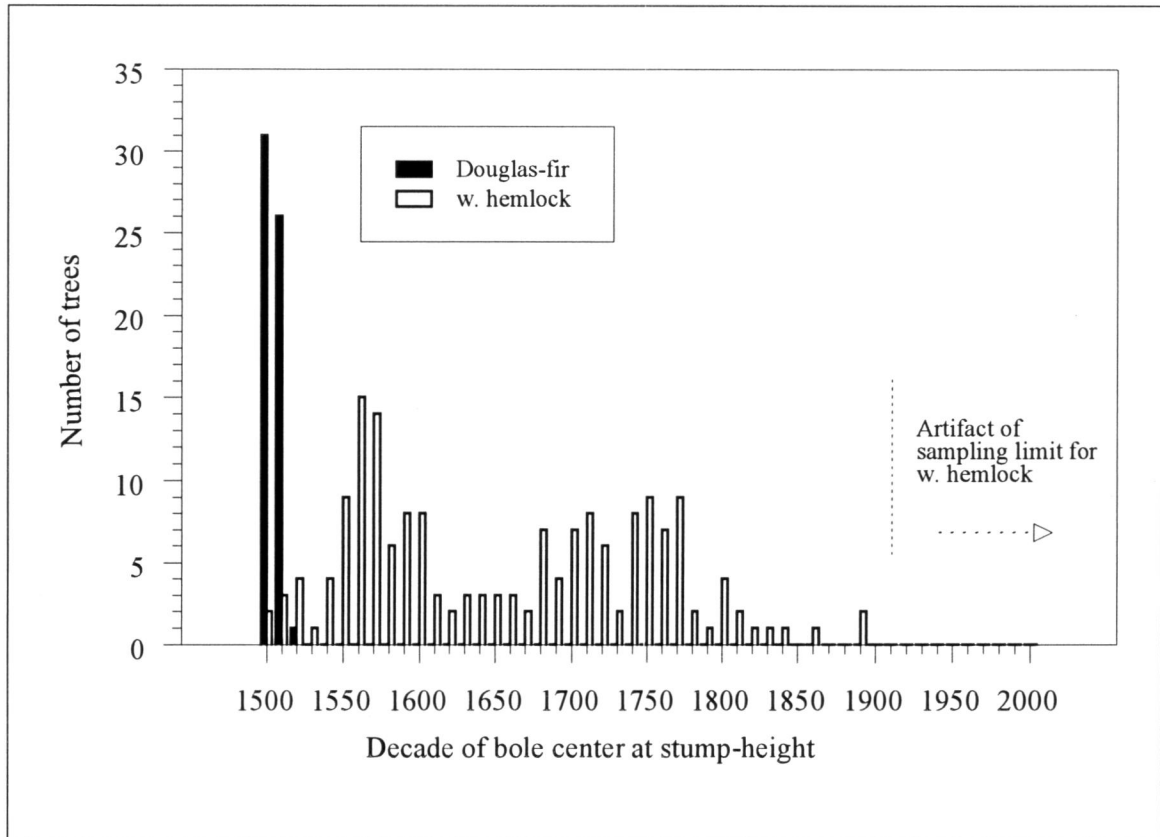
Figure 8. Establishment history.

Establishment history for all Douglas-fir (n = 58) and western hemlock (≥ 40 cm dbh, n = 175) with stump-height center dates, whether live or dead in 1992; see Table 1.
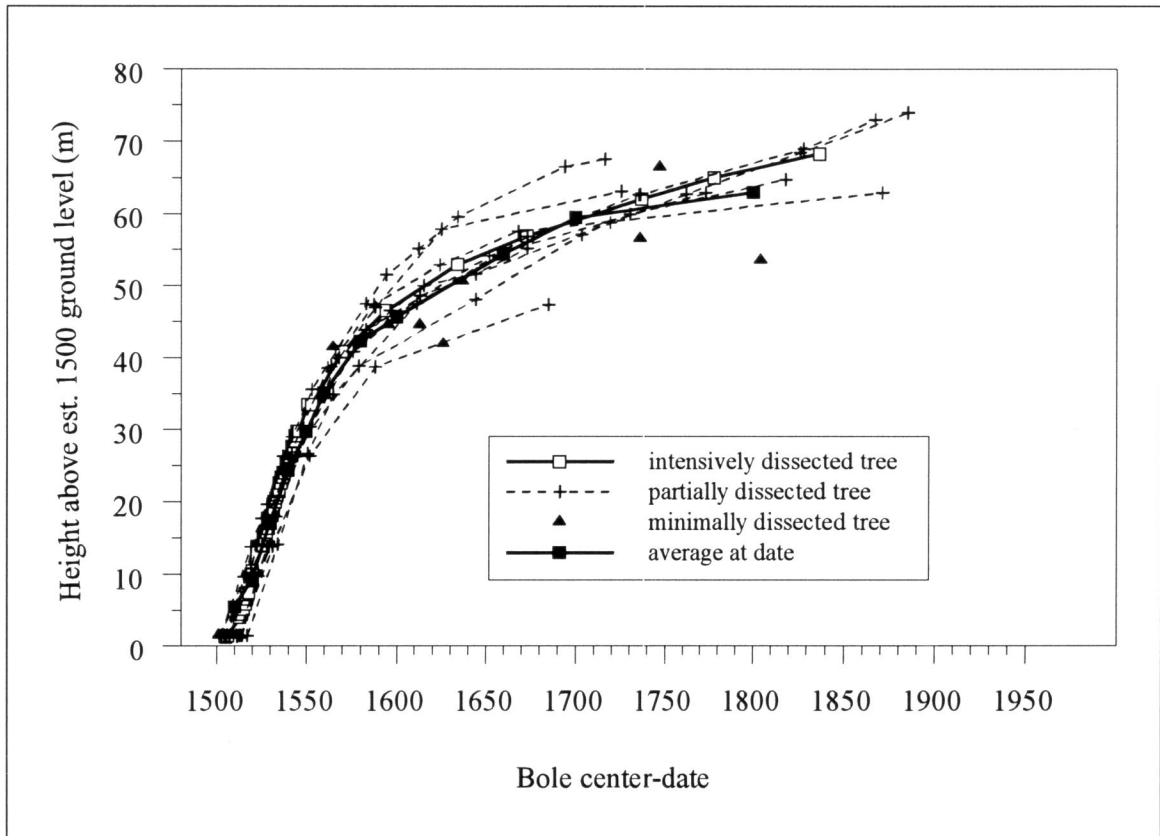
Figure 9. Reconstructed tree heights.

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 Dbh_{avg}-vs-$Height_{Dom}$ values, and the individual dbh-vs-height values (Figure 11, Figure 12). The uppermost sampled height for each tree is not the full 1992 height. The averages were computed for dates with reconstructed dbhs (Figure 10) and were used as $Height_{Dom}$ values for the stand at those dates.
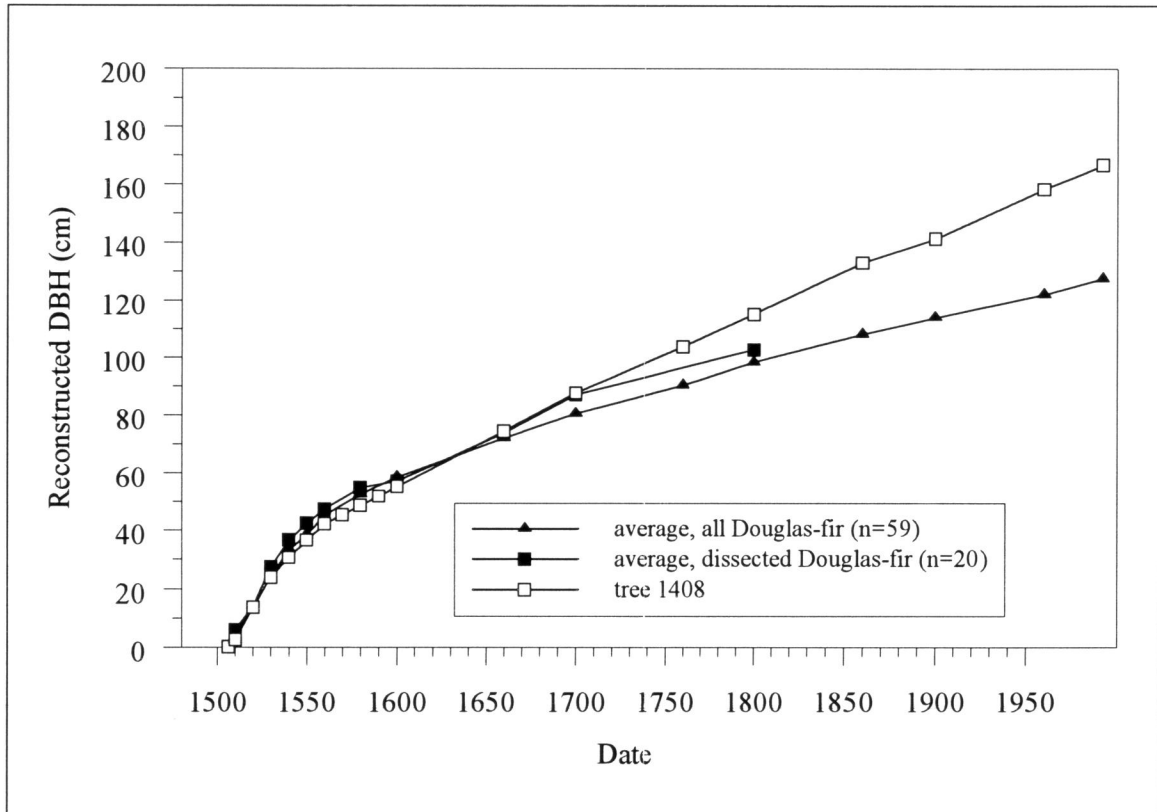
Figure 10. Reconstructed dbhs.

Yellowjacket reconstructed average 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. Dbhs were reconstructed for every decade present in the samples, but only selected dates are shown for simplification. The dbh averages for the dissected Douglas-fir are those used to construct the Dbh_{avg}-vs-$Height_{Dom}$ values (Figure 11; see Methods), and are not shown for dates past 1800 because corresponding average heights were not available past 1800 (Figure 9). The averages for all Douglas-fir include the dissected trees.
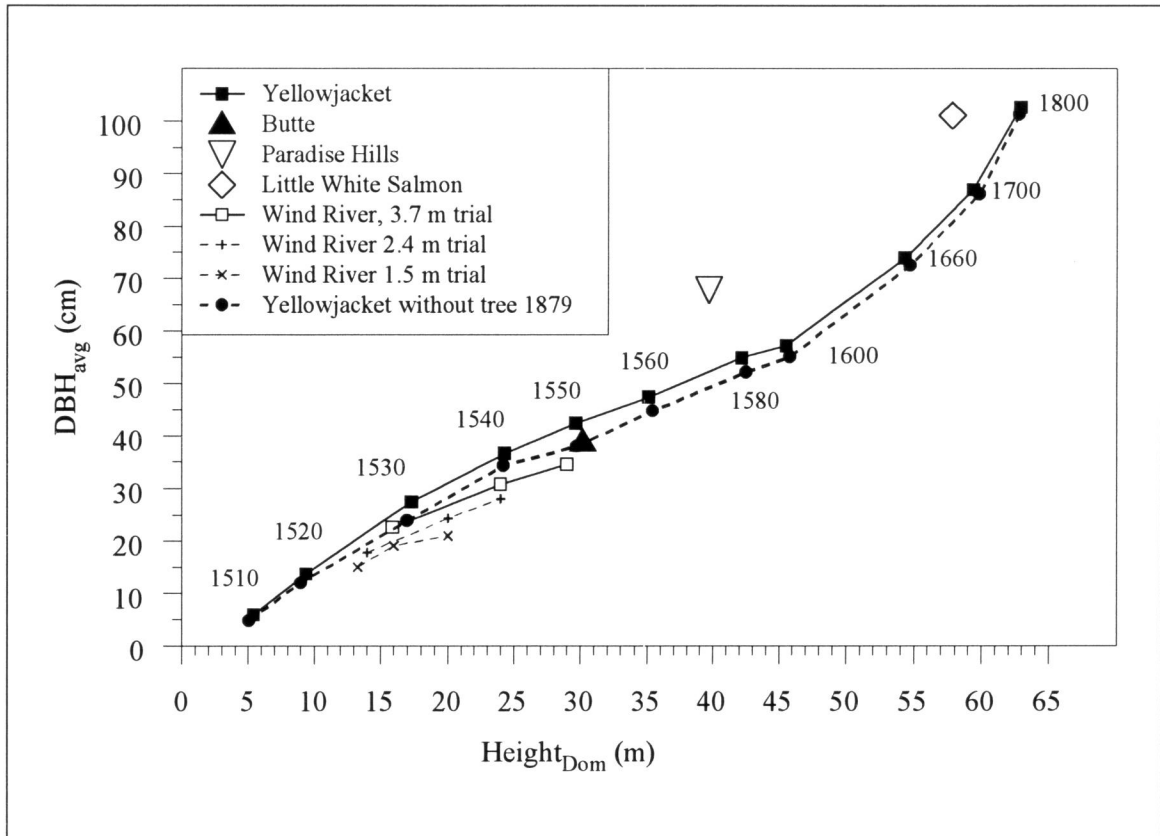
Figure 11. DBH$_{avg}$-vs-Height$_{Dom}$ curves.

DBH$_{avg}$-vs-Height$_{Dom}$ 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. Height$_{Dom}$, or 'Dominant height', is the average measured tree height for representative dominant (or largest 250/hectare) Douglas-fir at any given time. Each point represents a DBH$_{avg}$-vs-Height$_{Dom}$ value at a point in time for dominant Douglas-fir in a stand, although time is not otherwise a critical variable for the analysis. See Methods for sources of data. Also shown is the DBH$_{avg}$-vs-Height$_{Dom}$ curve for Yellowjacket with one extreme tree (#1879) removed from the averages (Figure 12).
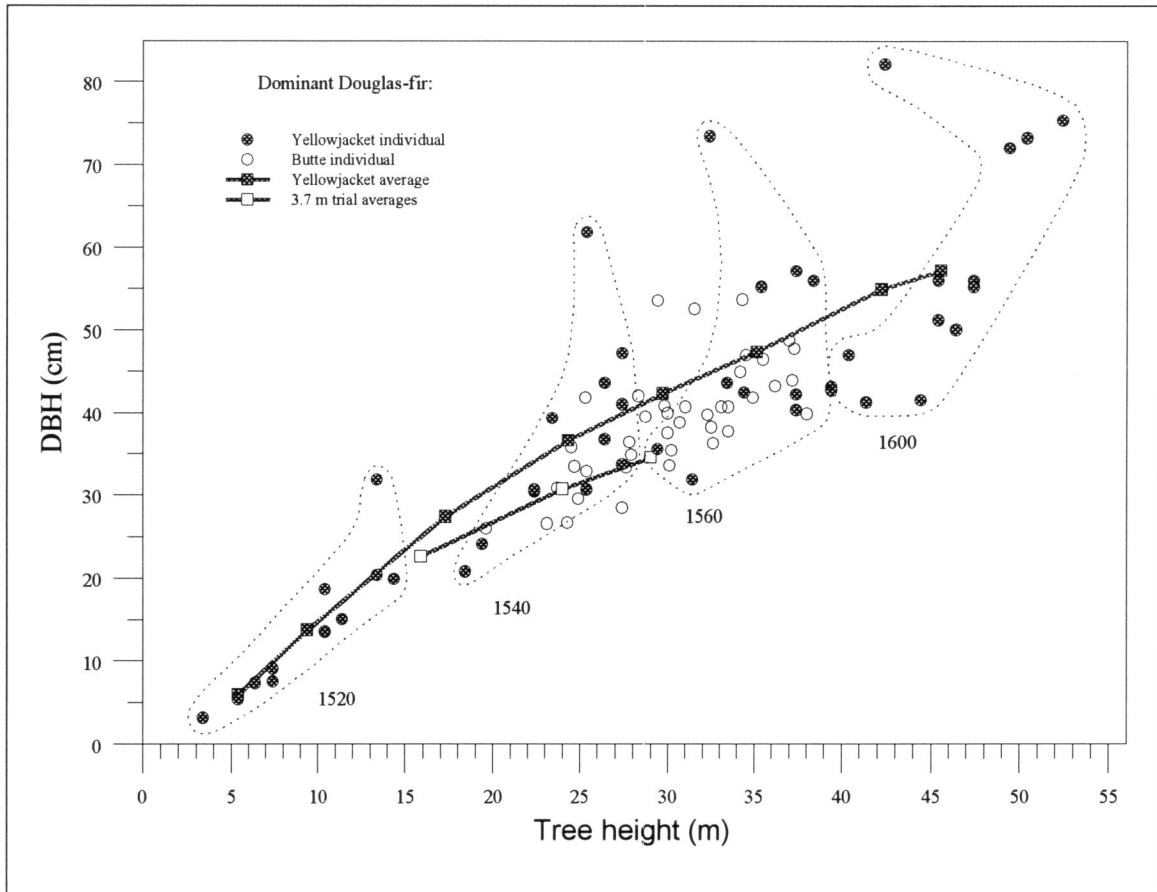
Figure 12. Dbh vs tree-height for individual trees.

Dbh vs tree-height for individual dominant Douglas-fir trees at Yellowjacket and Butte. The Yellowjacket values are for the dissected Douglas-fir at the annotated dates. 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 (#1879). The Butte values are for dominant Douglas-fir at a single stand age, ca 70 yr (see Methods for sources of data). The average curves for Yellowjacket and the Wind River are the same as shown in Figure 11.
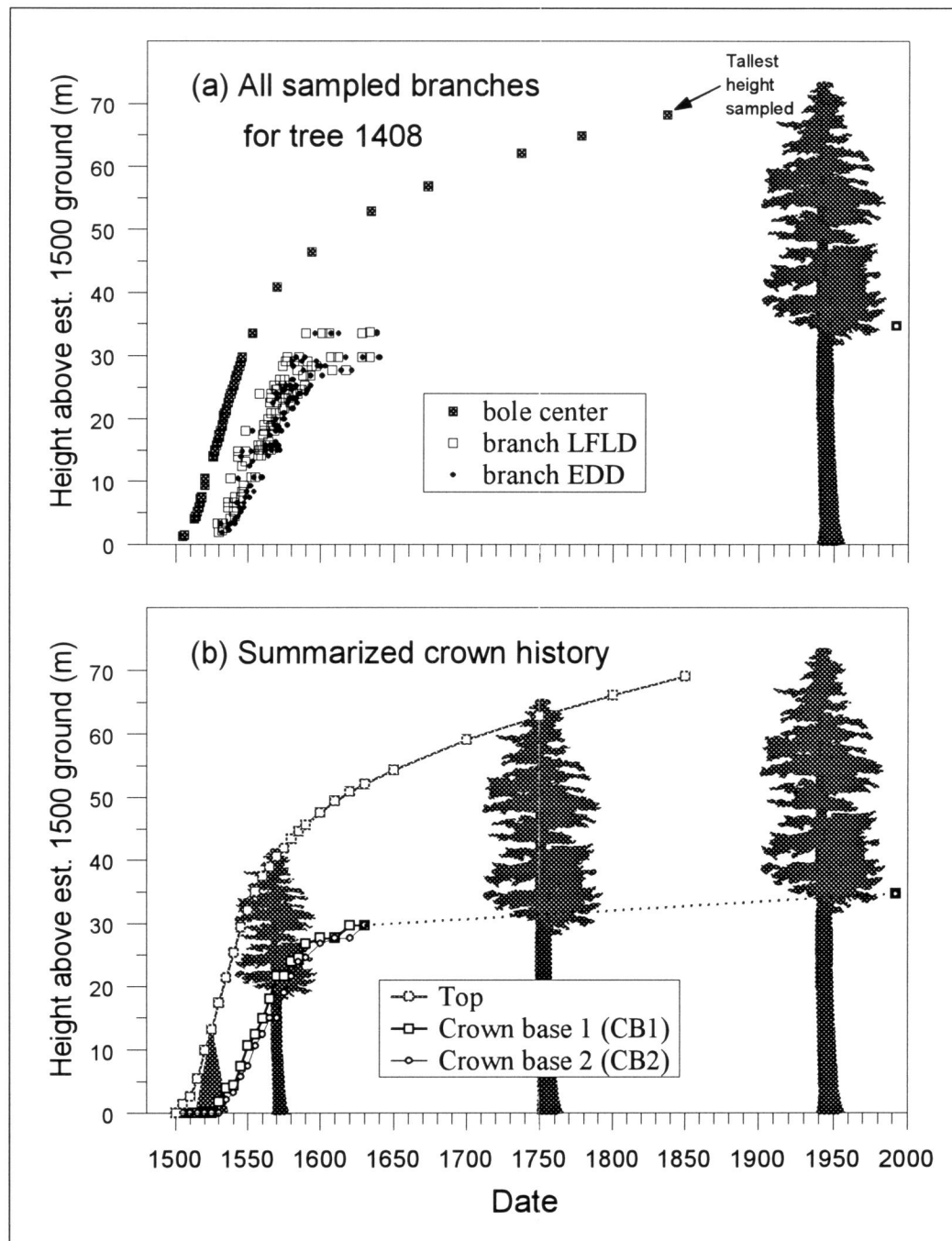
Figure 13. Crown development for Douglas-fir 1408.

a) Raw data for all branches: bole center date, LFLD (Latest Functionally Live Date), and EDD (Earliest Dead Date). b) Summarization of raw data showing at each of a series of dates the tree's reconstructed height (Top) and the heights to the reconstructed crown bases (CB1 and CB2). CB1 is the base of the functionally live crown at a date. CB2 is the base of a lower zone of dying branches just below the functionally live crown. See Figure 4 for sampling scheme.
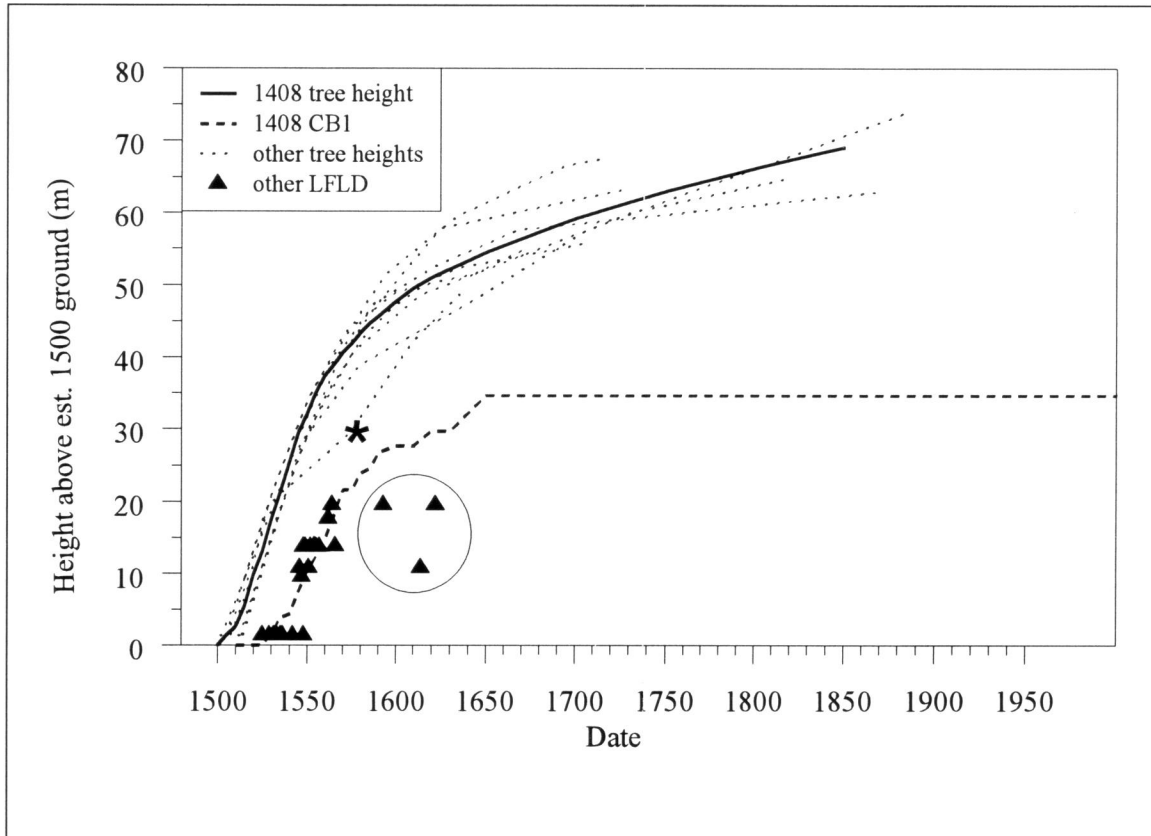
Figure 14. Crown history comparison.

Crown history for tree 1408 compared to limited crown data for other dominant Douglas-fir at Yellowjacket. The crown history for tree 1408 is as shown and described in Figure 13. 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 #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.
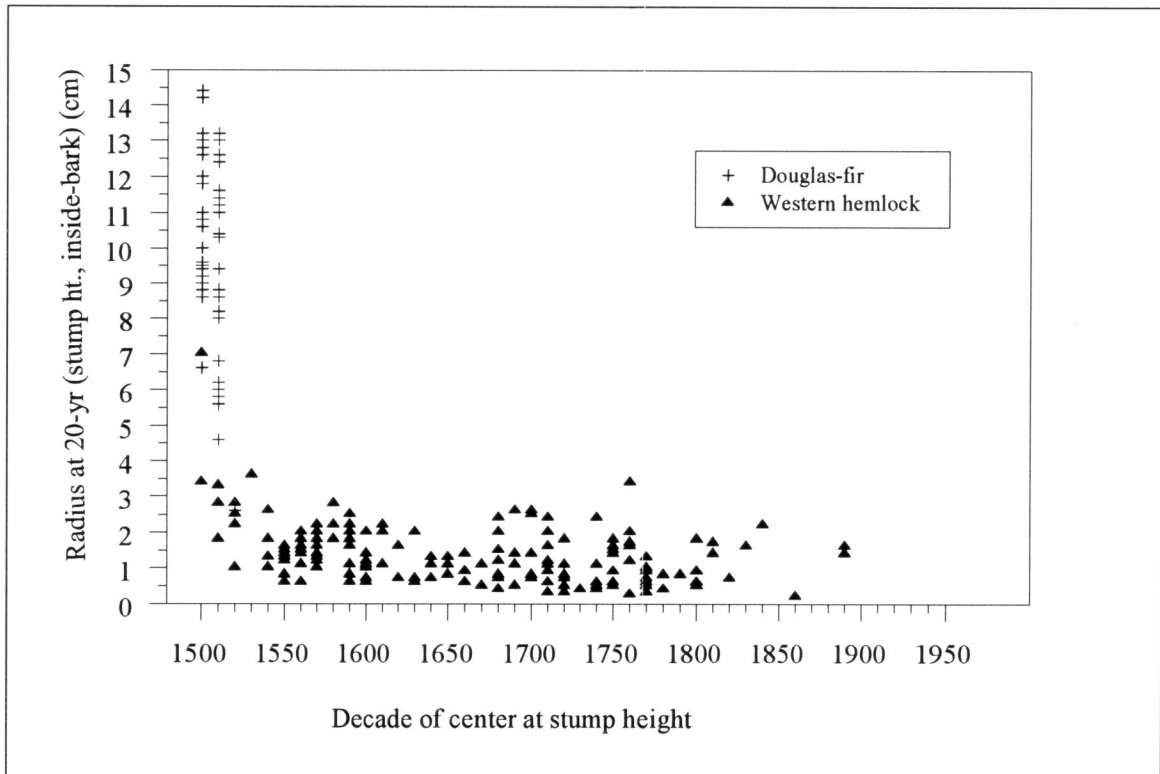
Figure 15. Juvenile radial growth rate.

Juvenile radial growth rate (represented by radius at 20-yr, stump-height and inside bark) versus decade of establishment (represented by decade of center at stump-height) for trees with stump-height center dates (Table 1): n = 58 Douglas-fir, n = 172 western hemlock (3 western hemlock with centers were missing data for radii at 20-yr).
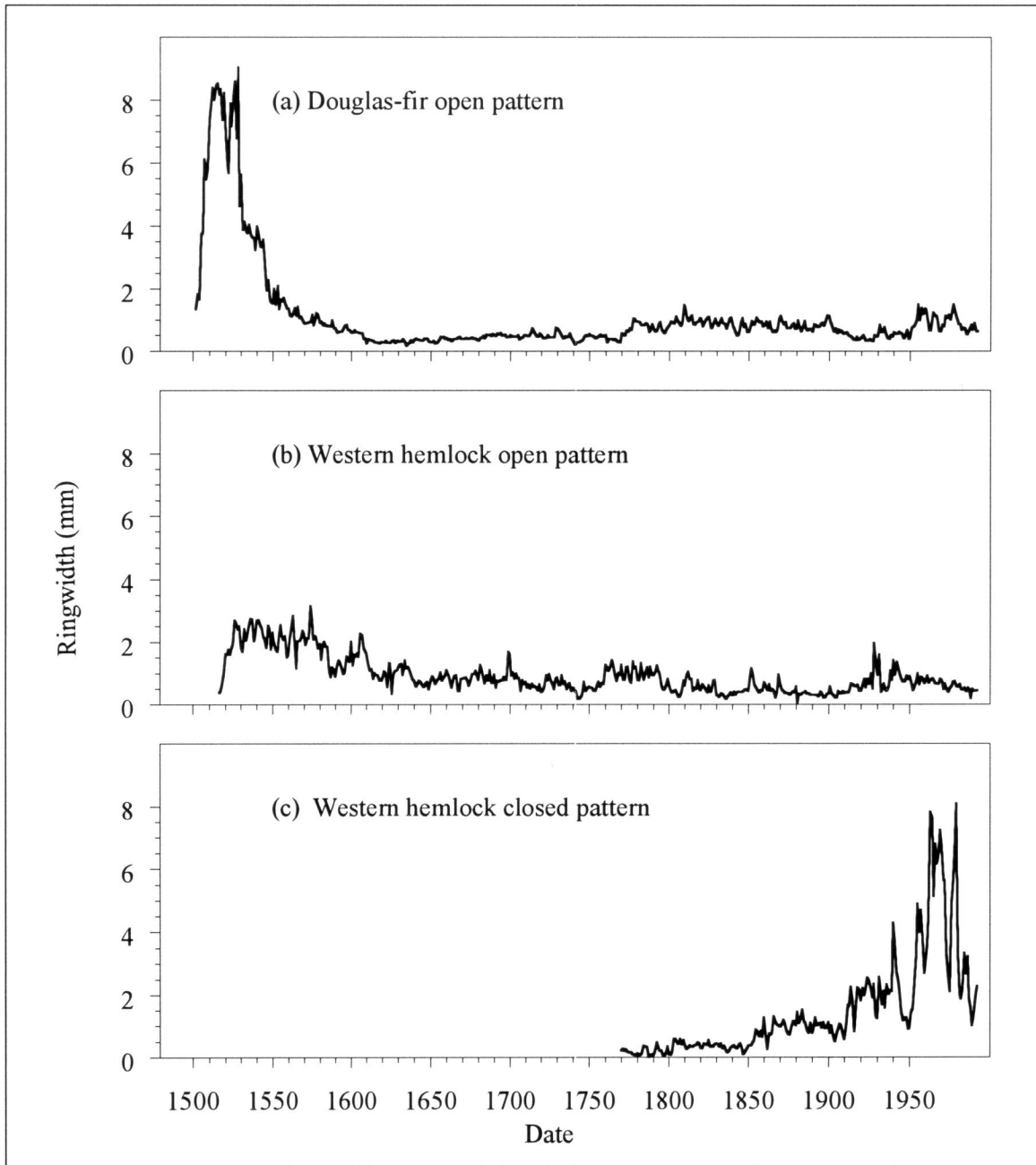
Figure 16. Examples of ringwidth patterns.

Examples of open (a, b) and closed (c) ringwidth patterns. These examples are from Douglas-fir (a) and western hemlock (b and c) stump-samples that were measured for individual ringwidths. Most samples were not measured at a yearly resolution (see Methods), but the yearly measurements are shown here to illustrate the characteristics shared by all trees classified as having an open or closed ringwidth pattern. For these 3 trees, the ringwidth pattern types were assigned based on the criteria used for trees that were not measured for individual ringwidths (see Methods). For all three figures, the earliest year is the center date.

Table 1. Number of trees sampled.

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

			Exact, estimated or missing center date assigned			
Category of trees	Present in plot	Stump sample collected and evaluated	Missing >1cm center: no center date	Pith present: exact center date determined	No pith, <1cm center missing: center date estimated	Total for which stump ht center date assigned
Douglas-fir, live in 1992	46	45**	2	42	1	43
Douglas-fir snag	74	16**	1	15	0	15
W. hemlock, live > ca 40 cm dbh*	254	224**	52	165	7	172
W. hemlock snag	44	4**	1	2	1	3
w. white pine snag	3	1**	0	1	0	1
snag, species not identified	110	0**	0	0	0	0

*12 w. hemlock slighly <40 cm dbh were sampled and evaluated.
** 1 live Douglas-fir was not sampled because it was not felled. 30 live western hemlocks >= 40 cm dbh were not sampled and evaluated due to post-logging conditions, or due to tree rot.
Snags were sampled only if they had a sufficient amount of sound wood.

Table 2. Characteristics of DEMO stands.*

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

*From Halpern et al, 1999; Halpern, personal communication
** Trees >5.0 cm dbh. Ranges are based on mean values for each of six 13 ha treatment units comprised of 32, 0.04 ha plots each.
*** Tree species codes: Abam = Abies amabilis, Abgr = A. grandis, Conu = Cornus nuttallii,
Psme = Pseudotsuga menziesii, Thpl = Thuja plicata, Tshe = Tsuga heterophylla

Table 3. Number of trees by ringwidth pattern.

Number of trees with open, closed, or other ringwidth patterns. Period of establishment is based on stump-height center dates.

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

CHAPTER 3
HISTORY OF CANOPY DISTURBANCES

INTRODUCTION

Old-growth Douglas-fir forests in the Pacific Northwest typically originated following stand-replacing fires, then developed for centuries as closed forests (Agee 1991, Spies and Franklin 1989). During the long intervals between catastrophic events, these closed forests likely experienced less severe disturbances that shaped stand structures by thinning the canopy over areas of various sizes without destroying the stands (e.g. Spies and Franklin 1991, McComb et al. 1993). The focus of this study is to increase knowledge of these "canopy disturbances" over the lifetime of old-growth Douglas-fir forests. This knowledge will be an important tool for forest managers in the Pacific Northwest where policies now have an increased emphasis on maintaining and developing old-growth forests. To implement these policies, some forest managers have begun to design silvicultural and restoration prescriptions intended to mimic natural disturbance processes (McComb et al. 1993, Aubry et al. 1999).

The suggestion that canopy disturbances have played a role in the development of old-growth forests is based largely on the observable structures of existing old-growth forests. Structures indicative of canopy disturbances include gaps in the main canopy, snags, broken topped trees, accumulations of large woody debris, wide ranges of Douglas-fir ages, and spatial variability in the distribution of these structures (Franklin and Hemstrom 1981, Franklin and Waring 1980, Spies and Franklin 1991, McComb et al. 1993, Tappeiner et al. 1997). This last feature in particular is suggestive of past disturbances to the canopy. For example, Spies and Franklin (1989) suggest that large catastrophic disturbances may lead to extensive patches of even-aged trees, with subsequent canopy disturbances creating a mosaic of smaller patches varying in forest structures. This "patchiness", although not commonly cited in definitions and standards for old-growth forests (e.g. Marcot et al. 1991), is frequently observed by researchers

who work in these forests (J.F. Franklin personal communication, personal observation), and has been documented for tree sizes and densities in several studies (e.g. Stewart 1986 a,b, Van Pelt 1995, Freeman 1997, Tappeiner et al. 1997). Forest patches and canopy disturbances occur across a continuum of sizes, with an arbitrary division provided by McComb et al. (1993; small < 0.2 ha, and large > 4 ha).

Research concerning the occurrence and effects of canopy disturbances over the lifetime of old-growth Douglas-fir forests is limited to a) recently occurring (ca. 75 years) small-sized events (e.g. Stewart 1986b, Franklin and DeBell 1988, Spies et al. 1990, McComb et al. 1993, Van Pelt 1995, 1999, Gray and Spies 1996, 1997), and b) reconstructed low- to moderate-severity fires that thinned canopies over large areas in relatively dry portions of the range (e.g. Stewart 1986a, Morrison and Swanson 1990, reviewed in Agee 1991). Given the great age of old-growth Douglas-fir forests, and the fact that low- to moderate-severity fires are uncommon over much of the range for this forest type (Agee 1991), the existing studies portray only a hint of the role of canopy disturbances during the extended life of these forests. A primary goal of the present study was to address this lack of information by using tree-ring records to reconstruct a detailed and continuous history of canopy disturbances over the entire lifetime of the "Yellowjacket" old-growth Douglas-fir stand in the Gifford Pinchot National Forest, western Washington Cascades. The reconstruction is based primarily on the analysis of synchronous pulses of abrupt changes in radial growth rates, as exhibited by changes in ringwidth. My specific objectives were to:

1. Create a detailed record of all sudden changes in ringwidth for the studied trees within a 3.3 hectare plot,

2. Reconstruct the history of prominent canopy disturbances based on this record.

The reconstruction necessarily focused on disturbances prominent enough to leave a record that could still be reliably detected after centuries. In particular, events covering a small area may affect too few trees to be reliably detected after centuries of mortality events to those trees.

This study is the second in a two-part reconstruction of the history of the Yellowjacket stand. The first part of the reconstruction (Chapter 2) showed that Yellowjacket originated after a stand-replacing disturbance in the late 1400s. All of the Douglas-fir still living in 1992 established between 1500 and 1521, while growth conditions were very open. A minor component of sampled western hemlock were also initial colonizers. Growing space filled as tree crowns widened, and by 1540 the stand had attained closed forest conditions. At this time, it appears that Douglas-fir trees were spaced on average ca. 3.5 m (800 trees/ha) from rapidly growing neighbors (likely other Douglas-fir). This is within the range of initial spacings for Douglas-fir in currently young stands in the Pacific Northwest. Most of the sampled western hemlock established after 1540 in the understory in a few broad intervals of higher (pre-1610, 1680-1779) and lower (1610-1679, 1780+) numbers with no sharp synchronous peaks. These trees had reached the canopy by 1992, but the vast majority of trees that established in the understory likely died without leaving a trace. By 1992, most initial colonizers had also died. Of the inferred 800/ha initial colonizers (likely mostly Douglas-fir) present at the end of stand initiation in 1540, only ca. 17/ha (14/ha Douglas-fir, 3/ha western hemlock) remained alive in 1992. Although this natural thinning of the initial colonizers was substantial over the centuries following crown closure, the closed forest was never opened enough to allow further Douglas-fir establishment or open ringwidth patterns for establishing western hemlock. By reconstructing the occurrence of canopy disturbances over the lifetime of the forest, the current study suggests ways in which these disturbances shaped the stand's development from its early structure in the 1500s to that in 1992.

METHODS AND RATIONALE

Study site

The Yellowjacket study site (lat. 46°21.7'N, long. 121°51.5'W, elev. 670 to 730 m) was established in a pre-harvest timber-sale (Gifford Pinchot National Forest) located in an old-growth Douglas-fir forest in the Western Hemlock Zone (Franklin and Dyrness 1973) of the western Washington Cascade Mountain Range (Figure 2). Its physical and

vegetative characteristics, described in detail in Chapters 1 and 2, are summarized here. Prior to cutting, the stand was dominated by Douglas-fir and western hemlock, with structural features meeting the definition for old-growth Douglas-fir stands (Franklin et al. 1981, Marcot et al. 1991, Chapter 1). The canopy was irregular in height and fairly closed, with occasional small gaps containing snapped or uprooted trees. Vegetative and physical characteristics at Yellowjacket varied continuously across the stand, but with trends toward groupings of features. Three distinctive, although not sharply delimited, areas could be easily observed. These medium-sized areas varied in tree sizes and densities, amount of coarse woody debris, amount and type of understory vegetation and environmental features. The absence of charcoal on the bark of any trees, and ring counts of the site's fire-sensitive Pacific yew (Burns and Honkala 1990), show that fire had not entered the forest since at least the mid-1700s. However, charcoal associated with the Douglas-fir roots suggests that the stand originated following a catastrophic fire. This fire probably affected an area much larger than the study plot, as the structure of the Yellowjacket stand is similar to surrounding stands. The stand was free of intrusive management until it was clearcut in 1992.

Pre-harvest field methods

Prior to harvest, a 3.3 ha plot was established with somewhat irregular borders determined by natural and man-made boundaries. Within this plot, all live western hemlock ≥ ca. 40 cm dbh, all live Douglas-fir and many snags were tagged and mapped, including elevations at the base of each tree (Figure 17, Figure 18; Table 1). All of the trees were in the main canopy, although the western hemlock varied considerably in height. Each tagged tree was evaluated for species, dbh, and crown class. Field checking revealed the mapping error to be < 0.5 m in the X and Y directions, and < 1 m in elevation.

Post-harvest field methods

After commercial felling, two types of tree-ring samples were cut from the mapped stems:

1) *Stumps.* The stumps of the mapped stems were sampled as detailed in Chapter 2 and Table 1, to be used as the primary source of data for reconstructing past disturbances. Each stump-sample was cut to include a full radius from pith to bark whenever possible, and was up to 20 cm wide. The broad width facilitated the assessment of ringwidth changes.

2) *Dissected trees.* Samples were collected from multiple heights of 20 dominant Douglas-fir and 4 western hemlock boles as detailed in Chapter 2. These were used for height-growth reconstruction, allowing the evaluation of the relative competitive status of the two species throughout the life of the stand.

Sample preparation, crossdating, and measurement of ringwidths.

All samples were trimmed, reinforced against breakage, finely sanded on a cross-sectional surface until cell structure was visible, and crossdated according to standard dendrochronological methods (Stokes and Smiley 1968, Ferguson 1970, Fritts 1976, Holmes et al. 1986, Yamaguchi 1991, Chapter 2). Ringwidths of 52 samples were measured with a Henson-Bannister Incremental Measuring Machine (accuracy ±0.01mm). The measured series were used in developing the master ringwidth series for crossdating (Chapter 2), and to provide a check on the study's visual methods of identifying abrupt changes in ringwidth (see below).

Evaluation of individual samples

Each stump-sample was evaluated for center date, radii at the beginning of each decade, ringwidth pattern, and growth-changes.

Center date. For stump-samples containing the pith (n = 225), the center date was assigned as the calendar year of the ring surrounding the pith (Chapter 2, Table 1). For samples missing ≤ 1 cm of the center (n = 9), the center date was assigned as the estimated decade of the center. 56 samples were missing > 1 cm of the center, and were not assigned center dates.

Radius at the beginning of each decade. For each stump-sample, radii were measured (± 0.5 mm) from the pith to outer edge of the first ring in each decade, and to the outermost ring (1992).

Long-term ringwidth pattern. This is a description of the life-long pattern of ringwidths for a stump-sample, designated as "open", "closed" or "other" (Chapter 2). The open pattern, characterized by fast early radial growth (wide rings) and slower later growth (narrow rings), is typical of trees that established in an area with no canopy overhead, i.e. open conditions. The closed pattern is characterized by slow early growth and faster later growth, and is typical of tree establishment beneath a closed canopy of trees or shrubs. Other ringwidth patterns, fitting neither of these descriptions, may represent establishment in other conditions.

Growth-changes. Numerous reconstruction studies have used "growth-changes", i.e. abrupt and sustained increases or decreases in ringwidth, as evidence of past disturbance, sometimes referring to such changes as "releases" and "suppressions" (e.g., Lorimer 1980, 1985, Glitzenstein et al. 1986, Lorimer and Frelich 1989, Canham 1990, 1985, Payette et al. 1990, Cho and Boerner 1995, Nowacki and Abrams 1997). In the current study, growth-changes were used as the primary evidence of past canopy disturbances. The terms "growth-change", "growth-increase", and "growth-decrease" are used herein to mean only abrupt and sustained changes in ringwidths, and to differentiate them from the other types of ringwidth changes (e.g. gradual or not sustained).

Growth-changes, particularly growth-increases, are frequently associated with disturbances to the canopy. However, to use them as indicators of past disturbances they must be distinguished from other types of variation in the tree-ring record such as age and

size related trends, climatically related signals, and unexplained year-to-year variability (e.g., Lorimer 1985, Cook 1987, Nowacki and Abrams 1997). Numerous studies have sought to distinguish disturbance-induced growth-increases by applying 3 criteria intended to screen out ringwidth variation associated with age trends, size trends and climate (e.g., Lorimer 1980, 1985, Glitzenstein et al. 1986, Lorimer and Frelich 1989, Canham 1990, 1985, Payette et al. 1990, Cho and Boerner 1995, Nowacki and Abrams 1997). Generally, these studies required a growth-increase to be abrupt, sustained, and of a magnitude exceeding a specified value, in order to be accepted as being disturbance induced. These criteria are necessarily approximate in nature, and vary widely among studies. The requirement of a sustained change ranged from 4 to 15 years among most studies. The minimum magnitude for a growth-increase generally varied from 25-100%, however some of these studies specified a fixed ringwidth instead (i.e. 0.5mm); above this value was a release, below this value was a suppression.

In the current investigation, criteria modified from the above studies were used to visually identify growth-changes on the prepared surface of all stump-samples (Appendix D). For a change in ringwidths to be accepted as a growth-change (Figure 19-Figure 24): 1) the increase or decrease had to be abrupt, achieved within ca. 3 years, and 2) the change had to be sustained, i.e. the ringwidths prior to and following the change had to each be relatively constant for ≥ 10 years. In contrast to previous studies, a criterion for a minimum magnitude of the change was not used, largely because there has been no general agreement about what the minimum should be for a disturbance-induced growth-change.

In this study, I assigned seven descriptive variables to each identified growth-change: 1) Type: increase or decrease, 2) Date of occurrence: calendar year of the earliest ring of the growth-change, 3) Radius at the date of occurrence, 4) Tree age at date of occurrence, 5) Magnitude: ratio of the average ringwidth for the 10 years following-vs-the 10 years preceding the date of occurrence, 6) Abruptness: the number of years it took to change from the preceding to the following 10 years average ringwidth, 7) Number of years

following the growth-change until the next growth-change, a measure of the length of time that the growth-change was sustained.

The reproducibility of this study's methods for visually identifying growth-changes was tested in two ways. First, 8 samples with a total of 79 growth-changes were evaluated by two investigators, myself and an independent researcher. Comparison of the two evaluations showed that dates of growth-changes detected by the visual methods were highly reproducible. Second, for the 52 samples that were measured for individual ringwidths, growth-changes identified using the visual methods closely matched those detected by a running 10-yr ratio (i.e., for each date, the following 10-yr average ringwidth divided by the preceding 10-yr average ringwidth), similar to the method used by Nowacki and Abrams (1997).

An important factor contributing to the reproducibility of identifying growth-changes, and to the clarity of the results, was the width and crossdating of the samples. On wide (avg 7 cm) samples, growth-changes could be distinguished from inter-annual and localized fluctuations more clearly than would be possible on narrow core samples or on graphs of measured series. For example, in the western hemlock samples, changes in ringwidth were frequently observed that only occurred across a small arc of the sample width (Figure 25). Changes such as these were not taken to represent growth-changes and were not entered in the data set.

Reconstruction of canopy disturbances

Growth-changes identified by the above methods were considered to have been caused by a canopy disturbance only when multiple western hemlock synchronously showed a growth-increase. By itself, an individual growth-increase was not considered a definitive indicator of a canopy disturbance for the following reasons:

1. Although the criteria used in this and other studies to identify growth-changes are intended to help distinguish disturbance-induced changes from other causes of ringwidth variation, there is no one set of criteria that has been proven to ensure that

all non-disturbance causes of ringwidth variation will be excluded. Since there are no rigorous data to guide the selection of these criteria, the exact values vary widely among the different studies, as detailed above, and among classes of trees within studies (e.g. Lorimer 1980, Lorimer and Frelich 1989, Nowacki and Abrams 1997).

2. Some disturbance-induced growth-changes that occurred in individuals when they were small understory trees could be due to very localized subcanopy events rather than being due to canopy disturbances. For example, elk grazing, branch-falls or the toppling of decaying snags could remove vegetation immediately surrounding a small understory tree that survived the event. Although there are no clear data documenting that growth-changes do or do not occur in response to such localized understory events, it is reasonable to expect suppressed understory trees to show a growth-increase in response to the sudden increased availability of local growing space caused by such events.

3. Some growth-changes may simply represent the unexplained random variations exhibited by all natural processes. Examples of this type of variation include groups of rings that, while wide along part of the circumference, are narrow along other parts of the circumference (Figure 25). If this inconsistency was not visible in the part of the ring arc included with the sample, a growth-change might be mis-identified. A similar effect was sometimes observed when the same rings were sampled at different heights on the tree.

Thus, while canopy disturbances can generally be expected to induce growth-changes, it cannot be expected that every identified growth-change is the result of a canopy disturbance. Consequently, for this study, additional criteria were used to identify more definitively those growth-changes that were likely to have been caused by a canopy disturbance.

For the purposes of this study, to infer that a canopy disturbance had occurred, I required a prominent and transient peak, or pulse, in which the number of individual western hemlock experiencing synchronous growth-increases clearly exceeded the observed

background level. The requirement for the occurrence of a prominent pulse is because when many trees experience synchronous growth-changes, such changes are more likely due to a discrete event, perhaps a disturbance (e.g. Glitzenstein 1986, Cook 1987, Lorimer 1980, 1985) and are less likely due to random variations, localized subcanopy event, or any other causes that are not expected to occur synchronously. The additional requirement that the growth-changes are specifically western hemlock growth-increases is based on western hemlock's ecological role as a shade-tolerant species (Chapter 2). Most western hemlock established in the understory after the Douglas-fir (Chapter 2). Western hemlock establishing at progressively later dates were not only far beneath the Douglas-fir, but they were also below other western hemlock trees with even denser foliage (Figure 26). Thus, throughout their lives, most western hemlock would experience overriding growth limitations from the canopy above. Consequently, if a canopy opening(s) was suddenly created, many subcanopy western hemlock would respond to the increased light with growth-increases. In contrast, localized understory events or unexplained random variations would cause a relatively small number of trees to exhibit growth-increases. Therefore, if many more western hemlock than usual synchronously experienced growth-increases, a canopy disturbance was inferred to have occurred at, or shortly before, the growth pulse. If all or most sampled trees were involved in the pulse, climate change might be an alternative cause. The exact time of the inferred canopy disturbance could not be pinpointed because there may be lags between disturbance and tree responses (Oliver and Larson, 1990). The ecological significance of pulses of other types of growth-changes (i.e. western hemlock growth-decreases, Douglas-fir growth-increases and decreases) is less clear. However if these types of pulses occurred within 2 decades of a pulse of western hemlock growth-increases, they were interpreted as possibly related to the same canopy disturbance that caused the western hemlock growth-increases, and were used to corroborate the disturbance.

Methods for identifying and characterizing pulses of western hemlock growth-increases consisted of:

1. *Identification.* The data were examined at progressively smaller spatial scales to determine whether there was a scale at which strong pulses were evident, and if so, to use that scale for the identification of pulses. First, a histogram was made for the whole plot showing a) numbers of western hemlock trees with growth-increases in each decade, and b) numbers of western hemlock trees with records for each decade. The decadal resolution was judged adequate because lags and variability in tree responses to disturbance are expected (Oliver and Larson 1990). This histogram suggested three peaks in the numbers of western hemlock with growth-increases. The plot was then subdivided into approximate halves (ca. 1.6 ha) and then into approximate quarters (ca. 0.8 ha), and histograms were prepared for the data in each subdivision. At these smaller scales the three peaks were more evident than in the histogram for the whole plot, and at the scale of the quarter plot were very strong (> 40% of the trees with records) in some quarters. The results of further subdivision did not enhance these peaks, and revealed no additional peaks, therefore they were not included in this study.

   Thus plot quarters (ca 0.8 ha each, Figure 27) were used as the subdivision for the identification of pulses, and 0.8 ha should be considered the approximate lower limit of studied disturbances. The histograms corresponding to each plot quarter were examined. A pulse was identified if, in at least one plot quarter, > 40% of the western hemlock with records had growth-increases in a particular decade. This stringent criterion was based on preliminary examination of the data, and was designed to select only peaks that were far above the background level of growth-increases.

2. *Associated pulses of growth-changes.* Once a pulse of western hemlock growth-increases was identified, the possibility of associated (± 2 decades) pulses of other types of growth-changes was explored (i.e. western hemlock growth-decreases, Douglas-fir growth-increases and growth-decreases). Pulses of other types of growth-changes were identified using methods similar to those used for detecting pulses of western hemlock growth-increases, except that a) histograms were made only for the entire plot, and b) the threshold used to identify pulses of Douglas-fir growth-changes

was 25% of the trees with records in a particular decade. As for the western hemlock, this threshold was based on preliminary examination of the data, and was designed to select only peaks that were far above the background level of growth-changes. If pulses of other types of growth-changes occurred within 2 decades of a pulse of western hemlock growth-increases, they were referred to as "associated pulses" and were interpreted as possible responses to the same canopy disturbance that caused the western hemlock pulse.

3. *Tree locations.* – Maps were made showing the locations of trees (both species) with growth-increases in the decade of each identified pulse of western hemlock growth-increases, and in adjacent decades. These maps show detailed information about the area affected by each inferred canopy disturbance, and the proximity of trees responding to the disturbance. This allows an event to be more confidently identified as a canopy disturbance. The actual size of a canopy disturbance reconstructed in this way is approximate because understory trees somewhat beyond the edges of gaps also respond to the creation of canopy openings. Further, for disturbances that extended beyond the plot boundaries, the reconstruction shows only the part of the disturbance included in the study site.

This method allowed for the identification of the most prominent pulses. The maps associated with each of these pulses supports the initial conclusion that these were the result of canopy disturbances. A number of statistical approaches were considered for this analysis (e.g., either point pattern analysis or spatial autocorrelation analysis: Upton and Fingleton 1985, Ripley 1987, Legendre and Fortin 1989, Duncan and Stewart 1991). These approaches were problematic due to complexities in the data (e.g., multiple and variable numbers of growth-changes per tree, changing numbers of trees with records per decade). Fortunately, the clarity of the data available in this study did not require evaluation by complex statistical methods to realize the stated objectives, and thus were not used. A variety of additional results may be achievable from further analysis of the extensive data set, but will be deferred to a later study.

Locations of trees according to sizes and establishment dates

Western hemlock were classified by their 1992 size and age, and separate maps were prepared showing the locations of each class. These were used to explore structural patchiness in the stand, and as aids in interpreting disturbances. The western hemlock age-class divisions were selected to reflect the four broad intervals of: higher establishment, pre-1610, 1680-1779; and lower establishment, 1610-1679, 1780+ (Figure 8). The western hemlock 1992 dbh classes were 40-69, 70-99, and ≥ 100 cm. For the purpose of these maps, all Douglas-fir were grouped with the largest western hemlock dbh class.

RESULTS

Growth-changes of individual trees

Growth-increases were common in both species, with 89% of the Douglas-fir and 99% of the western hemlock experiencing one or more growth-increases (Table 4). On average, increased growth rates were sustained 34 years in Douglas-fir and 37 years in western hemlock. Growth-increases occurred at a greater average tree age and radius and had a lower average magnitude for Douglas-fir than for western hemlock (Table 4). There was no trend in magnitude of growth-increases related to tree age for either species (not shown). Growth-decreases were more common in Douglas-fir than in western hemlock (Table 4), and were sustained for an average of 42 years in Douglas-fir and 46 years in western hemlock (Table 4). The average magnitude of growth-decreases was similar for Douglas-fir and western hemlock (Table 4).

The cumulative effect of growth-changes on long-term ringwidth trends differed for the two species. In Douglas-fir, the growth-changes contributed to a general trend from wider to narrower ringwidths. Of the 58 Douglas-fir with centers, 57 had open ringwidth patterns (Table 3 and Figure 16) and the first growth-change experienced was a decrease, followed by up to 5 more decreases before the first growth-increase at an average age of 172 years. In western hemlock, growth-changes usually contributed to a trend from

narrower to wider ringwidths. Of the 175 western hemlock with centers, 149 had closed ringwidth patterns (Table 3, Figure 16; Chapter 2) and the first growth-change was an increase occurring at an average age of 52 years. Only two western hemlock had open ringwidth patterns, and these trees established early in the history of the stand when conditions were fairly open (Chapter 2).

The competitive status of trees at the time of growth-increases (inferred from relative radii), also differed between species. At any given time, western hemlock experiencing growth-increases had much smaller radii than did Douglas-fir experiencing growth-increases, and than the average for all Douglas-fir (Figure 28). For example, in the 1760s the average radius of western hemlock trees experiencing growth-increases was 10.9 cm compared to 28.8 cm for Douglas-fir experiencing growth-increases, and 38.9 cm for all Douglas-fir. This is consistent with the lesser heights of western hemlock compared to Douglas-fir throughout the life of the stand (Figure 26).

Pulses of western hemlock growth-increases

Three pulses of western hemlock growth-increases were identified: the late 1500s pulse, the 1760s pulse and the 1930s pulse.

Late 1500s pulse

Identification of pulse (Figure 29). This pulse was identified in the SW quarter of the plot where 8 (53.3%) of the western hemlock with records for the decade experienced growth-increases in the 1580s and 8 (47%) western hemlock experienced growth-increases in the 1590s. In decades immediately preceding and following this period, only 0-3 western hemlock experienced growth-increases in this quarter. A weaker peak occurred in the SE quarter where 10 (34.5%) trees had growth-increases compared to ≤ 5 trees in nearby decades.

Associated pulses (±2 decades). The late 1500s pulse was fairly close in time to a long (1520-1560s) and strong pulse(s) of Douglas-fir growth-decreases, peaking in the 1560s

when 38 (63%) of the Douglas-fir experienced growth-decreases plotwide (Figure 30). This relatively broad pulse may represent a few events, as many of the growth-decreases (40%) occurred in 3 years: 1529, 1546 and 1565. Noteworthy in this interval was that one Douglas-fir experienced a massive injury in 1560 (fortuitously sampled) when the cambium was killed along 32 cm of the stem circumference at a height of 18.2 m. This tree also had a very strong growth-decrease (magnitude 0.25) in 1561, and possessed a very long double top in 1992.

Locations of trees with growth-increases. The western hemlock with growth-increases in the 1580s tended to be located in the southern half of the plot (Figure 32), but these trees were not tightly grouped and were intermingled with many western hemlock without growth-increases. In the 1590s, the western hemlock with growth-increases were more loosely grouped. In the three decades preceding and one decade following the 1580-1590s, lower numbers of western hemlock experienced growth-increases. A few Douglas-fir showed growth-increases in the 1550-1600s, and these were interspersed among the western hemlock with growth-increases. The Douglas-fir with growth-decreases in the associated pulse of the 1520-1560s were dispersed throughout the plot (not shown).

1760s pulse.

Identification of pulse (Figure 29). This pulse was identified in the NE quarter where 26 western hemlock (43%) had growth-increases in the 1760s, compared to 1-14 (0-19.7%) trees with growth-increases in all non-pulse decades. In the SE quarter there was a weaker peak of western hemlock growth-increases in the 1760s (14 trees, 25%). There was no peak in the other quarters in this decade. Plotwide, 83% of the western hemlock growth-increases in this pulse occurred in 1760 and 1761.

Associated pulses (±2 decades). The 1760s pulse was close in time to pulses of Douglas-fir growth-increases in the 1750s and 1770s when 16 (28%) and 24 (42%) trees, respectively, showed growth-increases plotwide (Figure 30). In the year 1760 one Douglas-fir had two moderately large (7, 7.4 cm along the ring) areas of cambial death at

a height of 12.57 m, and another had many small (< 0.5 cm) cambial scars at a variety of stem heights (injuries were fortuitously sampled). Each of these trees had a strong growth-decrease in 1761 (magnitudes of 0.3, 0.42) followed by a strong growth-increase in the 1770s (magnitudes of 2.3, 2.0).

Locations of trees with growth-increases. In the 1760s, most western hemlock with growth-increases were conspicuously clustered in a 1.5 ha area along the eastern edge of the plot (Figure 33). Many of these trees were nearest neighbors to each other and to four of the five Douglas-fir with growth-increases in the 1760s. The two injured Douglas-fir, neither of which showed growth-increases, were nearest neighbors to each other and to western hemlock with growth-increases. In contrast to the 1760s, nearby decades had no strong grouping of trees experiencing growth-increases.

1930s pulse.

Identification of pulse (Figure 29). This pulse was identified in the NE quarter where 46 (64%) western hemlock had growth-increases in the 1930s. There was also a strong peak in the 1930s in the NW quarter (13 trees, 41%), but there were not even small peaks in the SW and SE quarters for this decade. At a plotwide resolution, growth-increases occurred in all years of the decade, with 75% in 1931-1934.

Associated pulses (±2 decades). In the 1920s there was a weak peak of western hemlock growth-increases in the SW quarter (21 trees, 33%. Figure 29), and a pulse of Douglas-fir growth-increases (15 trees, 31%. Figure 30).

Locations of trees with growth-increases. Most of the western hemlock with growth-increases in the 1930s were conspicuously clustered in the north-northeast area of the plot, covering an area of ca. 0.8 ha within the plot (Figure 34). Many of these trees were nearest neighbors. The nine Douglas-fir with growth-increases in the 1930s were dispersed across the plot. In the two preceding and three following decades no strong groupings of trees with growth-increases were evident, although trees with growth-

increases in the 1920s were somewhat more concentrated in the southern portion of the stand.

Growth-changes outside the 3 main pulses

Of the 781 western hemlock growth-increases documented by this study (Table 4), 80% (626) occurred in non-pulse decades, i.e. decades outside the decades of the 3 main pulses. These non-pulse growth-increases were fairly evenly distributed in time across the life of the stand. The spacial grouping of non-pulse growth-increases was assessed by preparing maps for all decades. In all except 4 of the non-pulse decades the western hemlock with growth-increases were widely dispersed across the plot. In the remaining 4 decades (1650s, 1770s, 1820s and 1920s), the spatial grouping was weak.

Other types of growth-changes also occurred in non-pulse decades. Western hemlock growth-decreases occurred in many decades, but with no pulses (Figure 31). Douglas-fir growth-changes occurred in most decades (Figure 30), with two pulses of increases (1710s, 1800s) and a few pulses of decreases not associated with the 3 main pulses of western hemlock growth-increases. The most notable of these was the pulse in the 1730s when 25 (43%) Douglas-fir showed growth-decreases; 21 of these occurred in 1739. The Douglas-fir with growth-increases and decreases were never distinctly spatially grouped.

Spatial distributions of age and size classes

Western hemlock 1992 age classes (Figure 35). The oldest western hemlock (established 1500-1609, n = 74) were distributed throughout the plot but were less common in the northeast and southwest corners. Those establishing 1610-1679 (n = 19) did not show distinct spatial patterns. The youngest age classes of sampled western hemlock (establishing 1680-1779 and 1780-1897, n = 82) were largely restricted to the northeast and southwest corners of the plot.

Large, medium and small trees in 1992 (Figure 36). In 1992, large trees (all live Douglas-fir, n = 45; western hemlock ≥ 100 cm dbh, n = 49) were densest in a broad diagonal

band extending from the northwest to the southeast across the middle of the plot, and were relatively sparse in the northeast and southwest corners. Douglas-fir were particularly dense toward the southeast. The medium-sized western hemlock (70-99 cm dbh, n = 67) were dispersed across the plot. The smallest western hemlock sampled (40-69 cm dbh, n = 108) tended to be dense in the northeast and southwest corners, and sparse in the diagonal middle band. Although the spatial distributions of large, medium and small western hemlock are somewhat similar to the distributions of old, medium and young age classes, respectively, they are not entirely equivalent because in general, large western hemlock were old, but a small western hemlock could be a wide range of ages (Figure 37). For example, establishment dates for the smallest dbh class of sampled western hemlock ranged from 1550 to 1897.

DISCUSSION

Reconstructed disturbances

This study shows that, in the four and a half centuries following crown closure (ca. 1540), the Yellowjacket stand experienced at least two medium-sized (ca. 0.8 ha) and one perhaps larger-sized (> 0.8 ha) disturbances to the canopy. These 3 canopy disturbances likely represent a thinning of canopy trees across large portions of the study plot, but did not create gaps large enough to allow Douglas-fir establishment (Figure 8), or to allow open ringwidth patterns for establishing western hemlock (Table 3).

Mid-to-late 1500s disturbance(s)

Despite the small number of trees with records, the late-1500s pulse of western hemlock growth-increases was distinct (Figure 29). The western hemlock in this pulse had much smaller radii than did Douglas-fir at this time (Figure 28), and were probably far below the canopy (Figure 26), thus their synchronous growth-increases likely indicate damage and/or mortality of canopy trees in or slightly preceding this period. The inference of canopy disturbance(s) is additionally supported by evidence of the massive injury to one

Douglas-fir in 1560. This injury was fortuitously included in the dataset and other surviving trees may have been injured at the same time. Based on the distribution of western hemlock with growth-increases in the late 1500s (Figure 32), the disturbance likely affected the canopy over an area > 3.3 ha (the plot size). This damage apparently thinned the canopy but did not create single gaps large enough to result in Douglas-fir establishment or open ringwidth patterns for western hemlock establishing afterwards.

One of multiple possible scenarios for this disturbance(s) is suggested by the strong pulse(s) of Douglas-fir growth-decreases in the 1520s-1560s (particularly in 1529, 1546 and 1565) (Figure 30). In the mid-1500s, closed stand conditions were just developing and the Douglas-fir were rapidly growing, closely spaced, canopy trees (Chapter 2). The western hemlock were younger and much smaller than the Douglas-fir (Figure 26, Figure 28). Perhaps a series of events (e.g. wind or ice storms that broke tops) damaged and thinned main canopy trees in the mid-1500s, causing growth-decreases in the Douglas-fir that survived, and growth-increases in western hemlock at lower levels in the stand. The western hemlock responses may have lagged behind the time of the canopy damage, particularly if portions of the canopy died gradually. The broad wave of western hemlock establishment beginning in ca. 1550 (Figure 8) might have also been a response to overstory thinning, although this establishment was gradual and not suggestive of intense thinning.

The question arises why the surviving Douglas-fir did not show a pulse of growth-increases in the late 1500s as did the western hemlock. It is possible that there were no uninjured trees among the surviving Douglas-fir. However, even if there were, these trees would not necessarily show growth-increases in response to a thinning because at this time they were relatively young and their radial growth was in a gradual steep decline associated with the recent crown closure (Figure 16). The results of Reukema (1962) indicate that when young (ca. 40-50 years) Douglas-fir stands are thinned, many of the surviving Douglas-fir do not show radial growth-increases, although there may be a lessening in the rate of decline in radial growth.

1760s disturbance

The spatially restricted pulse of western hemlock growth-increases in the 1760s (mostly in 1760, 1761) is indicative of a canopy disturbance in or shortly preceding this decade (Figure 29). This conclusion is supported by the strong synchrony of the growth-increases, the sub-canopy stature of the responding western hemlock trees, and the large injuries (fortuitously sampled) to at least 2 Douglas-fir in 1760. Judging from the locations of western hemlock with growth-increases (Figure 33), the disturbance impacted canopy trees in an area of ca. 1.5 ha along the eastern edge of the plot (plus an unknown area beyond the plot boundaries). Based on the distribution of Douglas-fir still living in 1992 (Figure 18, Figure 36), the damage and mortality of canopy trees in this area did not result in a single large (ca. 1.5 ha) canopy gap, but rather in moderate thinning of the main canopy trees, with perhaps multiple smaller gaps. This is supported by the following:

1. The living Douglas-fir in this area in 1992 were main canopy trees in 1760 (Figure 26, Chapter 2), at which time they were 239 to 260 years old (Figure 8). If the disturbance in the 1760s had created a single large canopy gap, there would be a corresponding large hole in the 1992 distribution of Douglas-fir.

2. Given that Douglas-fir can establish on mesic sites in gaps > 0.075 ha (Spies and Franklin 1989, Spies et al. 1990), the absence of Douglas-fir establishment following the 1760s disturbance (Figure 8) indicates the 1.5 ha disturbed area was not characterized by openings of this size.

3. None of the western hemlock establishing after 1760 had open ringwidth patterns associated with establishment in relatively open conditions (Table 3).

The different ecologies and competitive states of the two species may explain why Douglas-fir did not respond by growth-increases in the 1760s as did western hemlock. For example, many western hemlock were far below the canopy at this time. When a canopy tree fell or was damaged, many subcanopy western hemlock would experience increased light and soil resources, and respond by increasing radial growth. In contrast, at

this time the Douglas-fir were 239 to 260 years old (Figure 8) main canopy trees (Figure 26, Chapter 2), and likely fairly separated from other canopy trees. Given the small number of directly competing canopy neighbors, the death or damage of a given Douglas-fir would probably affect few other Douglas-fir trees. It is not surprising, therefore, that a canopy disturbance in the 1760s would result in growth-increases of many more understory western hemlock than dominant Douglas-fir. This is also consistent with the study by North et al. (1996) showing that for at least six years following stand thinning, mature (120 to 145 years) overstory Douglas-fir did not show increased diameter growth. It is more difficult to interpret the spatially dispersed pulses of Douglas-fir growth-increases in the 1750s and the 1770s (Figure 30, Figure 33). These pulses may be related to the 1760s disturbance, or they may be responses to independent events.

1930s disturbance.

The spatially restricted pulse of western hemlock growth-increases in the 1930s indicates a canopy disturbance in or shortly preceding this decade (Figure 29). As for the two earlier canopy disturbances, this conclusion is supported by the strong synchrony of the growth-changes and by the sub-canopy stature of the responding western hemlock. The surviving Douglas-fir did not respond with a strong pulse of growth-increases in the 1930s, for similar reasons as argued for the 1760s disturbance. The significance of the associated pulse of Douglas-fir growth-increases in the 1920s is unclear.

Judging from the locations of the western hemlock with growth-increases, the 1930s disturbance was strongest in the NE quarter of the plot where it impacted ca. 0.8 ha, plus an unknown area beyond the edges of the plot (Figure 34). Similar to the 1760s disturbance, the damage to and mortality of canopy trees did not result in a single large canopy gap covering the disturbed area, but rather in moderate thinning of the main canopy, perhaps with small canopy gaps up to ca. 0.16 ha in size. This suggestion is also based on the 1992 distribution of Douglas-fir. At the location of the 1930s disturbance, the largest hole in the 1992 distribution of Douglas-fir was ca. 0.16 ha in size. Although

this hole may not have been created by the 1930s event, it does provide a maximum size for canopy openings created in that disturbance.

Based on historical records and on examination of the stand in 1992, the 1930s disturbance was likely a localized windthrow event. There are no reports of widespread events in the 1930s, such as large windstorms or insect outbreaks, that might have caused disturbances to forests in the western Cascades. However, isolated blowdowns of medium-sized patches occur on a fairly regular but unpredictable basis in forests near Yellowjacket, particularly where the ground is saturated (Buddy Rose, Randle District forester, personal communication). These blowdowns are generally attributed to microbursts (small, intense downdrafts), a phenomenon that is not necessarily associated with widespread weather events. The northeast portion of the plot is the wettest and steepest, making it more vulnerable to damage from microbursts, especially at older stand ages when the overstory trees are large and tall. In 1992, the northeast area was observed to have a high concentration of large logs and rootwads of all decay classes, showing that windthrow events were common in this area. One of the most recently fallen logs still had bark and its rings were dated. Although several of the outermost rings were rotten and could not be distinguished, crossdating allowed the outermost intact ring to be dated to 1923, suggesting that the death of this tree was likely associated with the 1930s canopy disturbance.

Other minor disturbances.

The three reconstructed events were the strongest canopy disturbances that occurred over the life of the stand, involving relatively large numbers of surviving trees, covering large portions of the plot, and were thus capable of leaving credible evidence, even after centuries. Additional, less evident, canopy and non-canopy disturbances likely occurred over the life of the stand, as suggested by the growth-changes that occurred outside the decades of the three reconstructed disturbances. The use of growth-changes in non-pulse decades to reliably reconstruct past disturbances is problematic and more limited than are

the highly synchronous pulses. However, they are a noteworthy feature of the stand and two examples are discussed below.

1. *Western hemlock growth-increases in non-pulse decades.* Eighty percent (626) of the western hemlock growth-increases were relatively isolated events, not part of the 3 reconstructed disturbances or part of visually obvious spatial groupings. Many of these individual western hemlock growth-increases may be due to canopy disturbances below the 0.8 ha resolution of the study, involving injury or mortality to a single or small number of canopy trees. However, many of these isolated increases may represent random variations, or may have had causes not related to canopy disturbances. For the identification of individual growth-changes, no data were found to guide in selecting a set of criteria that would unambiguously screen out all non-disturbance causes of ringwidth variation. This analysis relied on the synchronous occurrence of growth-changes among multiple trees for a more definitive identification of disturbance caused growth-changes (see Methods).

2. *Isolated pulses of Douglas-fir growth-changes.* Decades in which there were pulses of Douglas-fir growth-changes (both increases and decreases), but no corresponding pulses of western hemlock growth-increases are difficult to interpret. Particularly perplexing is the very strong pulse of Douglas-fir growth-decreases in the 1730s when 25 (43%) Douglas-fir scattered throughout the plot had growth-decreases; 21 of these happened in a single year, 1739. It could not be determined what type of event caused this or other isolated Douglas-fir pulses, but the absence of western hemlock growth-increases shows that significant thinning of the canopy was not involved.

Medium-sized forest patches

Prior to felling, the vegetative and physical characteristics at Yellowjacket were observed to vary continuously across the plot, but with trends toward groupings of features at a range of different spatial scales. These trends, combined with the reconstruction results, suggested three medium-sized patches differing in environmental features (including topography), and histories of canopy disturbances. In 1992, these patches were

distinguished by differing tree sizes, ages, and densities. The differing features of these areas likely arose from complex interactions among environmental features, canopy disturbance histories, and cumulative historical accidents. These patches, like their histories, were distinctive but not sharply delineated.

1. *Northeast patch*. This patch encompassed the northeast 1/4 to 1/3 of the plot. Environmentally, this was the wettest area of the stand, with a small seep, and moisture-requiring understory plants (e.g. Devils club) in places. It also had the steepest slope in the plot (ca. 50% slope, Figure 17). The forest of this area was distinctive for its relatively high densities of small western hemlock (57 trees, 40-70 cm; the smallest size class sampled), and its relatively low densities of Douglas-fir and large western hemlock (> 100 cm dbh) (Figure 36). Additional distinctive structural features included large accumulations of coarse woody debris and abundant western hemlock regeneration, particularly on the many large logs and rootwads. The age structure was also unique, with many young western hemlock trees (the youngest sampled age class, established 1680-1897) and few old trees (established 1500-1609) (Figure 35). This patch had the most dynamic disturbance history in the plot, having been heavily impacted by the canopy disturbances of the 1760s and 1930s (Figure 29, Figure 33, Figure 34).

At first glance, it might appear that the distinctive structural features of this patch were a direct result of its unique disturbance history. However, a clear relationship between reconstructed history and forest structure in this area could not be found. For example, although the cluster (n = 57) of small western hemlock had the appearance of a cohort that may have originated following one or both of the 1760s and 1930s canopy disturbances, these trees actually established over a wide range of dates (1580-1897) with none originating after 1930, and only 19 originating during a broad period after 1760 (1760-1897). This cluster was clearly not a cohort of similarly aged trees. Alternatively, the possibility was considered that this cluster of small trees might have been due to synchronous release from suppression by one or both of the canopy disturbances in this area. However, this possibility cannot totally explain the

cluster of small trees. Of the 57 trees in this cluster, 40 responded with growth-increases to the 1930s disturbance, 12 responded to the 1760s disturbance, 8 responded to both disturbances, and 13 responded to neither. While the 1930s and 1760s disturbances may have played a role in the success of small western hemlock, the causative relationships are apparently not simple or singular.

Since the distinctive structural features are not clearly the result of the unique disturbance history of the northeast patch, the forest structure here likely resulted from a complex interplay of factors. For example, the relatively moist conditions and steep slope of this patch may have been a factor contributing to its history of repeated canopy disturbances. In turn, the canopy disturbances would have shaped the character of the forest by thinning the largest overstory trees. This thinning would allow understory trees to survive and grow, and would also produce large woody debris that provided seedbeds for western hemlock regeneration. However, the establishment and growth of these understory trees were not directly related to the disturbances, and are perhaps due instead to the cumulative interactions of the historical accidents of climate, past individual treefalls, seedbed conditions, seedfall locations, etc.

2. *Central patch.* This patch encompassed a broad band running diagonally from northwest to southeast across the middle 1/3-1/2 of the plot. Environmentally, this patch had no extremes. There was no evidence of exceptionally wet or dry microsites, and the overall topography was gentle (ca. 25% slope), particularly toward its center, with a fairly sharp drop-off just beyond the southeastern edge of the plot (Figure 17). The forest in this patch was distinctive for: its relatively high density of Douglas-fir and large western hemlock (> 100 cm dbh) (Figure 36); its low density of small western hemlock (40-70 cm dbh, Figure 36); the relatively high density of very old trees (established 1500-1609, Figure 35); and the near absence of the youngest age class of sampled western hemlock (established post-1680, Figure 35). This patch was less impacted by the reconstructed canopy disturbances than was the northeast patch. It was not affected by the 1930s disturbance, was lightly affected along its eastern

edge by the 1760s disturbance, and was affected to an unknown degree by the disturbance of the late 1500s (Figure 29, Figure 32, Figure 33, Figure 34). The mild topographic and environmental features of this patch may have contributed to its less active disturbance history and favorable growing conditions, leading to the high density of large old trees. Although the steep drop-off just beyond the eastern boundary may have contributed to the disturbance near this edge in the 1760s, even here the Douglas-fir and large western hemlock were relatively dense (Figure 36).

3. *Southwest patch.* Judging from the generally sparse herb and shrub layer dominated by salal, this was the driest patch, with poorest growing conditions. The patch was also characterized by a steeper slope (ca. 35% slope, Figure 17) than the central patch. The forest was distinctive for: its relatively low density of very old trees (established 1500-1609, Figure 35); high density of the youngest age class of sampled western hemlock (established post-1680, Figure 35); relatively low density of Douglas-fir and large western hemlock trees (> 100 cm dbh, Figure 36); relatively high density of small western hemlock (40-70 cm dbh, Figure 36); low density of western hemlock regeneration; and scarcity of coarse woody debris. The cluster of small western hemlock had the deceptive appearance of a cohort of similarly aged trees. However, as in the northeast patch, these small trees established fairly evenly over a wide range of dates (1571-1840). The southwest patch was not distinctive with respect to canopy disturbance history, although it did have several western hemlock growth-increases in most decades, possibly caused by multiple, small-sized, disturbances (Figure 29, Figure 32, Figure 33, Figure 34). The drier conditions and poorer site quality of this patch probably played an important role in the development of forest structure and in the apparently low impact from the medium-sized canopy disturbances. For example, smaller trees on drier ground would be less prone to windthrow than larger trees on wetter ground.

Species-specific responses to canopy disturbances

Douglas-fir. At the stand level, the history of Douglas-fir involved centuries of growth and thinning as the dominant canopy species. The site was initially colonized in the early 1500s by an estimated 800 trees/ha, mostly Douglas-fir or Douglas-fir mixed with other fast growing species (Chapter 2). By 1992 only ca. 17/ha of the initial colonizers remained alive (14/ha Douglas-fir initial colonizers, 3/ha western hemlock initial colonizers). Although the amount of thinning of the pioneer trees was substantial over the life of the stand, this thinning never created canopy gaps large enough to allow Douglas-fir establishment, strongly synchronous pulses of western hemlock establishment, or open ringwidth patterns in establishing western hemlock. The thinning of Douglas-fir was facilitated by at least two medium-sized and one perhaps large-sized canopy disturbances. Many small canopy disturbances may have also occurred and contributed to the thinning, however these are less certain and the relative importance of small versus larger-sized canopy disturbances is difficult to assess.

Western hemlock. The overall history of western hemlock at Yellowjacket was one of establishment and slow growth in the understory, and gradual ascension to the canopy assisted by multiple growth-increases. The canopy disturbances likely accelerated the importance of western hemlock in the stand by thinning the canopy and releasing understory trees from suppressed growth. However, these disturbances did not directly affect the timing of western hemlock establishment. As was argued for the 1930s disturbance, tree establishment and subsequent survival likely involved cumulative interactions among many factors (e.g. understory light conditions, seedbed conditions, presence of woody debris, seedfall locations, individual treefalls, etc.).

Western hemlock successfully established slowly, but continuously, throughout much of the life of the stand, mainly in 5 broad intervals, but with fewer than 10 trees establishing in most decades and no strongly synchronous pulses (Figure 8). Many other western hemlock established but were not successful, and left no record, hence the following descriptions are for only the sucessful establishment. Except for the higher establishment

ca. 1540-1609, variations in establishment rates did not correspond to times of the reconstructed canopy disturbances. The low establishment ca. 1500-1539 may have been due to stem exclusion by the rapidly growing pioneers. The higher establishment rates ca. 1540-1609 may have been due to enhanced survival and growth related to moderate thinning of the main canopy in the mid- to late-1500s. Subsequent intervals with lower (1610-1679) and higher (1680-1779) establishment rates may have had more to do with the upper strata of western hemlock than with the Douglas-fir. By these times, the Douglas-fir crowns were far above the forest floor, and western hemlock in the sub-canopy would cause deep shade in the lowest levels of the forest. Hence the low establishment ca. 1610-1679 may have represented a stem exclusion stage under western hemlock (Oliver and Larson 1990), with a few trees successfully establishing on microsites with sufficient light, perhaps in tree fall gaps. The relatively higher establishment in ca. 1680-1779 may have represented an understory reinitiation stage, when branch or tree mortality in the aging upper strata of western hemlock allowed more light through to the forest floor. The low establishment identified after 1780 was an artifact of the 40 cm dbh lower limit for sampling western hemlock.

By 1992, many western hemlock trees that established in the understory had reached the canopy or were on their way up, thus diversifying the stand's horizontal and vertical complexity compared to its early structure. Most of these trees reached the canopy through multiple growth-increases. Although the measured growth-increases were for radial growth, they were likely associated with increased height growth, as photosynthate is allocated to height growth before diameter growth (Oliver and Larson, 1990). Some of the growth-increases were directly associated with the 3 reconstructed canopy disturbances. Many others were more isolated events, due either to smaller canopy events or other causes such as events in the understory, isolated branch falls, or random variations. Regardless of the causes of these isolated growth-increases, they may have influenced the general condition of western hemlock growth as much or more than did the medium-sized canopy disturbances. However, the reconstructed disturbances were likely the major contributors to the creation of the medium scale patchiness of the forest.

Management implications

This two-part reconstruction represents the most detailed history available for the entire lifetime of an old-growth Douglas-fir stand, and should be of considerable value for the management of old-growth Douglas-fir forests. In the Pacific Northwest, with the increased emphasis on maintaining and developing old-growth stands, researchers and managers have asked whether silvicultural interventions will be needed to promote the development of existing young stands into old-growth structures, and if so, what types of interventions are required (e.g. McComb et al. 1993, Thomas 1997, Kohm and Franklin 1997, DeBell et al. 1997, Tappeiner et. al 1997, Halpern and Raphael 1999, Aubry et al. 1999). The knowledge provided by the Yellowjacket reconstruction adds to the array of tools and ideas being used to address these questions. The first part of this study, the reconstruction of the stand initiation stage (Chapter 2) shows that at a large spatial scale and long time span, old-growth Douglas-fir structures may develop by multiple pathways. Yellowjacket started out fast and dense, similar to modern young stands, whereas previously reconstructed old-growth Douglas-fir stands apparently started very slowly and at low densities. Yet typical old-growth structures did develop from these very different beginnings. This finding led to the suggestion that many typical young stands might need only time to develop old-growth structures, and that silvicultural interventions such as thinning may not be required. However, for some other young stands, thinning may be chosen as an intervention to speed the development of structural complexity, or because the stands are considered too dense or undifferentiated. For these cases, the current study provides an example that may be useful for developing thinning guidelines, although the benefits of any intervention should be weighed carefully against the unintended ecological costs associated with silvicultural manipulations (e.g. disturbance to the ground and understory communities). Findings of this study relevant to the development of thinning guidelines include:

• Although the amount of thinning of the pioneer trees was substantial over the life of the Yellowjacket stand, the thinning was apparently gradual as evidenced by the fact that after the canopy initially closed, the stand was never opened up enough at any single time

and place to allow Douglas-fir establishment or open ringwidth patterns for establishing western hemlock.

- Some of the thinning at Yellowjacket was brought about by three canopy disturbances that thinned, but did not clear, the canopy over medium-sized areas. Other thinning likely occurred via individual tree deaths that left no or small canopy gaps, such as might occur due to competitive interactions.

- Some environmental patches within Yellowjacket were more impacted by the canopy disturbances than others. In particular, three medium-sized patches at Yellowjacket differed from one another in environmental characteristics, histories of canopy disturbances and forest structures. These patches represent differing developmental histories at medium spatial scales nested within the large patch set up by the initial catastrophic disturbance. Management should be sensitive to such patchiness at varying scales in these forests.

Given the strong linkages between forest structures and functions, variability in the pathways to old-growth structures is likely important for maintaining diversity in habitat and ecosystem functions at many scales, both spatial and temporal, across the landscape. Clearly, there is a continuing need for further research into the structural and functional characteristics of patchiness in these forests.

Figure 17. Contour Map.

Elevation contours for Yellowjacket study plot. The study plot was 3.3 ha in area. The irregular shape of the plot is due to natural and manmade boundaries: a dry streambed along the northern edge, a road along the western edge, the sale boundary along the southern edge, and cliff along the eastern edge. The elevation contours are for 5 m intervals, and were derived from elevations measured at the base of each tree. Some trees along the western edge of the plot were missing elevation data, and so there are no contours drawn for that area, however no topographic changes were observed here.

Figure 18. Location of live trees in data set.

Locations of all live (in 1992) Douglas-fir (45) and western hemlock (224) in the data set (Table 1). The western hemlock were ≥ 40 cm dbh except for 12 slightly < 40 cm dh. One additional Douglas-fir, and 30 live western hemlock ≥ 40 cm dbh were also in the plot but not sampled due to post-logging conditions or tree rot. The grid squares are 40 x 40 m.
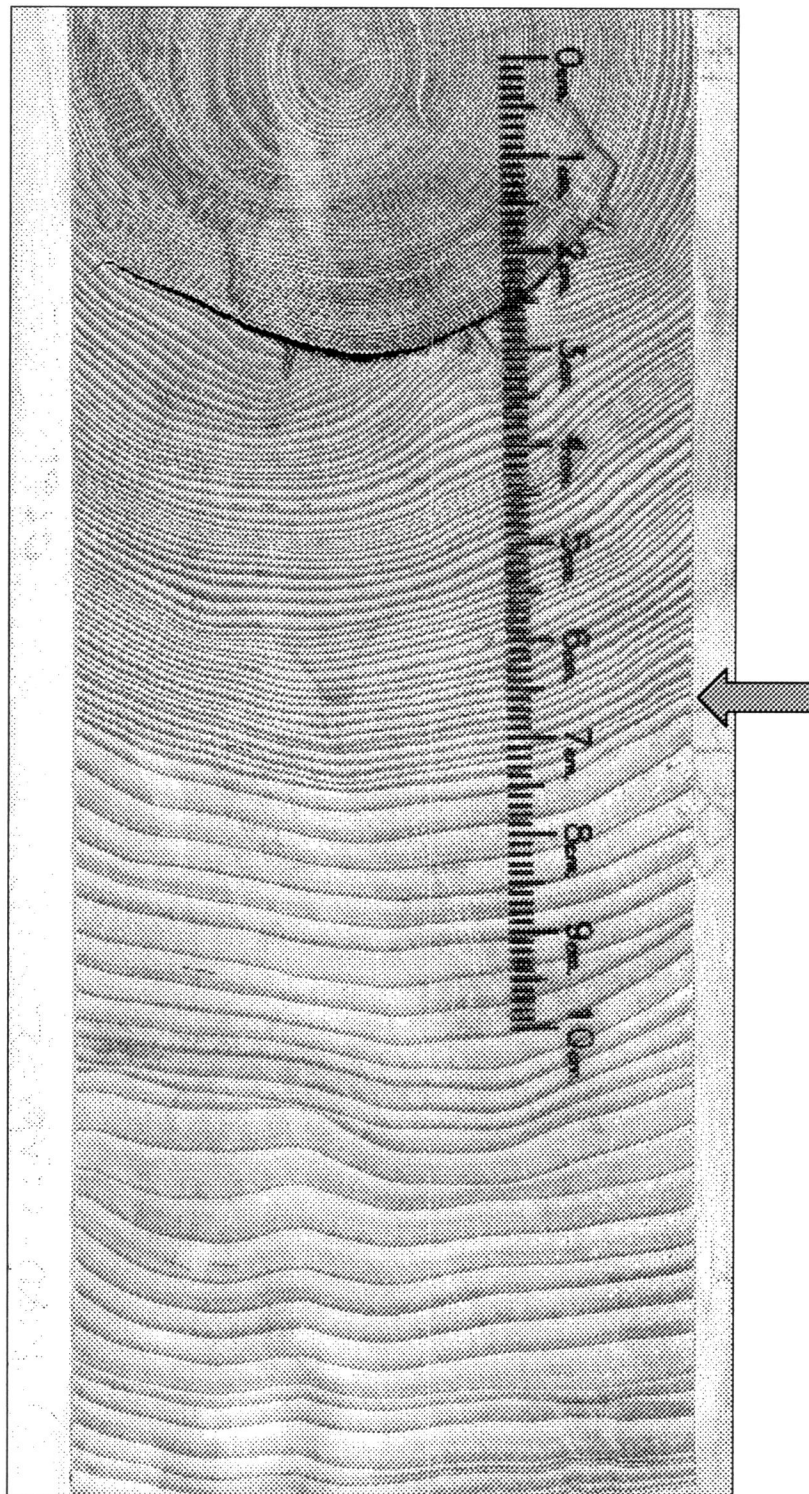
Figure 19. Stump-sample #1820.

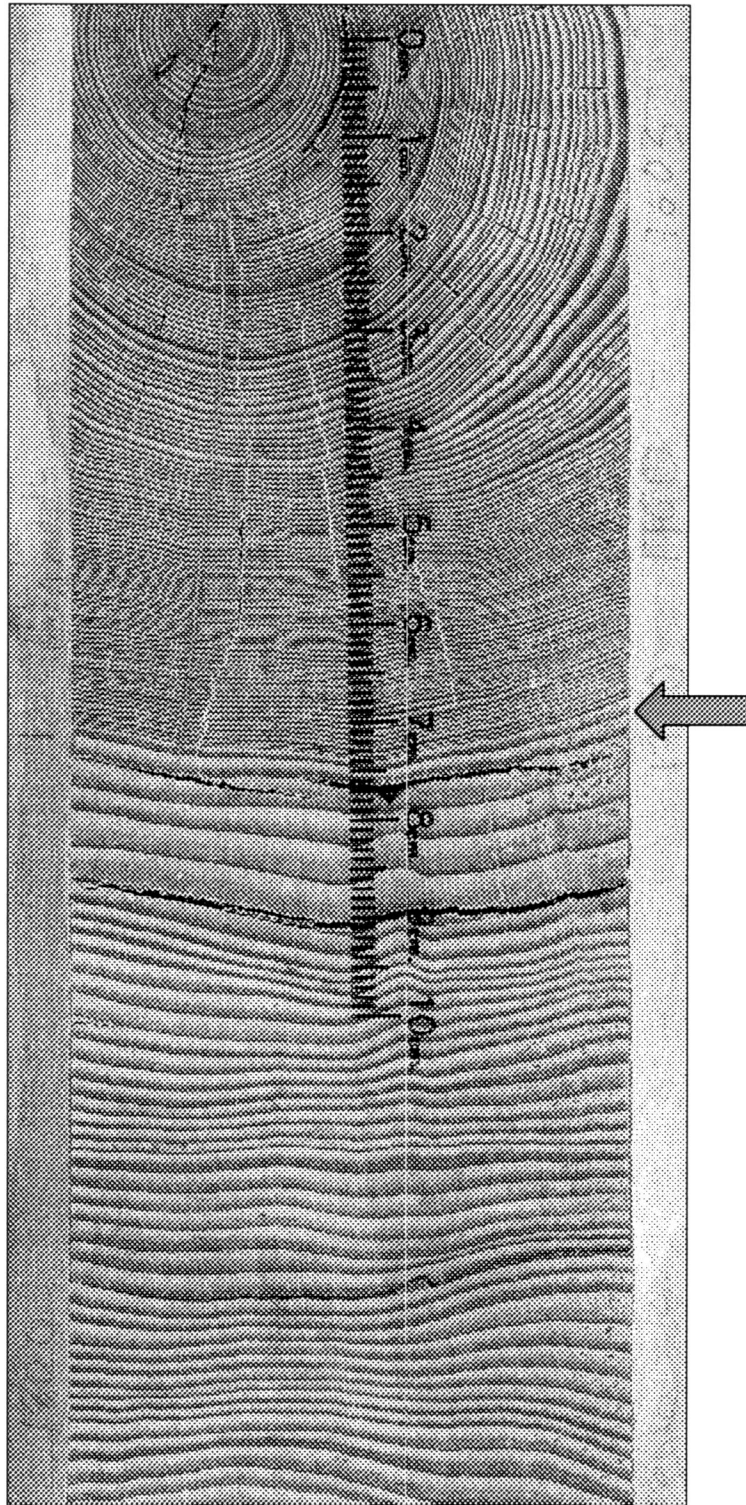Stump-sample from western hemlock #1820 showing growth-increase occurring in 1933.

Figure 20. Stump-sample #1900.

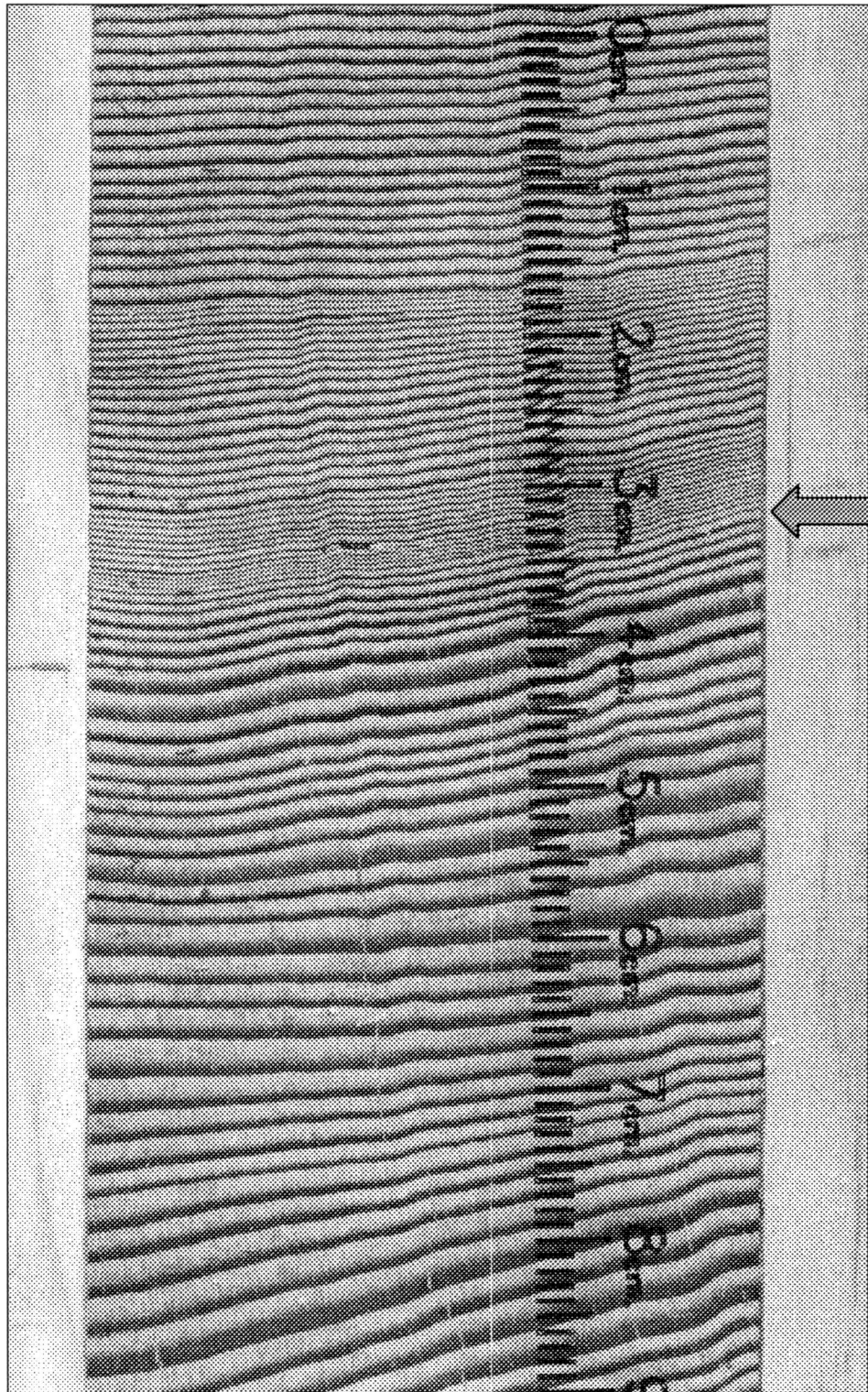Stump-sample from western hemlock #1900 showing growth-increase occurring in 1761.

Figure 21. Stump-sample #1977.
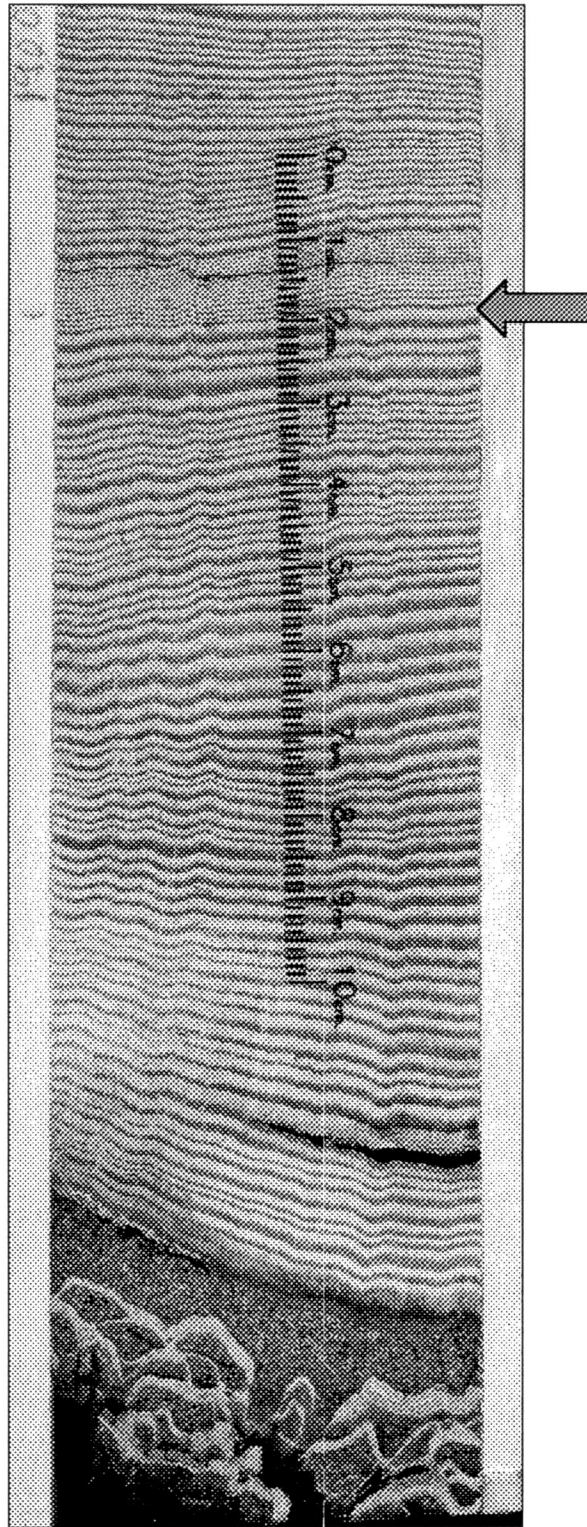Stump-sample from Douglas-fir #1977 showing growth-increase occurring in 1771.

Figure 22. Stump-sample #1477.
Stump-sample from Douglas-fir #1477 showing growth-increase occurring in 1931.
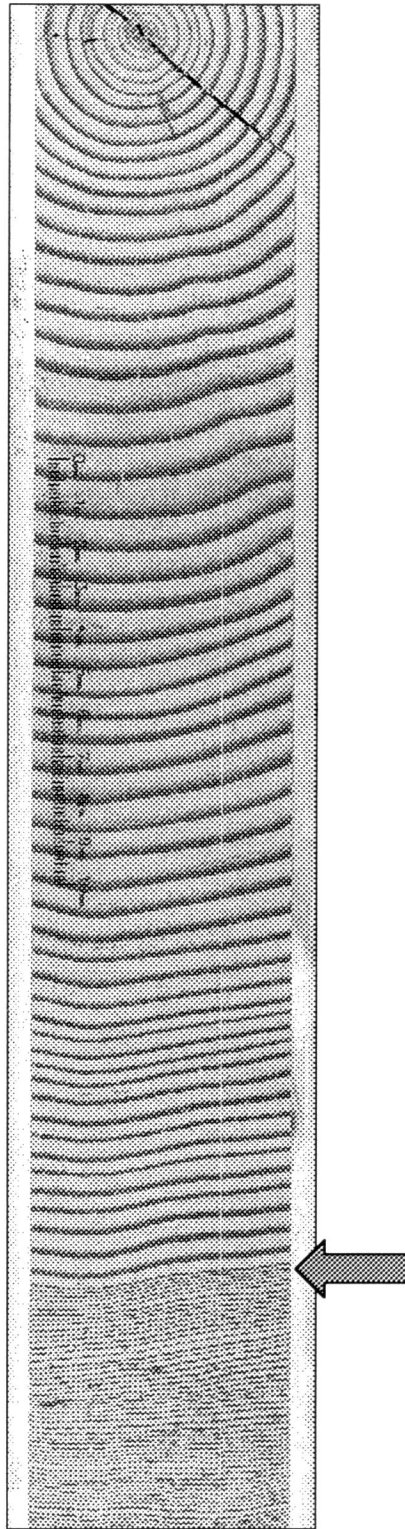
Figure 23. Stump-sample #1187.

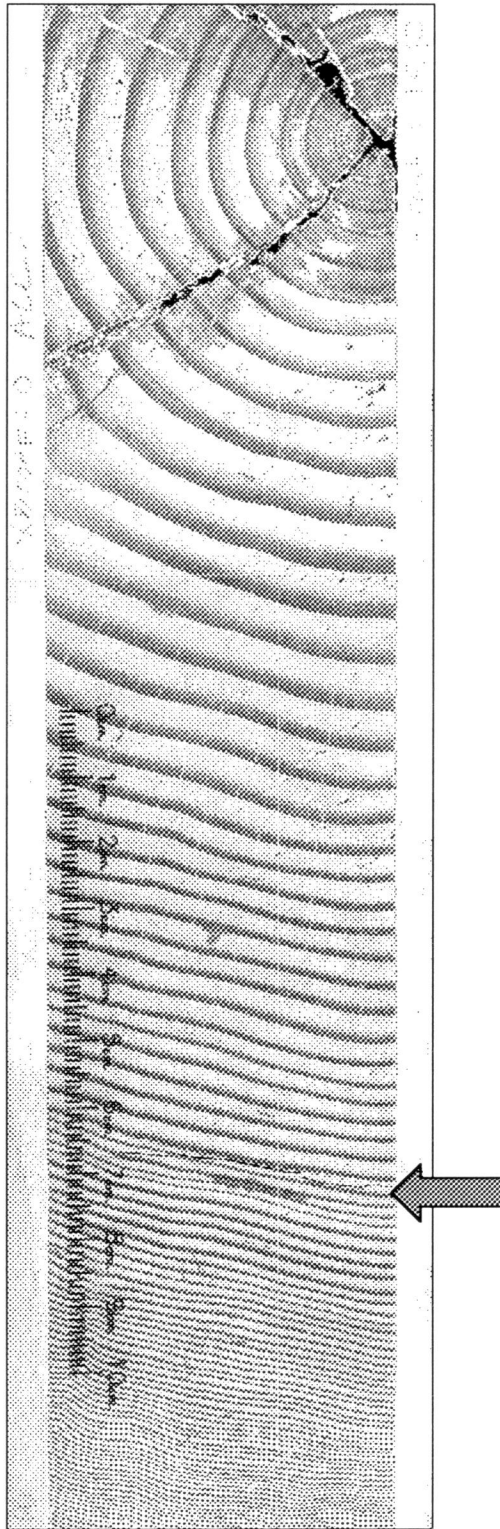Stump-sample from Douglas-fir #1187 showing growth-decrease occurring in 1561.

Figure 24. Stump-sample #1973.

Stump-sample from Douglas-fir #1973 showing growth-decrease occurring in 1543.
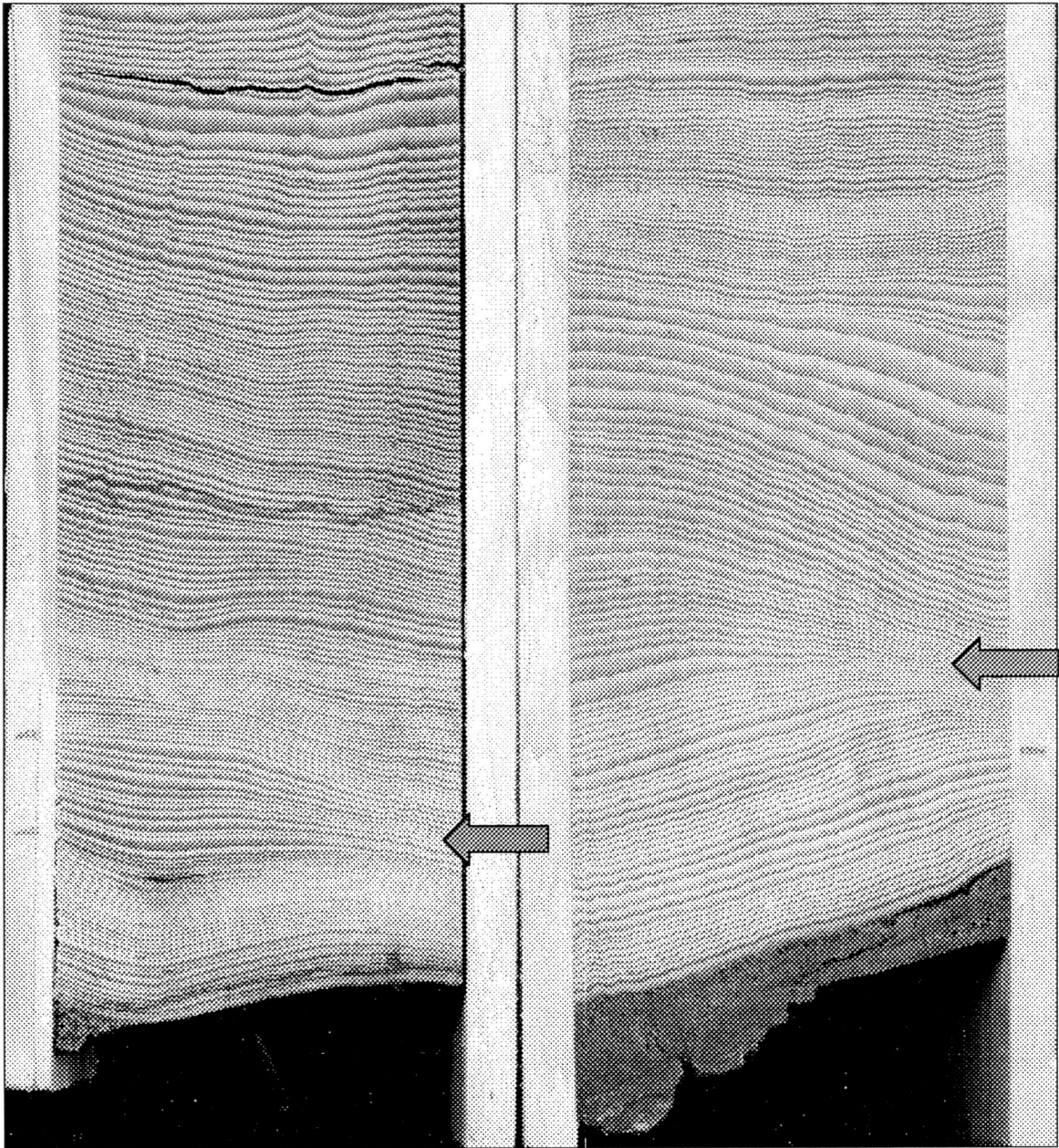
Figure 25. Western hemlock showing random variations.

Western hemlock stump-samples showing changes in ringwidth that are apparent along one side of the sample but not the other.
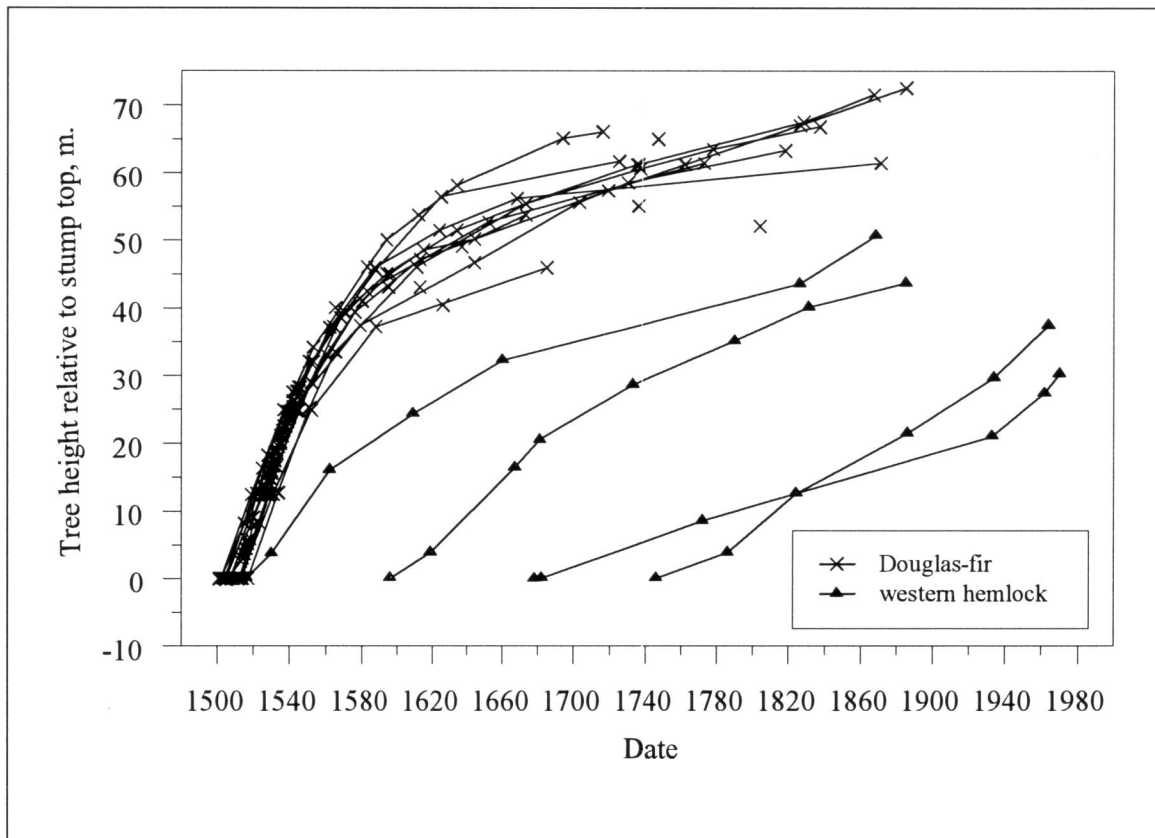
Figure 26. Reconstructed heights.

Reconstructed heights for the dissected Douglas-fir (n = 20) and western hemlock (n = 4) trees. The single isolated points are for the Douglas-fir that were sampled at only 2 heights each. The uppermost sampled height for each tree is not the full 1992 height.
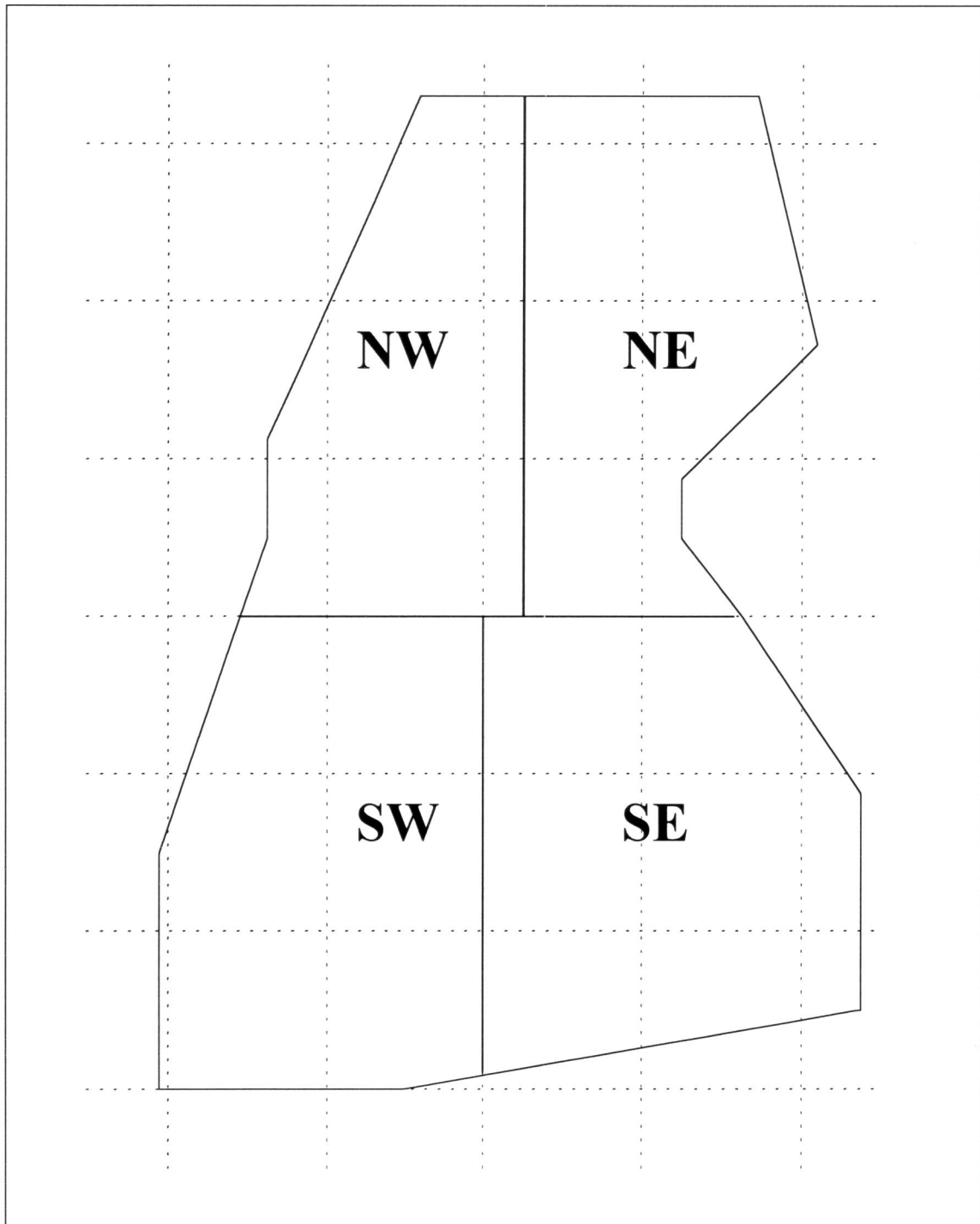
Figure 27. Boundaries for plot quarters.

The plot was divided, along north-south and east-west lines, into halves and quarters that were as similar in size as conveniently possible for the irregularly shaped plot. The exact sizes were not of importance to the analysis.
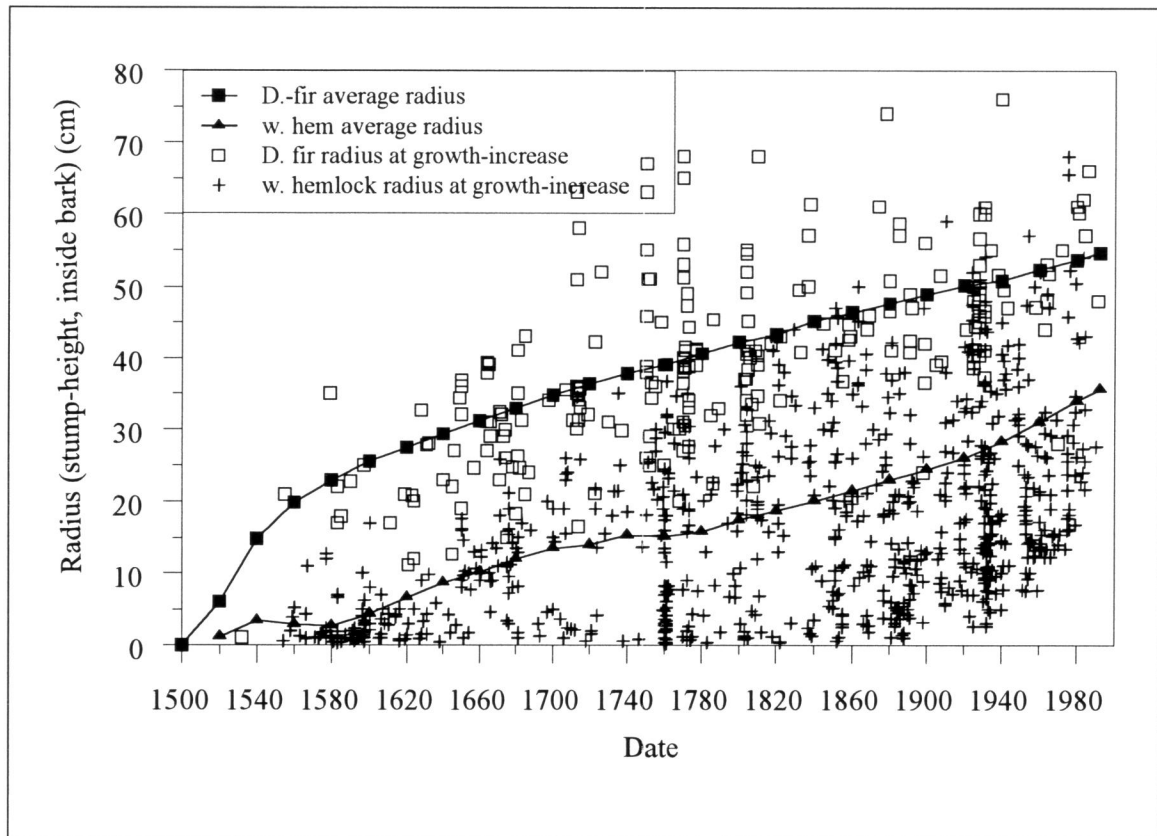
Figure 28. Radii of individual trees.

Radii (stump-height, inside bark) of individual western hemlock and Douglas-fir trees at the dates of their growth-increases; and average radii for Douglas-fir and western hemlock with records for selected dates. The radii were not converted to dbhs because this conversion, which requires a number of considerations (Chapter 2), was not necessary for the present analyses. Radii are considered to be approximate surrogates for the relative competitive states of these trees.
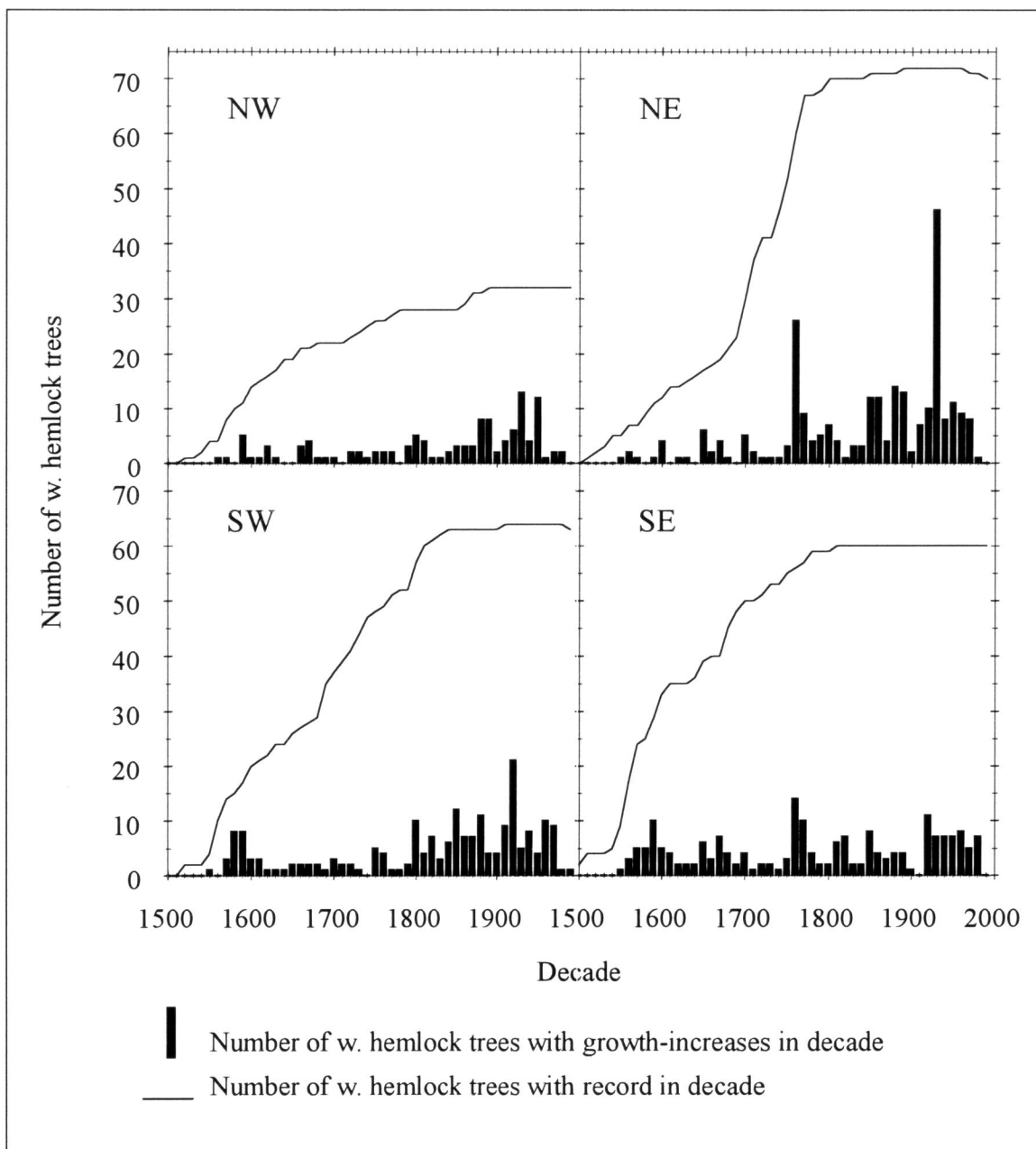
Figure 29. The number of western hemlock with growth-increases.

The number of western hemlock in each plot quarter that had growth-increases in each decade (bars), and the numbers of western hemlocks in each plot quarter with records in each decade (lines). A tree had a record for a decade if it had established in or prior to the decade and survived long enough that in 1992 it had datable tree-ring records for the decade.
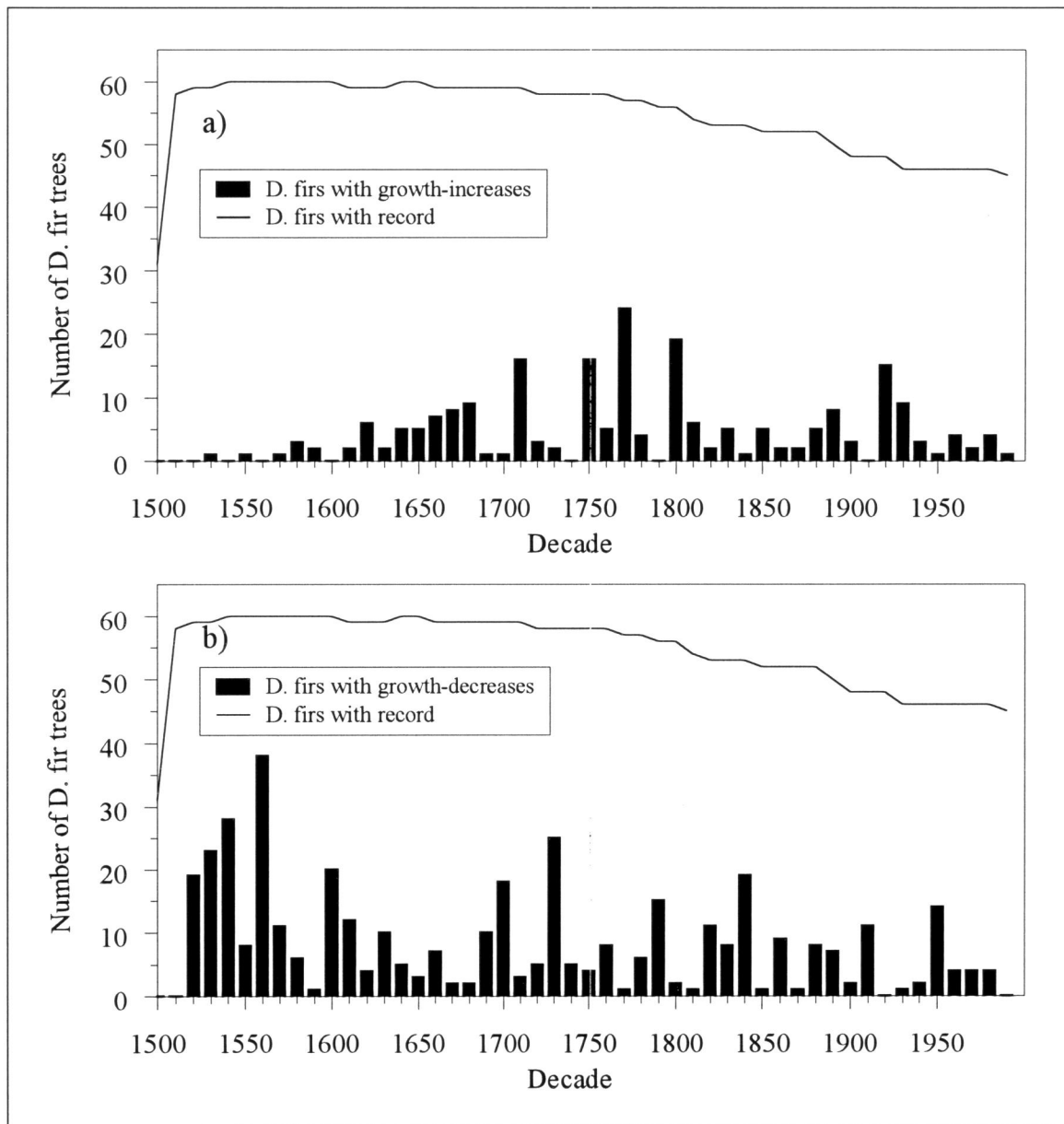
Figure 30. Douglas-fir with growth-changes.

The numbers of Douglas-fir trees in the whole plot that had a) growth-increases or b) growth-decreases in each decade, and the numbers of Douglas-fir in the whole plot that had records in each decade.
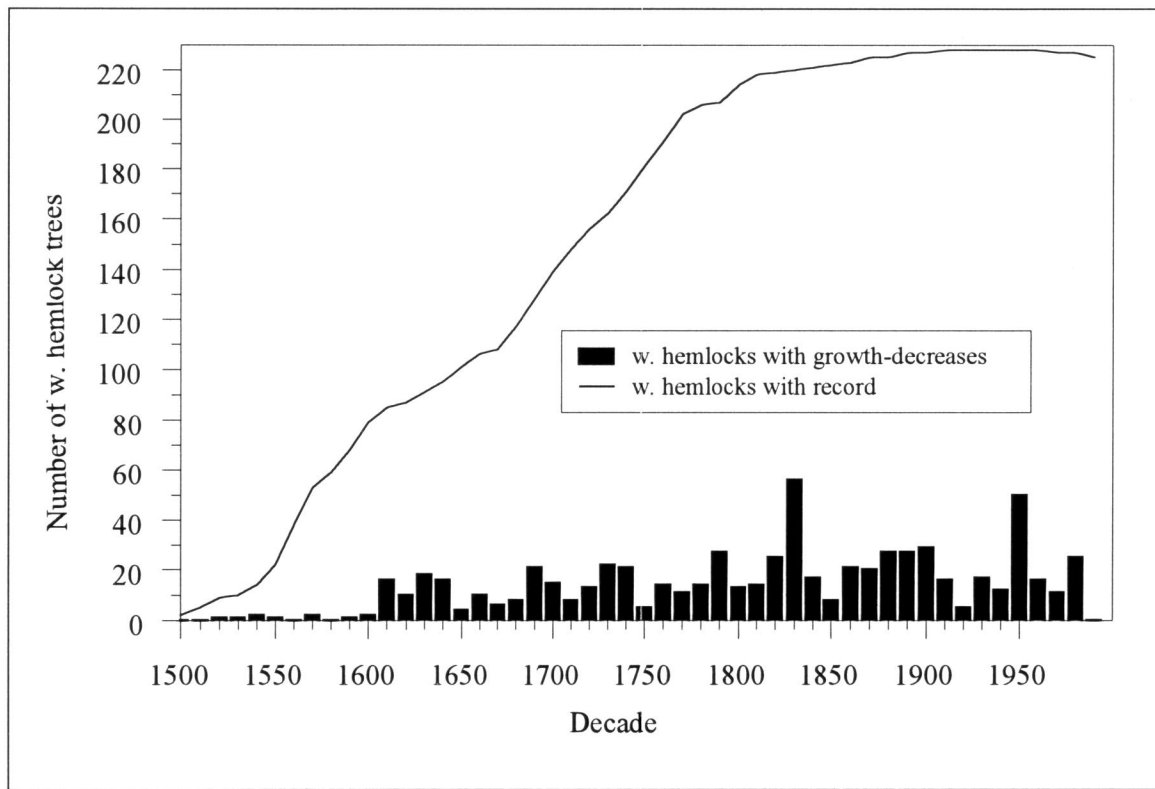
Figure 31. Western hemlock with growth-decreases.

The numbers of western hemlock trees in the whole plot that had growth-decreases in each decade, and the numbers of western hemlock in the whole plot that had records in each decade.
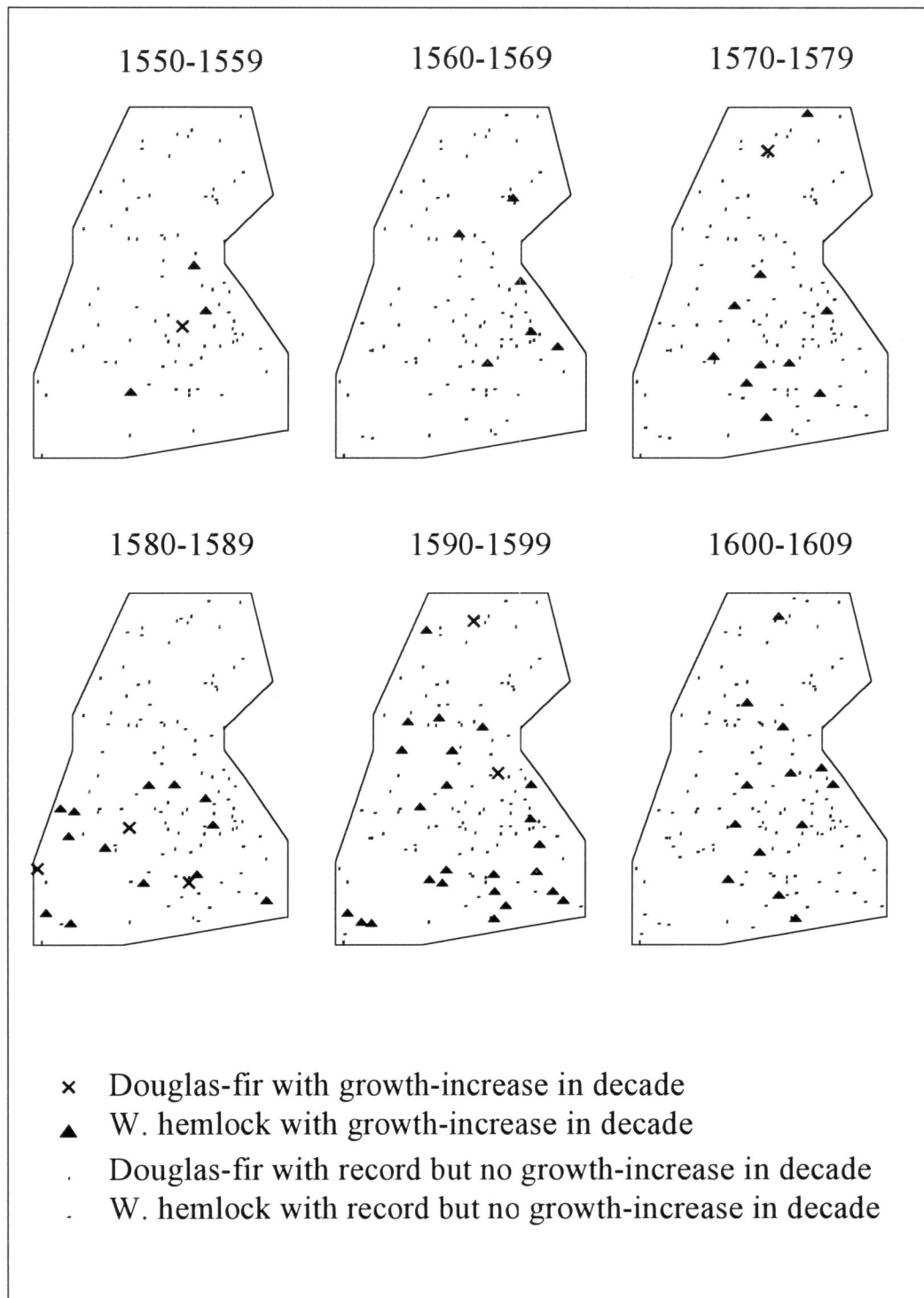
Figure 32. Locations of trees with growth-increases near 1590.

Locations of western hemlock and Douglas-fir trees with growth-increases in decades at and near the time of the 'late 1500s pulse' of western hemlock growth-increases. Also shown are the locations of all trees with records for these decades.
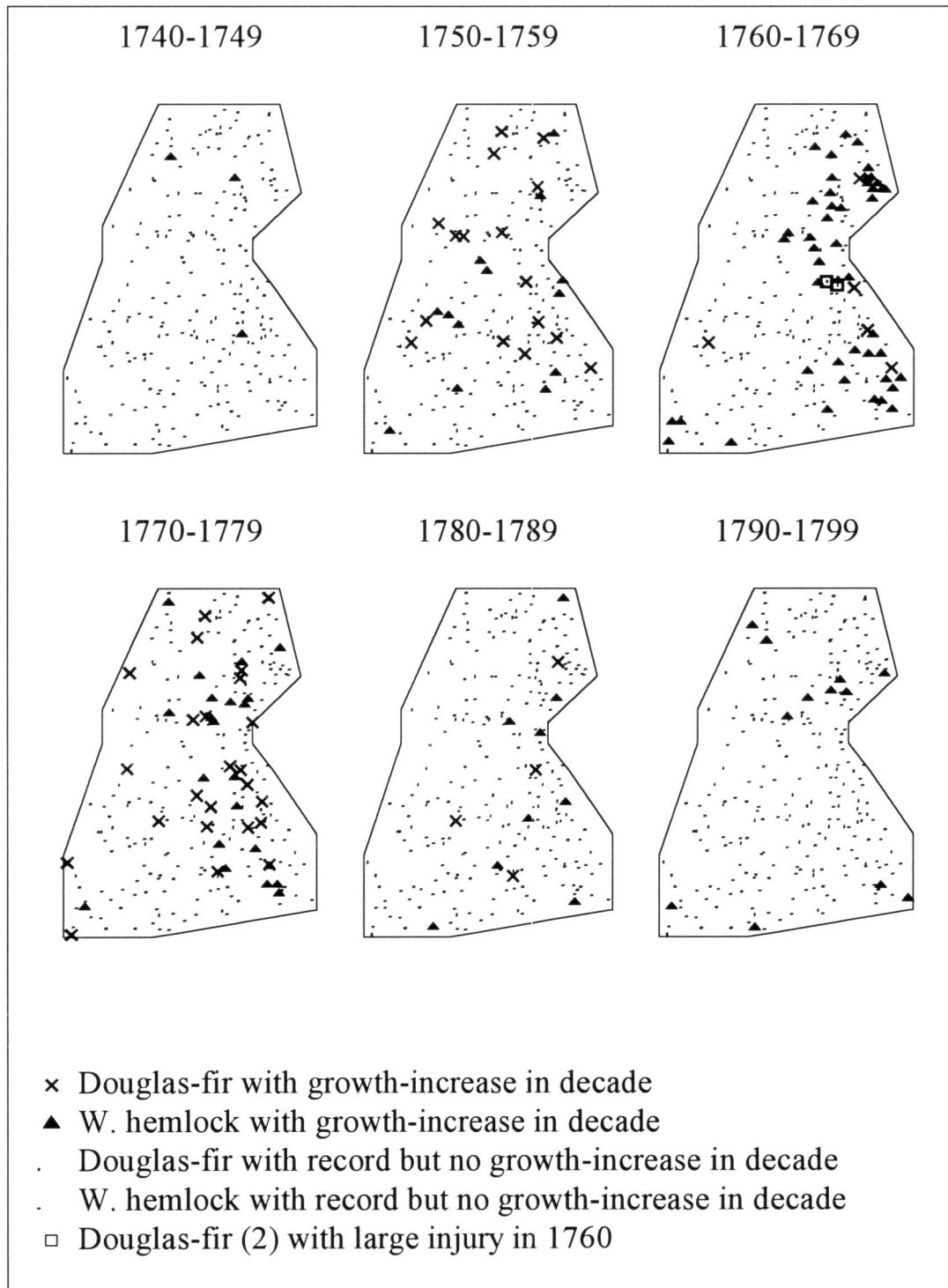
Figure 33. Locations of trees with growth-increases near 1760.

Locations of western hemlock and Douglas-fir trees with growth-increases in decades at and near the time of the '1760s pulse' of western hemlock growth-increases. Also shown are the locations of all trees with records for these decades.
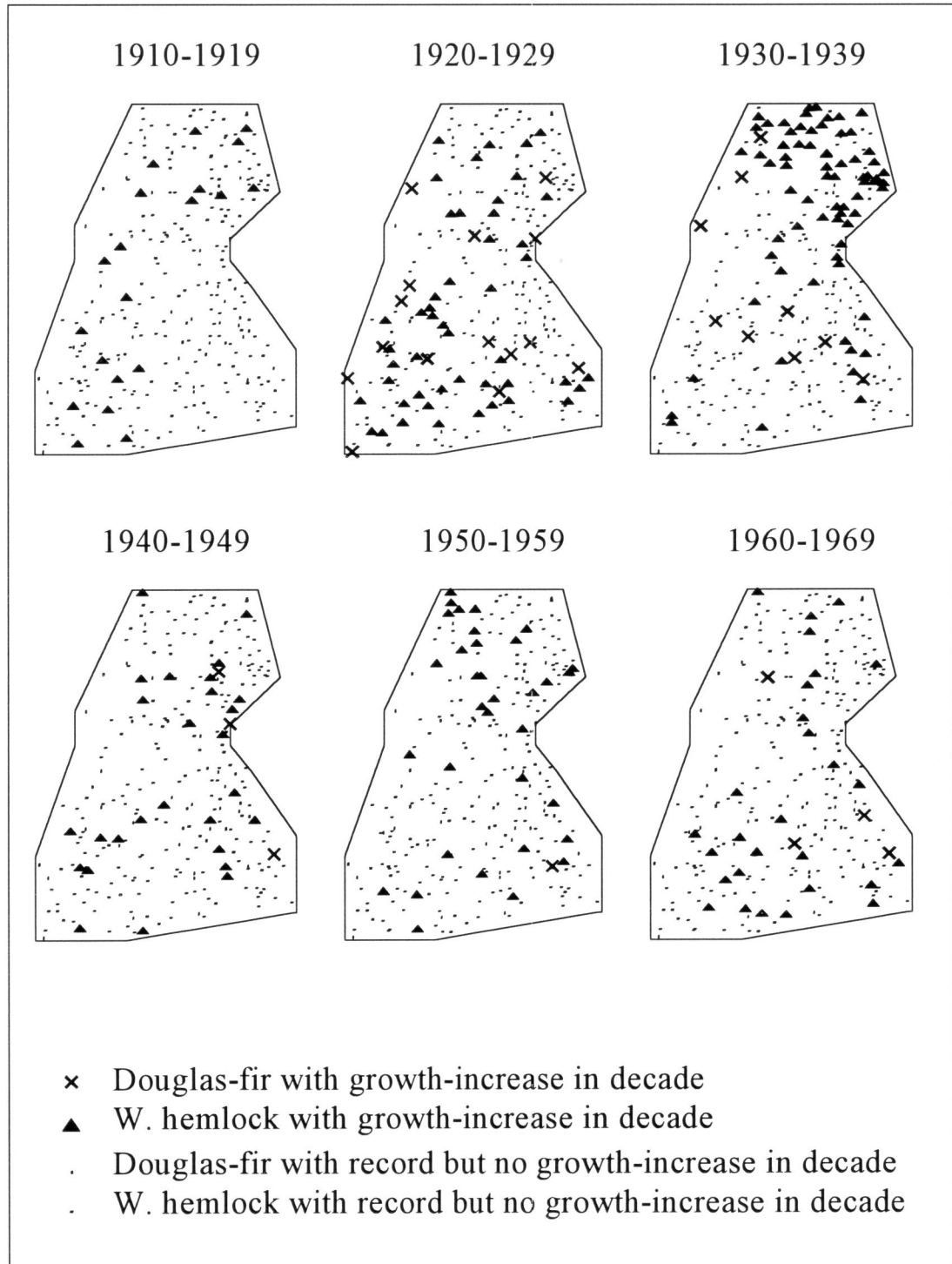
Figure 34. Locations trees with growth-increases near 1930.

Locations of western hemlock and Douglas-fir trees with growth-increases in decades at and near the time of the '1930s pulse' of western hemlock growth-increases. Also shown are the locations of all trees with records for these decades.
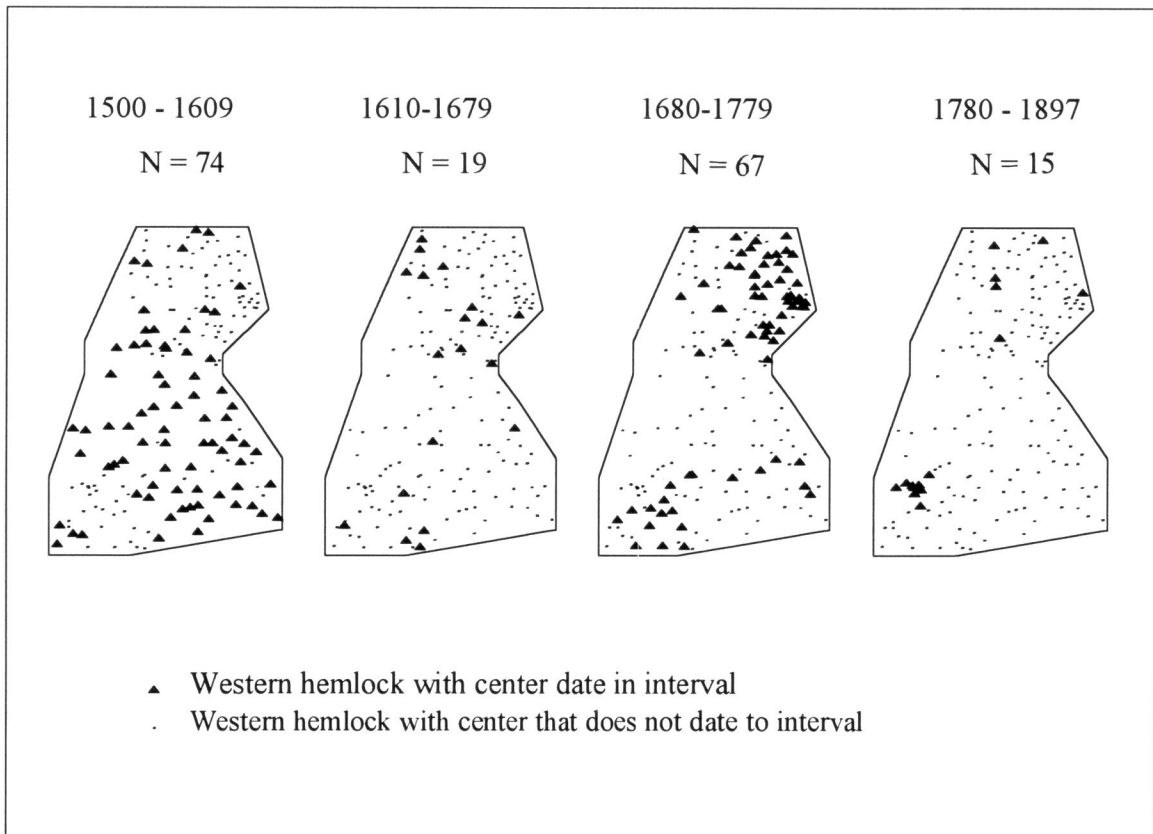
Figure 35. Locations of western hemlock establishment.

Locations of sampled live western hemlock that established (at stump-height) during 4 periods. The time periods reflect the broad intervals of higher and lower amounts of successful western hemlock establishment (**Figure 8**). Also shown for each period are the locations of sampled western hemlock with centers that did not date to the period; this set of trees is smaller than all western hemlock shown in Figure 18 due to trees without centers.
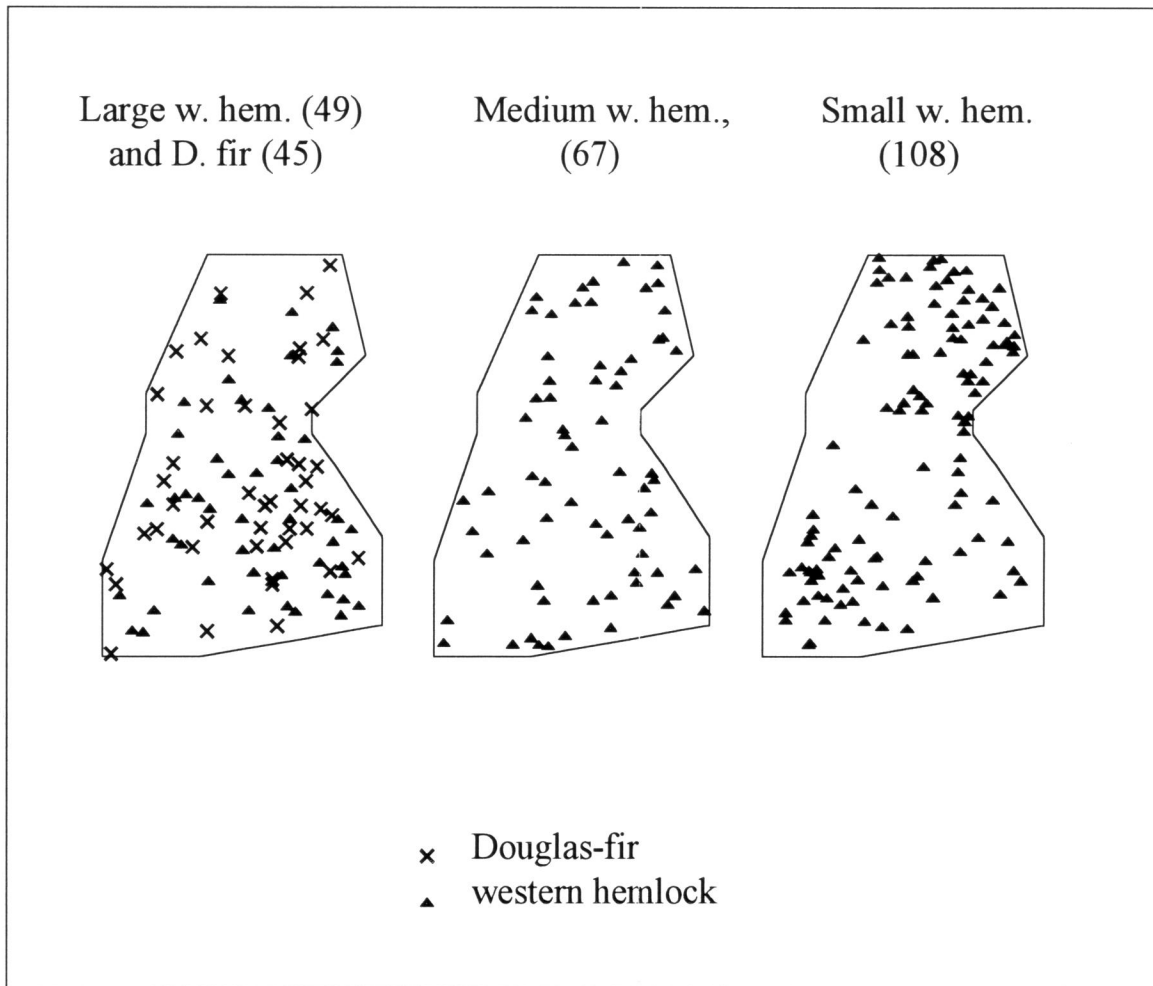
Figure 36. Locations of trees by 1992 dbh size classes.

Locations of sampled live western hemlock and Douglas-fir by 1992 dbh size classes (directly measured on the live trees). Western hemlock dbh size classes are: small, 40-69 cm; medium, 70-99 cm; large, ≥ 100 cm. The locations of all Douglas-fir are included in the map showing the large western hemlock.
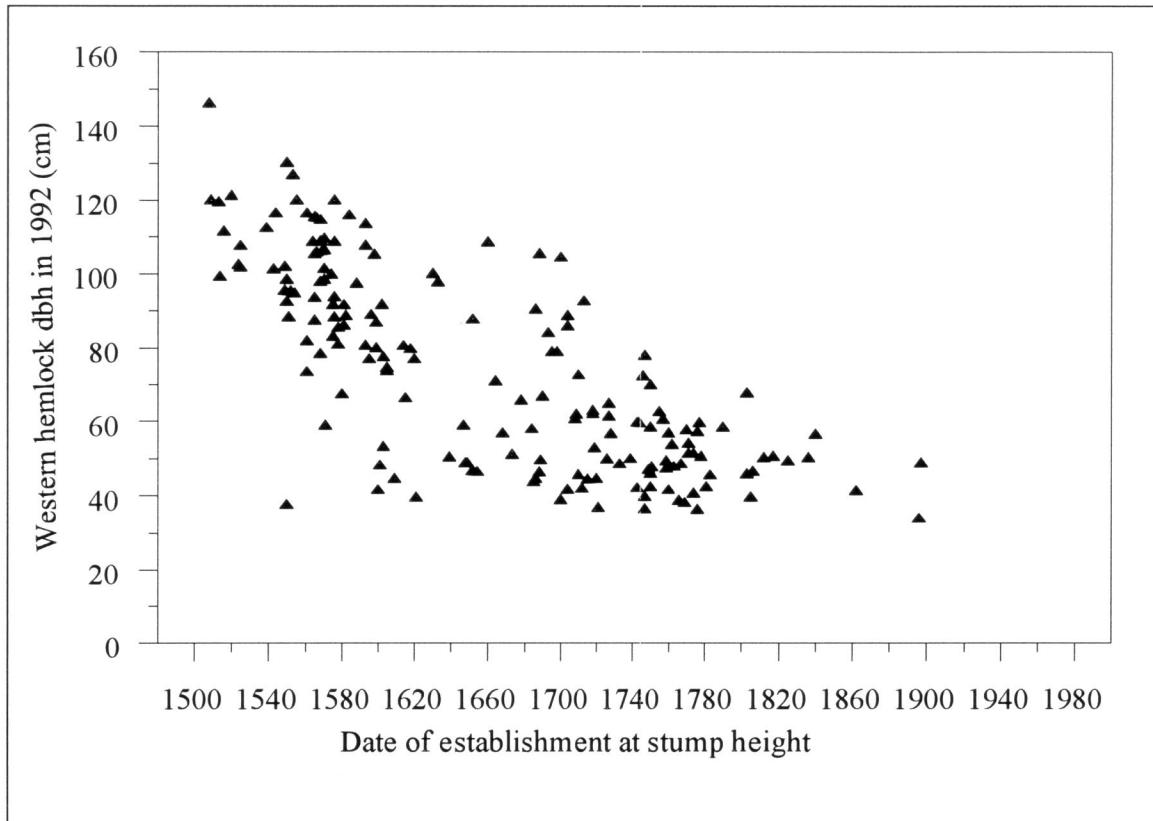
Figure 37. Western hemlock 1992 dbh versus date of establishment.

Western hemlock 1992 dbh versus date of establishment at stump height (n = 175). The dbhs were measured on the live trees in 1992. The establishment dates are the center-dates at stump-height.

Table 4. Growth-changes for Douglas-fir and western hemlock.

		Douglas-fir	Western hemlock
Number of trees evaluated		61	228
Growth-increases (GIs)			
Total number of GIs		223	781
% of trees of species with 1 or more GIs.		88.5%	98.7%
% of trees of species with no GIs.		11.5%	1.3%
Per tree characteristics of GIs:			
Number/tree	x	3.6	3.4
	SD	(2.4)	(1.7)
	range	0-10	0-9
Time following GI until next GI or GD, yr	x	34.1	36.6
	SD	(29.5)	(30.2)
Magnitude of GI	x	1.8	2.4
	SD	(0.6)	(1.2)
	range	1.1-4.8	1.1-12.7
Radius at GI, cm	x	39.3	17.2
	SD	12.9	(13.3)
	range	1.1-76	0.2-68
Tree age (stump ht) at GI, yr	x	273	172.6
	SD	107.1	(109.4)
	range	11-486	7-430
Growth-decreases (GDs)			
Total number		412	679
% of trees of species with 1 or more GDs.		100%	86.8%
% of trees of species with no GDs.		0%	13.2%
Per tree characteristics of GDs:			
Number/tree	x	6.8	3.0
	SD	(2.5)	(2.1)
	range	1-14	0-10
Time following GD until next GI or GD, yr	x	42.1 yr	45.5yr
	SD	(42.2)	(39.9)
Magnitude of GD	x	0.6	.5
	SD	(0.1)	(0.2)
	range	0.3-0.9	0.1-0.9
Radius at GI, cm	x	33.2	23.2
	SD	(15.8)	(13.5)
	range	4-77	2-64.2
Tree age (stump ht) at GI, yr	x	188.6	193.7
	SD	(137.8)	(106)
	range	13-484	13-458

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APPENDIX A:
FIELD TECHNIQUES FOR INTENSIVE DISSECTION
OF DOUGLAS-FIR 1408

One Douglas-fir, tree 1408, was intensively dissected for the purpose of reconstructing the development of its long crown. At the time of the stand felling (1992), the size and crown dimensions of this tree were visually representative of other dominant Douglas-fir in the stand. I dissected and sampled the tree in a way that would allow reconstruction of the cumulative height history, and recession of the live crown base up to its 1992 height. Accordingly, the dissection methods varied among 3 sampling zones along the bole (Figure 4; the following heights are relative to the stump surface):

1. *Stump surface to 28.3 m.* Intensively sampled clear bole. In this sampling zone, the bole was clear of emergent branches, with not even indents to mark the locations of embedded branches (i.e. branches that had long ago died, broken off, and been grown over by subsequent bole rings). To reconstruct the recession of the crown base to its 1992 height, I needed to locate and sample these embedded branches. In order to do this most effectively, in a way that preserved entire embedded branches, I needed to split the large, up to 2 m diameter bole along the pith. Don DeWitt was contracted to do this. He researched the project by first splitting smaller logs (ca. 1 m diameter, 3-6 m long), and by observing work of Bormann in which smaller logs (ca. 0.5 m diameter, ca. 3 m long) were split (Bernard Bormann, personal communication).

To achieve the splitting of the large diameter bole of tree 1408 (up to 2 m diameter, cut into 3-6 m long logs), Don DeWitt designed a device consisting of two L-shaped halves, which together housed a hydraulic cylinder capable of delivering up to 50,000 pounds of force (Figure 38). The halves were bolted to the lower face of a log with the bases of the "Ls" fitting into a cut slot. The cylinder was placed into the housing, and was attached to the pump by long hydraulic line. The splitting proceeded from the base toward the upper end of each log (Figure 39) in order to use the growth rings

to funnel the split toward the pith. This procedure was potentially dangerous, and multiple safety precautions were taken (e.g. placing blocks under the logs to prevent rolling during splitting, progressing the split slowly, keeping people sufficiently distant from the hydraulic cylinder by separating the pump from the cylinder via a length of hydraulic tubing). Once the bole logs were split, I found embedded branches by locating features in the pith that indicated probable locations of branch whorls (i.e. yearly termini or sharp angles in the pith), and also by locating distortions in the wood grain that indicated probable locations of underlying embedded branches. On the split surface, the pith and distortions in the wood grain were clearly visible (Figure 40). These locations were marked, and measured for height along the bole relative to the stump surface. At each marked location, a wide (ca. 10 cm) cross section was cut from one split half of the log. Each cross section contained 0-6 embedded branches. The cross sections were later split into smaller pie-shaped bole wedges (Figure 41), each containing one integrated branch (birth to death to incorporation wherever present), and, wherever possible, a full bole radius (wood from pith to bark). If a cross section had no branches, a bole radius was split out. For this intensively dissected section of the bole, we sampled a total of 51 heights; 45 of these sampled heights had 1-6 branches each, for a total of 100 sampled branches, with 6 of the sampled heights having no branches.

The reasons for sampling only half (180 degrees) of each split log were in order to a) limit the dissection to what was feasible in the allotted time, and b) save ½ of each log in reserve. Sampling only 180 degrees could be a problem if the tree had an asymmetric crown base during any portion of its life. However, due to rolling of logs prior to splitting, the particular 180 degrees that was sampled for each log was out of register with the 180 degrees sampled for adjacent logs. Thus if there was crown asymmetry, it would show up in the crown reconstruction as sharp changes in locations of the crown base across log boundaries. I examined the crown reconstruction results for any such indications of crown asymmetry across log

boundaries. The data did not suggest artifacts due crown asymmetry across log boundaries due to sampling only 180 degrees.

2. *Samples from 32-33.2 m.* Lightly sampled bole at and just below the 1992 crown base. In this section of the bole, we sampled a total of 6 branches from 3 heights. The highest of these sampled branches was the only live branch that was sampled. This was the base of the 1992 live crown. This branch was a large and complex branch system: 5-6 branches that merged, close to the trunk, into one branch stem that was 35 cm in diameter at its juncture with the trunk.

3. *Samples from 39.4 - 66.8 m.* Bole samples within the 1992 live crown, no branches sampled. The 1992 live crown extended from 33.2 m upward to the tree top at 70 m. Within this length of the bole, cross sections were taken from 7 heights (at 3-6 m intervals) for cumulative height-growth data. The only branch sampled from the 1992 live crown was the base at 33.2 m, as described above. The uppermost height sampled was 66.8 m; above this, the bole had broken apart during felling. The total height of 70 m was estimated from the reconstructed cumulative height-growth curve.

Figure 38. Log splitting mechanism.
Log splitting mechanism in place on a log of the intensively dissected tree 1408.

Figure 39. Log splitting mechanism in action.

Log splitting mechanism in action as Don DeWitt and Eric Miller monitor progress.
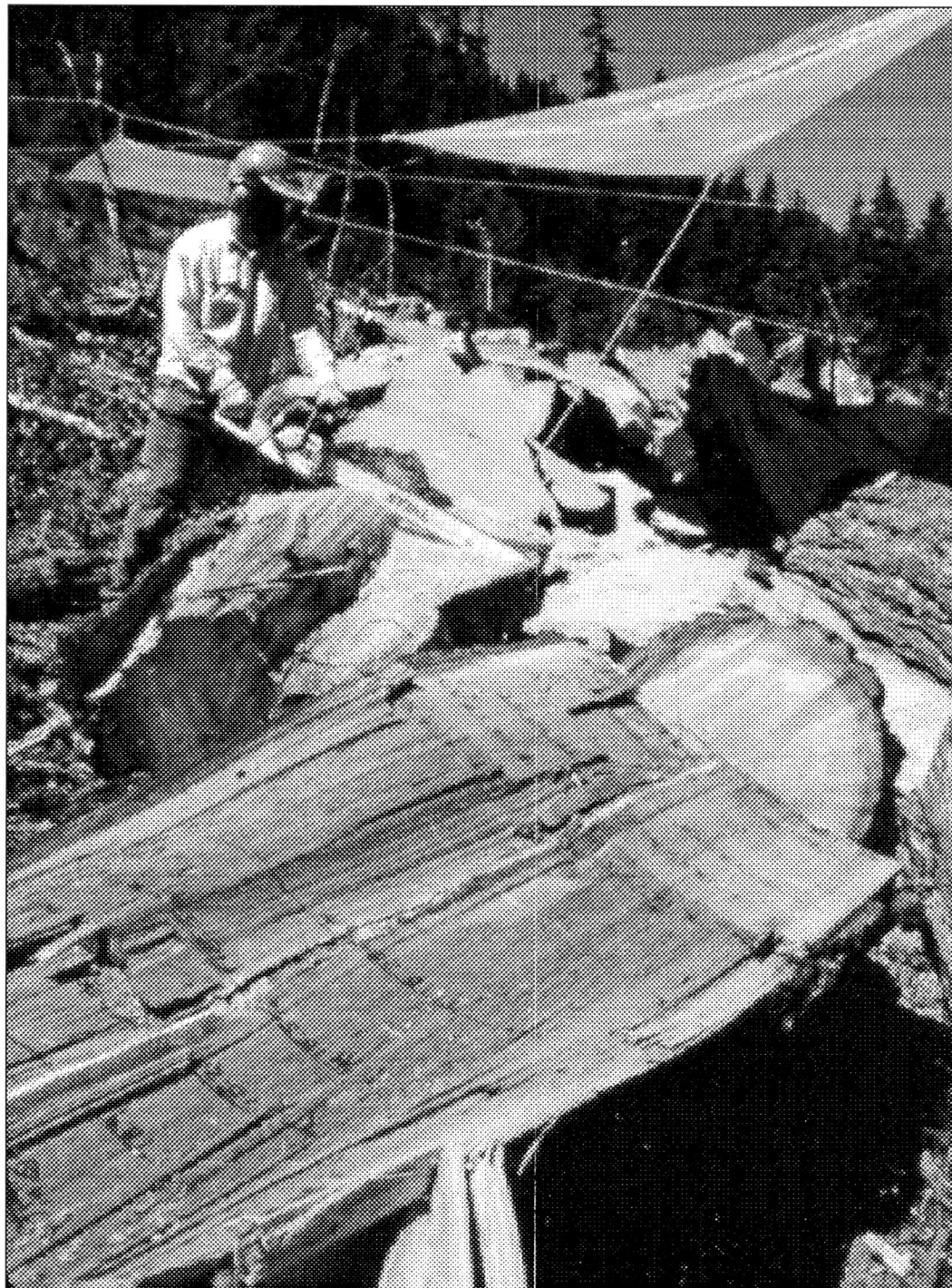
Figure 40. Sampling the split bole.

Once the potential locations of embedded branches were found by examining the wood in the vicinity of the pith (see Appendix A), the locations were marked, then cross sections were cut bracketing these locations. Don DeWitt is shown here cutting the sections. Note the visibility of the pith down the entire length of the log.

Figure 41. Raw branch samples.

Excess wood was cut away from branches embedded in the cross sections, and the samples were labeled in preparation for transport.

APPENDIX B:
RECONSTRUCTION OF DOUGLAS-FIR DIAMETERS AT "BREAST HEIGHT"

For each stump-sample, a stump-height radius inside-bark (SRIB) was measured for the beginning of each decade as the distance (± 0.5 mm) from the bole pith to the outer edge of the first ring in the decade. Each Douglas-fir SRIB was converted to a corresponding dbh (diameter outside bark at breast height), i.e. 1.4 m above the ground for the date, Figure 42) as follows:

1) Stump-height diameter inside bark (SDIB) was calculated as 2 * SRIB.

2) SDIB was converted to dbh by applying a correction for double bark thickness.

For SDIB ≤ 23cm: DBH = 1.104 * SDIB

For SDIB ≥ 23cm: DBH = 1.182 * SDIB - 1.8cm.

These bark thickness corrections were derived from regression equations that Johnson (1955) developed using Douglas-fir that were 20 to 466 years old and located in widely scattered locations in western Oregon and western Washington. Monserud (1979) shows that the Johnson regression results are similar to those developed for Douglas-fir from widely separated regions (N. Idaho, NW Montana, the eastside of the Cascade Range, and the Northern Rocky Mountain region). Thus the Johnson (1955) equations provide a good fairly estimate of bark thickness for the current study. As an alternative approach, the bark correction method used by DuVall (1983) was considered, i.e. $DBH_{date} = RIB_{date} / RIB_{1992} * DBH_{1992}$. A spot check of this method on individual trees showed that it gave similar results to the correction based on Johnson (1955). However, using this method would compound the estimate with errors in the 1992 dbh measurements made on the large trees.

In developing and using these methods for the reconstruction of dbhs, I was particularly heedful that reconstructed dbhs for dates in the youth (1500s; Figure 8) of the Douglas-fir would accurately reflect true dbhs for those dates (i.e. dbhs that would have been measured on the live trees at those dates, using standard methods). This was done to insure that the reconstructed dbhs could be compared fairly to dbhs measured on currently young stands. A few factors have the potential to cause errors in dbh reconstructions: 1) sample height relative to breast height for a reconstructed date, 2) bole asymmetry and 3) stem taper. These factors were evaluated using data from the soil pit, and data from measurements made on stumps:

1. *Sample height relative to breast height for a reconstructed date.* The position of the sample height relative to the breast height for a given date will influence whether the reconstructed dbh will accurately reflect the true dbh for a date. For example, if the sample position is below the breast height for the date, the reconstructed dbh may overestimate the true dbh dependent on the amount of stem taper at the date. A sample cut from the pith to bark of a stump represents a fixed position on the bole throughout the tree-ring record of a tree's life. However, for old trees the vertical distance between this fixed position and the ground has changed over time due to the accumulation of material that has fallen on the ground over the centuries. Thus the ground level has raised relative to the sample position, and the corresponding level of breast height has raised relative to the sample position. That is, if a sample in 1992 is taken at a height of X above the 1992 ground, the height of that sample above the 1500 ground will be X plus the depth of material that has accumulated on the ground since 1500. In order to evaluate the relationship between the stump-sample height, and breast height for the youth of the Douglas-fir (1500s), the following points were considered:

   d. *Height of the Douglas-fir stump-samples relative to the 1992 ground surface.* The large diameters of the Douglas-fir (and the older western hemlock) combined with sloping ground were such that individually measured sample heights were meaningless. That is, the Douglas-fir and the large western

hemlock stumps were on average 0.9 m taller, relative to the ground, on the tall side than on the short side. Samples taken at the same level on the stump, but on different sides of the stump could have considerably different measured heights relative the ground directly beneath the sample. Therefore, the approach I used was to cut each stump-sample from a level that would be ca. 0.8 m above the 1992 ground mid-slope for the stump. For example, if field conditions, or the requirement that the sample come from an average radius, meant that the sample had to be cut from the upslope side of the stump, an imaginary horizontal line would be visually approximated from the mid-slope 0.8 m level to the upslope side, and the sample would be plunge cut at the level of the imaginary line (which would be < 0.8 m relative to the ground on the upslope side). The value of 0.8 m was chosen because for the Douglas-fir and large western hemlock stumps, this was the average stump-height relative to the 1992 ground, based on measurement of the tall and short sides of each of 36 Douglas-fir stumps, and 37 large western hemlock stumps. These measurements were not complicated by mounds of debris at the base of the large trees, such as exist in many old-growth stands. In this stand, there were no such mounds.

e. *Depth of material that has accumulated since ca. 1500.* The soil pit at the base of a Douglas-fir revealed that the roots near the bole were buried beneath an average of ca half a meter of accumulated material (duff, litter, small bits of decayed wood, tephra, soil and pebbles). Since all sampled Douglas-fir successfully established over a short interval in the early 1500s (**Figure 8**), I take ca 0.5 m to be the depth of accumulated material since the early 1500s, i.e. the ground level of the early 1500s was approximately 0.5 m below the 1992 surface. This depth is more likely to be a slight overestimate than an underestimate.

f. *Relationship between the stump-sample height and "breast-height" for the youth of the Douglas-fir* (1500s; **Figure 8**). I estimate that for Douglas-fir, the

distance from the sample-height to the surface of their germination and youth was on average ca 1.3 m (average 0.8 m. above the 1992 ground, plus ca 0.5 m. of material that has accumulated since germination). Suspected sources of error (e.g. the depth of accumulated material) in this estimate are such that it may be a slight overestimate but not likely an underestimate. This estimate may place the average stump-sample height slightly below the 1500 breast-height, but not above it.

2. *Asymmetry.* When a single SRIB is used to estimate a corresponding SDIB, error might be introduced by bole asymmetry. For example, if a tree grew much faster on one side than the other, and it was sampled on the slow growing side, the reconstructed dbh for a given date would underestimate the true dbh, and visa versa if it were sampled on the fast-growing side. In order to minimize any such effects, stump-samples were taken from a visually estimated average radius for each stump.

3. *Stem taper.* For the youth of the Douglas-fir, i.e. the 1500s, the sample-height was estimated to be slightly below breast-height by perhaps an average of ca 0.1 m, as discussed above. If stem taper were large in the vicinity of the sample, this difference between sample-height and breast height could cause the reconstructed dbhs to be larger than the true dbhs. Samples collected from multiple heights for the intensively dissected tree 1408 suggested that when this tree was young, stem taper was small or absent near breast height. Tappeiner et al (1997) also examined the stem taper in young Douglas-fir by taking two increment cores from each of 20 trees, one at a height of 0.55 m and the other directly above at breast height. From these samples, Tappeiner et al. (1987) concluded that within this height range there was little or no stem taper. For the current study also, stem taper was likely small in the youth of the Douglas-fir, and the reconstructed dbh should not be much affected by the slightly below breast height location of the sample. However, if there was an effect due to sample position and stem taper, it would be in the direction of the reconstructed dbh being an overestimate of the true dbh.

Summary of evaluation: I estimate that for dates in the youth of the Douglas-fir (1500s), after the SDIBs were corrected for bark thickness as above, the reconstructed average dbhs are a close approximation to average dbhs that would have been measured for the live trees at those dates. If there was any systematic error in the reconstructions, it would be toward the reconstructed dbhs being somewhat larger than the true dbhs. For later dates (post 1600), the reconstructed dbhs were progressively lower relative to breast height, and the effects of stem taper on individual reconstructed dbh values may have increased somewhat. However, even for 1992 when these factors would have the greatest effect, reconstructed dbhs were a good approximation of true dbhs (i.e. measured on the live trees before they were felled; Figure 43).
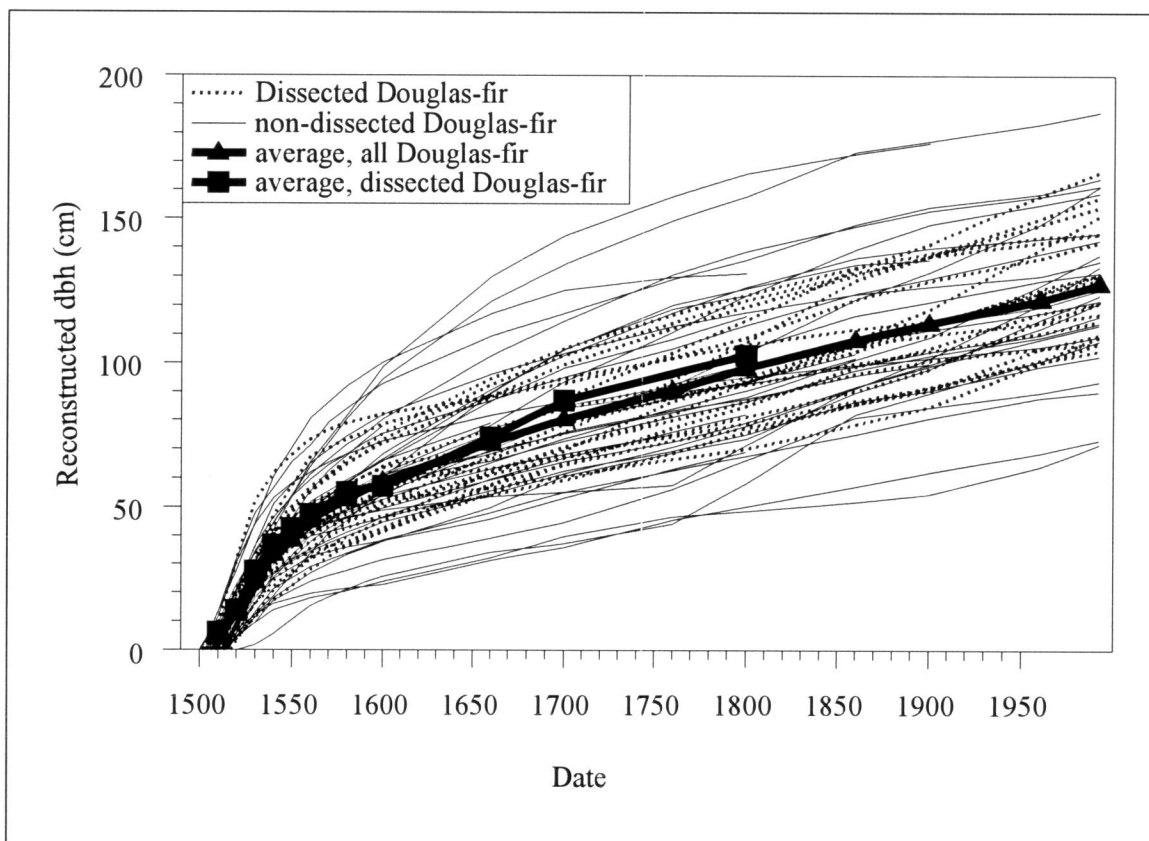
Figure 42. Reconstructed dbhs for Douglas-fir.

Individual dbh histories for dissected Douglas-fir (n = 20), individual dbh histories for non-dissected Douglas-fir (n = 39), average dbhs at dates for the dissected Douglas-fir, and average dbhs at dates for all Douglas-fir (n = 59). The dbh averages for the dissected Douglas-fir are those used to construct the Dbh_{avg}-vs-$Height_{Dom}$ values (Figure 11; see Methods), and are not shown for dates past 1800 because corresponding average heights were not available past 1800 (see Figure 9).
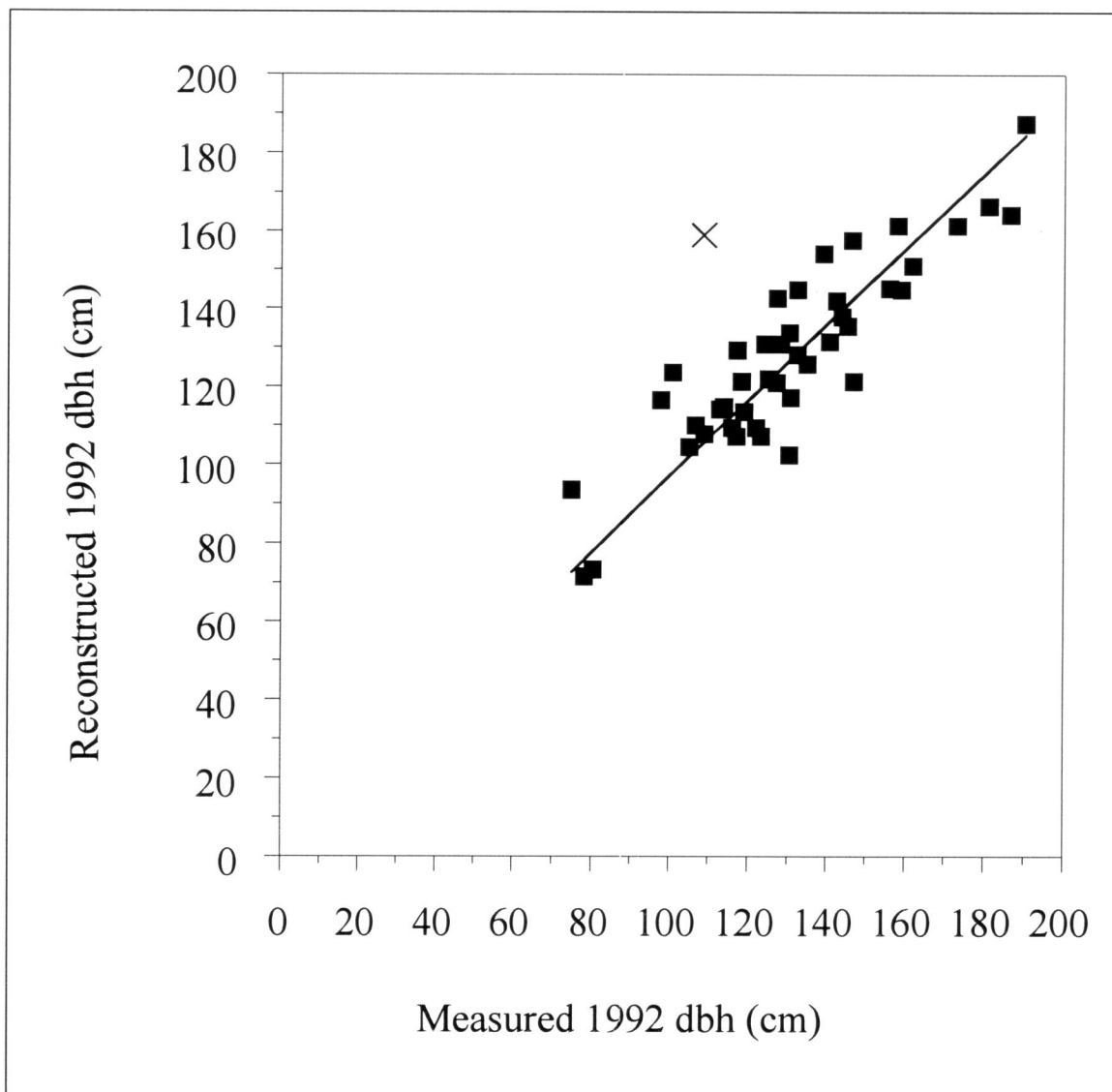
Figure 43. Douglas-fir reconstructed-versus-measured 1992 dbh.

Douglas-fir "reconstructed 1992 dbh" versus "measured 1992 dbh", and linear regression line. Douglas-fir "reconstructed 1992 dbh" versus "measured 1992 dbh", and linear regression line. The measured dbhs were done on the live trees in 1992. The regression line is: "reconstructed dbh" = 0 + 0.97 "measured dbh". R squared = 0.77. Forty-three trees (•) were included in the regression. The omitted tree (X) had a very sweeping bole and probably an extreme error due to asymmetry.

APPENDIX C:
IDENTIFICATION OF BRANCH DEATH DATES

Two variables were defined to span the interval over which a branch was gradually dying: 1) Latest Functionally Live Date (LFLD), i.e. the latest date at which the branch was producing rings and was hence functionally live, and 2) 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 rings but not yet clearly dead. The LFLD and the EDD are described further below. These variables were evaluated for each sample containing a branch by examining the area where the bole rings merged with or abutted the branch (branch–bole juncture). This evaluation was done with the aid of a dissecting microscope so that cell structure could be observed.

Latest Functionally Live Date (LFLD, Figure 6). This is the date of the latest bole ring in a sample that continued without interruption from the bole into the branch, where it became a branch ring. Preceding the LFLD ring, back to the formation of the bole pith, all bole rings were similarly continuous with the branch. Hence, up to and including the LFLD ring, the branch formed a tight knot within the bole wood. It is clear from this bole and branch structure that for all dates up to and including the LFLD, the branch cambium was continuous with the bole cambium, alive, and producing annual growth rings: i.e. the branch was functionally live. The LFLD thus marks the latest date at which the branch was "functionally live".

Earliest Dead Date (EDD, Figure 6). Following the LFLD 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 forming a tight knot. It appeared from the structure of these rings, at the juncture of the branch with the bole, that over this interval the branch was gradually dying; it was not producing rings at its base, but the branch had not yet clearly died. This interval ended with a bole ring that was abruptly discontinuous with the branch at the branch–bole juncture; this was defined as the EDD ring. All rings that followed the EDD ring were similarly discontinuous with the branch, hence this ring

marks the transition from a tight knot to a loose knot. The EDD as defined here is similar to definitions used in previous studies to identify the date at which branch mortality occurred (Andrews and Gill 1939, Maguire and Hann 1987). It is clear from the structure of the bole–branch juncture that at the EDD, and at each date subsequent it, the branch cambium was dead at the branch base.

To assess the repeatability of identification of the LFLD and the EDD for a branch, a subset of 63 branches with multiple prepared surfaces were evaluated. The EDDs identified on the different surfaces of the same branch differed by an average of 0.71 years (0-4 yr). The LFLDs on the different surfaces of a branch differed by an average of 1.63 years (0-6 yr) For branches with different EDDs or LFLDs identified on the different surfaces, the latest EDD or LFLD was assigned to the branch as a whole.

APPENDIX D:
DETECTION OF GROWTH-CHANGES
ON THE WOOD SURFACE

Some growth-changes are so dramatic that no guidelines are needed for detecting and dating them. However, many are less obvious and can be difficult to pick out against the background of the age trend and yearly variation in ringwidths. Following are the methods I used to detect and date the growth-changes on the surfaces of the wide samples. These are the instructions given to the independent researcher who helped test the reproducibility of the detection of growth-changes on the wood surfaces:

1. First look at samples, more than one, and get a general feel for the overall ringwidth patterns, yearly variation, and growth-changes.

2. For detecting growth-changes in a particular sample, start at the center and work outward. Use your 2 index fingers as a moving frame to help detect the growth-changes. Place the 2 index fingers on the sample, pointing along the rings, and about 2-3 cm apart along the radius. Slide the fingers slowly along the wood, maintaining the space between them, looking for sudden changes in the ringwidths. This method serves to keep your place on the wood, to filter out the noise of yearly variation, and to help zero in on abrupt changes. Observe and compare the number of rings across each finger (you do not need to count the rings, a visual impression will suffice). Where there appears to be an abrupt change, move the bracketing fingers forward and backward in time, and also try varying the distance between them, until the beginning of the change is zeroed in on. It also helps sometimes to view the sample at an angle rather than straight on. This in effect integrates the pattern across the sample. This method is deceptively simple, yet is very effective for utilizing the power of the eye and human brain for sorting out complex patterns. The growth-changes detected in the way were highly reproducible, as described in the Methods.

When you do find a sudden change in ringwidth, ask:

1. Does the new growth rate persist for 10 or more years?

2. Is the change from the old growth rate to the new growth-rate achieved within ca. ≤ 3 yr?

3. Are most rings after the change greater than (in the case of a growth increase) or less than (in the case of a growth decrease) most of the rings before the growth change? This question is to rule out changes that are shifts in variability rather than in overall growth rate.

4. Is the change apparent across the width of the sample? In the western hemlock samples, fluctuations in ringwidth often occurred across only a small arc of the circumference (Figure 25). When such fluctuations were apparent on the wide samples, they were not designated as growth changes.

If the answer to all these questions is yes, the observed change is accepted as a growth-change and evaluated for the 7 descriptive variables described in the Methods.

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