Canopy disturbances over the five-century lifetime of an old-growth Douglas-fir stand in the Pacific Northwest

Linda E. Winter, Linda B. Brubaker, Jerry F. Franklin, Eric A. Miller, and Donald Q. DeWitt

Abstract: The history of canopy disturbances over the lifetime of an old-growth Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stand in the western Cascade Range of southern Washington was reconstructed using tree-ring records of cross-dated samples from a 3.3-ha mapped plot. The reconstruction detected pulses in which many western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) synchronously experienced abrupt and sustained increases in ringwidth, i.e., "growth-increases", and focused on medium-sized or larger (≥0.8 ha) events. The results show that the stand experienced at least three canopy disturbances that each thinned, but did not clear, the canopy over areas ≥0.8 ha, occurring approximately in the late 1500s, the 1760s, and the 1930s. None of these promoted regeneration of the shade-intolerant Douglas-fir, all of which established 1500–1521. The disturbances may have promoted regeneration of western hemlock, but their strongest effect on tree dynamics was to elicit western hemlock growth-increases. Canopy disturbances are known to create patchiness, or horizontal heterogeneity, an important characteristic of old-growth forests. This reconstructed history provides one model for restoration strategies to create horizontal heterogeneity in young Douglas-fir stands, for example, by suggesting sizes of areas to thin in variable-density thinnings.

Résumé : L'historique des perturbations du couvert pendant toute la durée de vie d'une forêt ancienne de douglas (*Pseudotsuga menziesii* (Mirb.) Franco), dans la partie ouest de la chaîne des Cascades dans le Sud de l'État de Washington, a été reconstitué en utilisant des séries dendrochronologiques d'échantillons synchronisés provenant d'une placette cartographiée de 3,3 ha. La reconstitution a permis de détecter des évènements pendant lesquels plusieurs pruches de l'Ouest (*Tsuga heterophylla* (Raf.) Sarg.) ont subi des augmentations abruptes et soutenues de la largeur des cernes, c'est-à-dire des augmentations de croissance, et s'est concentrée sur des évènements d'envergure moyenne ou plus (≥0,8 ha). Les résultats montrent que le peuplement a subi au moins trois perturbations du couvert qui, chacune, ont éclairci mais n'ont pas ouvert le couvert sur des surfaces de plus de ≥0,8 ha aux alentours de la fin des années 1500, des années 1760 et des années 1930. Aucune d'entre elles n'a favorisé la régénération du douglas, une espèce intolérante; les individus de cette espèce se sont tous établis entre 1500 et 1521. Les perturbations ont peut-être entraîné la régénération de la pruche de l'Ouest mais leur effet le plus important a été de susciter des augmentations de croissance chez cette essence. Les perturbations du couvert provoquent la fragmentation ou l'hétérogénéité horizontale, une caractéristique importante des forêts anciennes. La reconstitution de cet historique fournit un modèle qui permet à des stratégies de restauration de créer une hétérogénéité horizontale dans les jeunes peuplements de douglas en suggérant, par exemple, la dimension des zones à éclaircir lors d'éclaircies à densité variable.

[Traduit par la Rédaction]

Introduction

Old-growth Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests in the Pacific Northwest typically originated following stand-replacing fires, then developed for centuries as closed forests (e.g., 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 existing old-growth forests

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and eventually developing old-growth forests from modern young and mature forests. These current policies developed after intense controversy over the ecological, social, and economic consequences due to a century of heavy logging of old-growth forests in the Pacific Northwest (Thomas 1991, 1997; Thomas et al. 1993; FEMAT 1993; Aubry et al. 1999). To implement the current policies, some forest managers have begun to design silvicultural and restoration prescriptions intended to emulate natural disturbance processes in these forests (e.g., McComb et al. 1993).

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, reported wide ranges of Douglas-fir ages in some forests, and spatial variability in the distribution of individual structures (Franklin and Waring 1980; Franklin and Hemstrom 1981; Spies and Franklin 1991; McComb et al. 1993; Tappeiner et al. 1997; Franklin et al. 2002). 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 (collective observations) and has been documented for tree sizes and densities in several studies (e.g., Stewart 1986*a*, 1986*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.

Previous research concerning the occurrence and effects of canopy disturbances over the lifetime of old-growth Douglas-fir forests is limited to (*i*) recently occurring (ca. 75 years) small-sized events (e.g., Stewart 1986*b*; Franklin and DeBell 1988; Spies et al. 1990; McComb et al. 1993; Van Pelt and Franklin 1999; Van Pelt 1995; Gray and Spies 1996, 1997) and (*ii*) reconstructed low- to moderate-severity fires that thinned canopies over large areas in relatively dry portions of the range (e.g., Stewart 1986*a*; 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 medium-sized or larger (≥0.8 ha) canopy disturbances over the entire 500-year lifetime of an old-growth Douglas-fir stand. The study stand, referred to as “Yellowjacket” after its resident drainage, is located in the Gifford Pinchot National Forest, in the western Washington Cascade Mountains. The reconstruction is based on the analysis of synchronous pulses of abrupt increases in radial growth rates, as exhibited by increases in ringwidth, and necessarily focuses 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.

Methods and rationale

Study site

The Yellowjacket study site (46°21.7′N, 121°51.5′W, elevation 670–730 m) was placed within a pre-harvest timber sale previously established by the Gifford Pinchot National Forest. The sale was in an old-growth Douglas-fir forest in the Western Hemlock Zone (Franklin and Dyrness 1973) of the western Washington Cascade Mountain Range. The forest at Yellowjacket was continuous with and surrounded by forests of similar structure covering a large area. Winter (2000) describes in detail the physical and vegetative characteristics of the study site, which are summarized here. Prior to cutting, the stand was dominated by Douglas-fir and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), with structural features meeting the definition for old-growth Douglas-fir stands (Franklin et al. 1981; Marcot et al. 1991). Douglas-fir – western hemlock stands such as that at Yellowjacket are one type of Douglas-fir old-growth and are the primary example of old-growth ecosystems in western Oregon and Washington (Franklin et al. 1981). In this forest type, Douglas-fir acts as the primary shade-intolerant pioneer, and the shade-tolerant western hemlock is the true climax species. The canopy at Yellowjacket was irregular in height and closed, with occasional small gaps containing snapped or uprooted trees. Douglas-fir were the tallest trees, ca. 65 m. Maximum diameters for Douglas-fir and western hemlock, respectively, were 190 and 146 cm. Vegetative and physical characteristics at Yellowjacket varied continuously across the stand but with trends toward groupings of features, i.e., patchiness. The absence of charcoal on the bark of any trees, and ring counts of the site’s fire-sensitive Pacific yew (*Taxus brevifolia* Nutt.; Burns and Honkala 1990), suggest that fire had not entered the forest since at least the mid-1700s. However, charcoal found surrounding the Douglas-fir roots suggests that the stand originated following a catastrophic fire. The stand was free of logging disturbance until it was clearcut in 1992 for the timber sale.

Pre-harvest field methods

Prior to harvest, we established a 3.3-ha plot with somewhat irregular borders determined by natural and man-made boundaries. Within this plot, all live western hemlock ≥40 cm diameter at breast height (DBH), all live Douglas-fir, and many snags were tagged and mapped (see Table 1 for numbers). All of the tagged and mapped live 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.

Post-harvest field methods

After commercial felling, the stumps of 290 mapped stems were sampled (see Table 1 for breakdown by species) to be used as the primary source of data for reconstructing past disturbances. At the time of felling, 269 of these were

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

Category of trees	Present in plot	Stump-sample collected and evaluated*
Douglas-fir, live in 1992	46	45
Douglas-fir snag	74	16
Western hemlock, live, approximately >40 cm DBH†	254	224
Western hemlock snag	44	4
Western white pine snag	3	1
Snag, species not identified	110	0

*One live Douglas-fir was not sampled, because it was not felled. Thirty 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.

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

live. Only 21 of the mapped snags had sufficient sound wood to be sampled. For each sampled stump, a level plunge-cut was used to take a sample from a representative radius at about 0.8 m (i.e., "stump-height") above the 1992 ground level. Each such "stump-sample" was cut to include a full radius from pith to bark whenever possible and was up to 20 cm wide.

Sample preparation, cross dating, and measurement of ringwidths

All samples were trimmed, reinforced against breakage, and finely sanded on the cross-sectional surface until cell structure was visible, according to standard dendrochronological methods (e.g., Stokes and Smiley 1968; Ferguson 1970; Fritts 1976). All samples were examined under a binocular microscope, and each bole ring was assigned a calendar year by cross-dating samples against master ringwidth dating series, one each for Douglas-fir and western hemlock. The master series were developed from 19 Douglas-fir and 6 of the least suppressed western hemlock by measuring ringwidths with a Henson–Bannister incremental measuring machine (accuracy ±0.01 mm) and using the program COFECHA (Holmes et al. 1986) combined with visual confirmation (e.g., Fritts 1976; Yamaguchi 1991). Ringwidths of an additional 27 representative samples were also measured. The 52 samples measured for ringwidths were used to provide a check on the study's visual methods of identifying abrupt changes in ringwidth (see below).

Methods for reconstruction of canopy disturbances

Rationale

The approach used here to reconstruct canopy disturbances was a two-step process: (*i*) identify abrupt and sustained increases in ringwidth in all sampled individual western hemlock, and (*ii*) identify pulses in which many western hemlock synchronously experienced these increases. We inferred that any such pulse had been caused by a canopy disturbance that occurred at or shortly prior to the pulse. The rationale for this approach is as follows.

Numerous reconstruction studies have used abrupt and sustained increases in ringwidth as evidence of past disturbance, sometimes referring to such changes as "releases" (e.g., Lorimer 1980, 1985; Glitzenstein et al. 1986; Lorimer and Frelich 1989; Canham 1990, 1985; Payette et al. 1990; Cho and Boerner 1995) or as other terms including "radial-growth changes" and "radial-growth increases" (Nowacki and Abrams 1997). In the current study, the term "growth-increase" is used herein to refer to an abrupt and sustained increase in ringwidths. Growth-increases are frequently associated with disturbances to the canopy. However, to be used as indicators of past disturbances they must be distinguished from other types of tree-ring variation, such as age- and size-related trends, climatically related signals, and unexplained year-to-year variability. For this reason, previous reconstruction studies have sought to distinguish disturbance-induced growth-increases by applying criteria intended to screen out ringwidth variation associated with non-disturbance related causes (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 (4–15 years in the various studies), and of a minimum percentage increase (25–100% in the various studies) to be accepted as being disturbance induced.

Although such criteria screen out many non-disturbance related causes, it still cannot be assured that every identified individual growth-increase is the result of a canopy disturbance. Some individual growth-increases may simply represent unexplained random variations in ringwidth. 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, an occurrence observed frequently for western hemlock (collective observation). Other growth-increases may be due to events occurring in the understory rather than due to canopy disturbances. Consequently, for this study, additional criteria were used to identify more definitively those growth-increases that were likely to have been caused by a canopy disturbance. Specifically, to infer a canopy disturbance, we required that (*i*) the growth-increases occurred in western hemlock trees, and (*ii*) there was a prominent peak, or pulse, in which the number of individual western hemlock experiencing synchronous growth-increases clearly exceeded the numbers occurring in surrounding decades.

The requirement that the growth-increases occurred in western hemlock is based on the shade tolerance of this species. Most western hemlock established in the understory after the Douglas-fir, where they grew slowly for years to decades (Winter 2000). Western hemlock establishing at progressively later dates would have been far beneath both Douglas-fir and other western hemlock trees with dense foliage. Thus, throughout their lives, most western hemlock would experience overriding growth limitations from the canopy above and would likely respond with growth-increases if a gap was created in the canopy. The requirement for the occurrence of a prominent pulse is because synchronous changes in growth rates 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 events, or any other causes that are not expected to occur synchronously. If a canopy opening was suddenly created at any time over the life of the stand, it would be expected that many western hemlock would respond to the increased light with a pulse of synchronous growth-increases. Therefore, if the data showed a prominent pulse of western hemlock growth-increases, we inferred that a canopy disturbance occurred at, or shortly before, the pulse.

The ecological significance of pulses of other types of sudden changes in ringwidth is less clear (i.e., Douglas-fir growth-increases, and sudden decreases in the ringwidths of western hemlock or Douglas-fir). Although these other types of changes were also evaluated on the samples, they are not reported in this paper, because they did not contribute to the interpretation of canopy disturbances.

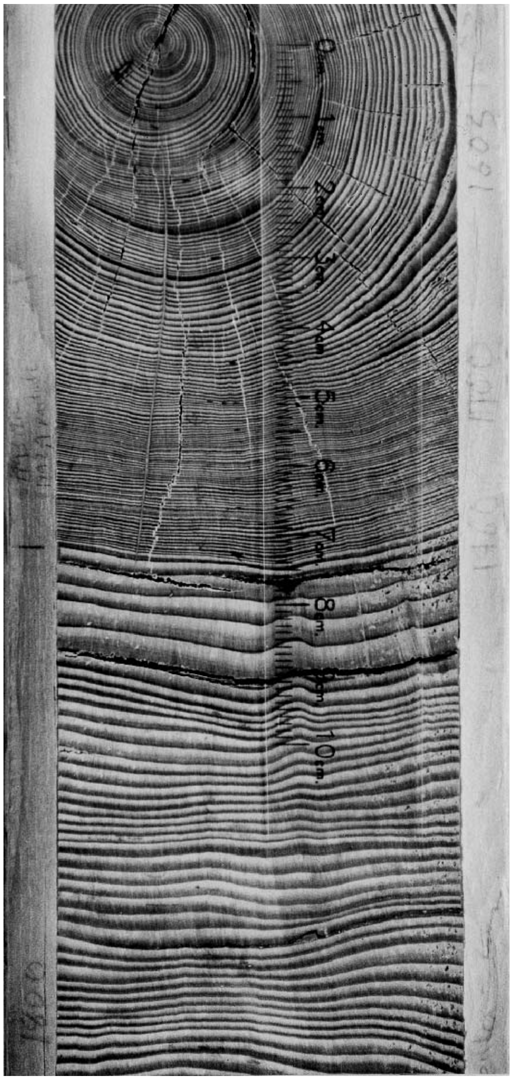
Given the above rationale, the process for estimating the time and approximate extent of canopy disturbances involved the two steps noted above and explained further below.

(1) Identification of growth-increases in individual western hemlock

Criteria adopted from previous studies (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) were used to visually identify growth-increases on the prepared surfaces of the stump-samples from all sampled western hemlock (n = 228). In this study, to be accepted as a growth-increase (Fig. 1): (*i*) the mean ringwidth for the 10 years following the change had to be at least 25% greater than the mean ringwidth for the 10 years preceding the increase (Nowacki and Abrams 1997); (*ii*) the increase had to be sustained, i.e., the ringwidths prior to and following the change had to each be relatively constant for ≥10 years; and (*iii*) the increase had to be abrupt, achieved within ca. 3 years. Once a growth-increase was identified, its date of occurrence was assigned as the calendar year of the earliest ring of the increase in ringwidth.

The reproducibility of this study's methods for visually identifying growth-increases was tested in two ways. First, 8 samples were evaluated twice: once by an author and once by an independent researcher. Comparison of the two evaluations showed that dates of growth-increases detected by the visual methods used here were highly reproducible. Second, for the 52 samples that were measured for individual ringwidths (the only samples measured in this way), growth-increases identified using the visual methods closely matched those detected by a running 10-year ratio (i.e., for each date, the following 10-year mean ringwidth divided by the preceding 10-year mean ringwidth), similar to the method used by Nowacki and Abrams (1997). An important factor contributing to the reproducibility of identifying growth-increases was the width and cross dating of the samples. In the western hemlock samples, very localized fluctuations in ringwidth were frequently observed that only occurred across a small arc of the wide (mean 7 cm) samples. We would not accept such a localized fluctuation as a growth-increase. In contrast, a narrow core sample might

Fig. 1. Example of a growth-increase in a stump-sample from a western hemlock. This was a representative tree in that all western hemlock were long-lived shade-tolerant trees and most established under closed-canopy conditions, such as this tree did. However, not all growth-increases were as distinct as this example. That is part of the reason for the requirement of strong synchrony among multiple growth-increases to infer a canopy disturbance. This particular growth-increase occurred in 1761 and so was part of the 1760s pulse of western hemlock growth-increases.



capture a localized fluctuation, and it might be mistaken for a growth-increase.

(2) Identification of pulses of western hemlock growth-increases

To identify pulses, a histogram was made for each plot quarter showing (*i*) numbers of western hemlock trees with growth-increases in each decade and (*ii*) numbers of western hemlock trees with records for each decade. A pulse was identified for a decade if, in at least one plot quarter, there was a peak in which >40% of the western hemlock with records had growth-increases in the decade. Peaks occurring in the identified decade in other quarters were considered to be extensions of that pulse, regardless of their size. The stringent 40% threshold was based on preliminary examination of the data and was designed to select only peaks that were visually obviously far above the level of growth-increases in surrounding decades. The scale of the plot quarter was selected for the identification of pulses after examination of the data at various spatial scales. This examination showed that peaks in the histograms were strongest at the scale of plot quarters, and further subdivision did not reveal any additional peaks. Since plot quarters (ca. 0.8 ha each) were used as the subdivision for the identification of pulses, 0.8 ha should be considered the approximate lower limit of studied disturbances.

Maps were made showing the locations of western hemlock with growth-increases in the decade of each identified pulse 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 size of a canopy disturbance reconstructed in this way is approximate. For example, it does not distinguish between the "actual gap" and the "expanded gap" (Runkle 1982). Further, for disturbances that extended beyond the plot boundaries, the reconstruction shows only the part of the disturbance included in the study site.

Methods for determining establishment and growth in relation to identified canopy disturbances

An establishment history was reconstructed for Yellowjacket by using stump-height centre dates to approximate the decades of tree establishment. The centre dates were determined as follows. For 225 (167 western hemlock, 57 Douglas-fir, 1 western white pine snag) of the 290 sampled trees, the stump-samples had pith present, and an exact stump-height centre date was assigned as the calendar year of the ring surrounding the pith. For each of 9 trees (8 western hemlock, 1 Douglas-fir) whose stump-samples were missing the centre by ≤1 cm, a stump-height centre decade was estimated by extrapolation. For 56 trees (53 western hemlock, 3 Douglas-fir) whose stump-samples were missing >1 cm, stump-height centre dates were not assigned. Similar to the convention followed by Cho and Boerner (1995), establishment dates are expressed as dates at stump-height and are used at a decadal resolution. As a measure of the error this introduces with respect to germination dates, we estimate from reconstructed height–growth curves that it took Douglas-fir at Yellowjacket 3–7 years to grow from the stand establishment surface to stump-height (Winter 2000). Western hemlock likely took longer than Douglas-fir to reach stump-height.

The establishment history reconstructed in this way was examined for evidence of increased recruitment at or closely following the time of the reconstructed disturbances. As a further aid to assessing the impact of the reconstructed disturbances on recruitment and growth, western hemlock were classified by their 1992 size and age, and separate maps were prepared showing the locations of each class. The western hemlock age-class divisions were selected to reflect four broad intervals that varied in the amount of establishment: 1500–1609, 1610–1679, 1680–1779, and 1780+. The western hemlock 1992 DBH classes were 40–69, 70–99, and ≥100 cm. For the purpose of the maps of DBH classes, all Douglas-fir were grouped with the largest western hemlock DBH class.

Results

Growth-increases in individual western hemlock trees

There were 773 growth-increases distributed among 225 of the 228 sampled western hemlock. Only three western hemlock had no growth-increases. The average radius at the time of a western hemlock growth-increase was 17.3 cm (range 0.2–68 cm). For the western hemlock growth-increases, the mean percent increase between preceding and subsequent 10-year ringwidth mean was 140%. There was no trend in the size, i.e., percentage, of growth-increases related to tree age.

Pulses of western hemlock growth-increases

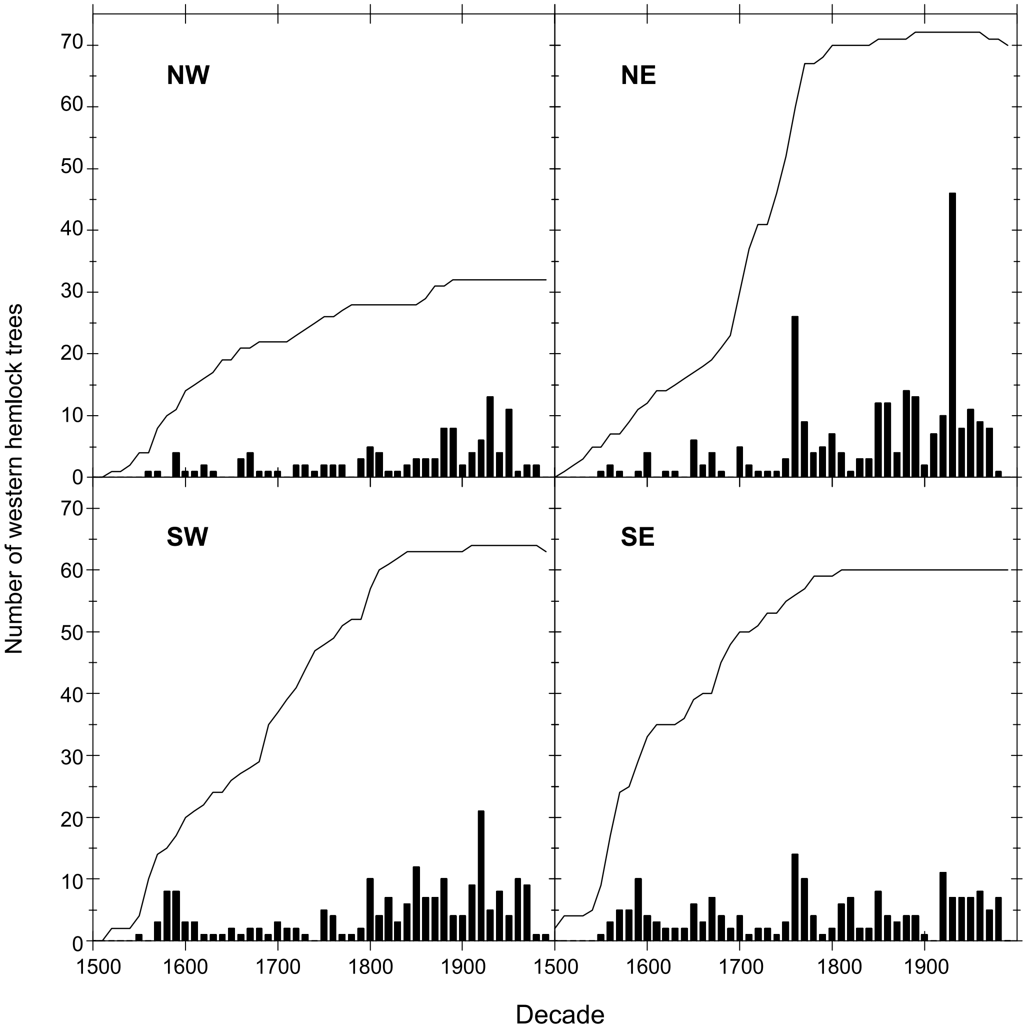
Identification of pulses

Three pulses of western hemlock growth-increases were identified (Fig. 2): the late 1500s pulse, the 1760s pulse, and the 1930s pulse. The pulse of the late 1500s was identified in the SW quarter of the plot where 8 western hemlock experienced growth-increases in the 1580s and another 8 had growth-increases the 1590s (Fig. 2). These numbers represented 53.3% of the western hemlock with records the SW quarter in the 1580s and 47% in the 1590s, compared with 0–25% in nearby decades. This pulse of the late 1500s extended into the SE quarter where a peak occurred in which 10 (34.5%) trees had growth-increases in 1590 compared with 5 or fewer trees (≤20%) in nearby decades. The pulse extended into the NW quarter also where in the 1590s a peak occurred in which 4 (36.4%) western hemlock experienced growth-increases in this decade.

The pulse of the 1760s was identified in the NE quarter where 26 western hemlock (43%) had growth-increases in the 1760s, compared with 0–14 (0–35%) trees with growth-increases in all non-pulse decades in this quarter (Fig. 2). This pulse extended to the SE quarter where a 1760s peak occurred in which 14 western hemlock (25%) had growth-increases. In this decade there was no peak in the other quarters. At a yearly resolution, plotwide, 83% of the western hemlock growth-increases in this pulse occurred in 1760 and 1761.

The 1930s pulse was identified primarily in the NE quarter where 46 (64%) western hemlock had growth-increases in the 1930s (Fig. 2). This pulse extended into NW quarter

Fig. 2. The numbers of western hemlock in each plot quarter that had growth-increases in each decade (bars), and the numbers of western hemlock 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.



where there was a 1930s peak in which 13 western hemlock (41%) had growth-increases. There were no 1930s peaks in the SW and SE quarters. At a yearly resolution, plotwide, growth-increases occurred in all years of the 1930s decade, with 75% occurring in 1931–1934. There was a 1920s peak (21 trees, 33%) in the SW quarter that was below the threshold for a pulse as defined for this study.

Locations of western hemlock with growth-increases in the pulses of the late 1500s, the 1760s, and the 1930s

The western hemlock with growth-increases in the 1580s tended to be located in the southern half of the plot (Fig. 3), but these trees were not tightly grouped and were interspersed with many western hemlock without growth-increases in the decade. In the 1590s, the western hemlock with growth-increases were more widely distributed. In the decades immediately preceding and following the 1580–1590s, lower numbers of western hemlock experienced growth-increases.

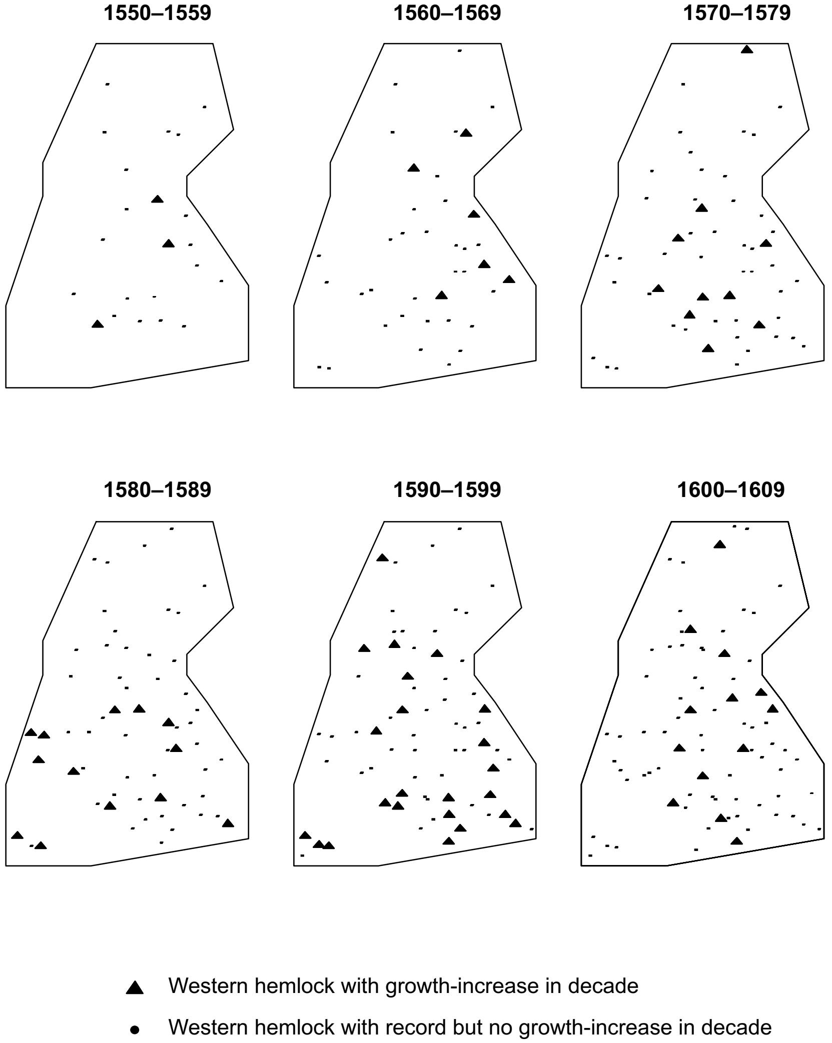
In the 1760s, most western hemlock with growth-increases were conspicuously clustered in a 1.5-ha area along the eastern edge of the plot (Fig. 4). Many of these trees were nearest neighbors to each other. In the 1770s also, western hemlock with growth-increases were grouped in the eastern portion of the plot, although there were fewer than in the 1760s. Other decades near the 1760s had no strong grouping of trees experiencing 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 (Fig. 5). Many of these trees were nearest neighbors. 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-increases outside the three main pulses

Of the 773 western hemlock growth-increases documented by this study, 80% (619) occurred in “secondary” decades, i.e., in decades outside the decades of the 3 main pulses of western hemlock growth-increases defined above. These secondary growth-increases were relatively evenly distributed in time across the life of the stand. Their spatial

Fig. 3. Locations of western hemlock 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 western hemlock with records for these decades.



grouping was assessed by preparing maps for all decades. In all except 4 of the secondary decades the western hemlock with growth-increases were widely dispersed across the plot. In the remaining 4 decades (1650s, 1770s, 1820s, and 1920s), there was only weak spatial grouping.

Establishment and growth in relation to identified pulses of western hemlock growth-increases

Establishment

All sampled Douglas-fir that had centre dates established (at stump-height) from 1500 to 1521 (n = 58) (Fig. 6). There was no Douglas-fir establishment following the pulses of western hemlock growth-increases. Sampled western hemlock with centre dates established from 1508 to 1897 (n = 175), predominately after 1540, in four broad intervals with greater and lesser numbers of establishing trees: 1500–1609, 1610–1679, 1680–1779, and 1780–1897. The decreasing numbers of establishment dates after ca. 1850 is an artifact of the 40-cm minimum DBH limit for sampling of western hemlock. At the time of or shortly following the pulses of western hemlock growth-increases, there was no prominent increased western hemlock establishment.

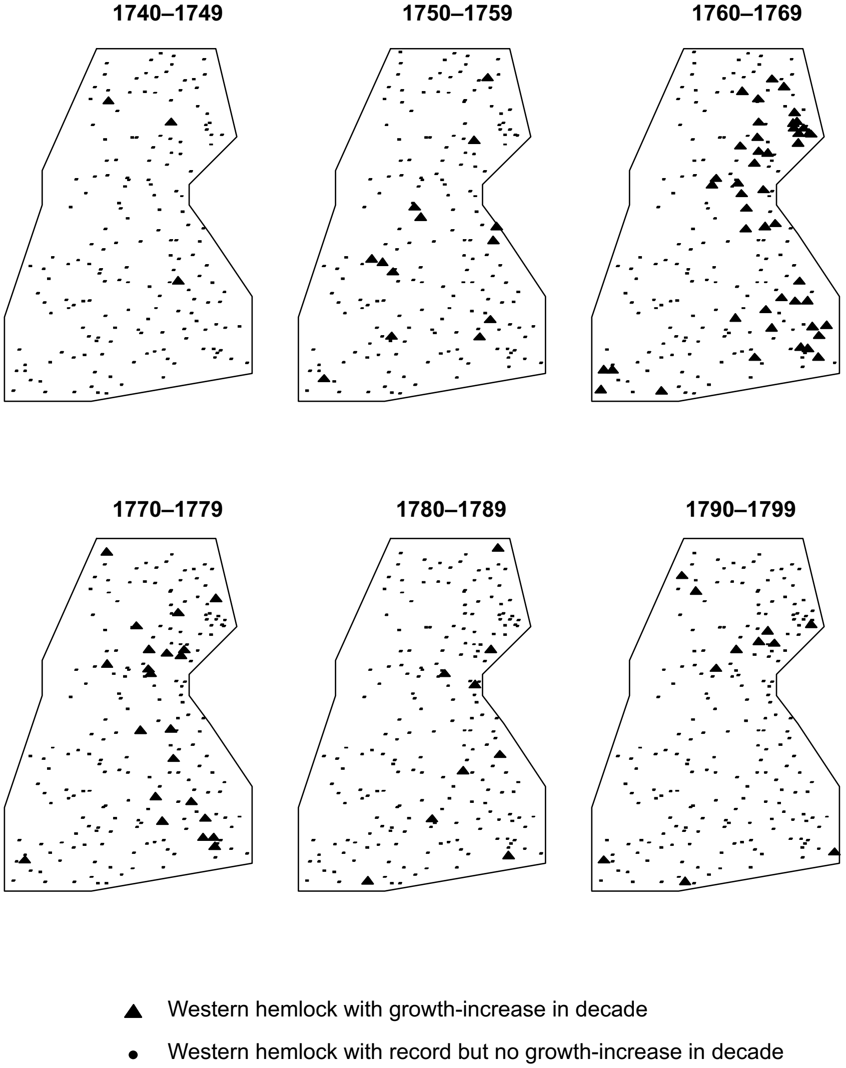
Western hemlock 1992 age-classes

The oldest western hemlock (established 1500–1609, n = 74) were distributed throughout the plot but were least dense in the northeast and southwest corners (Fig. 7). A similar distribution occurred for the trees in this group that established 1580–1609, i.e., at or shortly following the late 1500s pulse of western hemlock growth-increases. The middle age-class of western hemlock (established 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. Trees in this group that established 1760–1779, i.e., at or shortly following the 1760s pulse of western hemlock growth-increases, were also restricted to the northeast and southwest corners of the plot.

Spatial distribution of tree sizes in 1992

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 (Fig. 8). The medium-

Fig. 4. Locations of western hemlock 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 western hemlock with records for these decades.



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 small western hemlock spanned a wide range of ages (Fig. 9). For example, establishment dates for the smallest DBH class of sampled western hemlock ranged from 1550 to 1897.

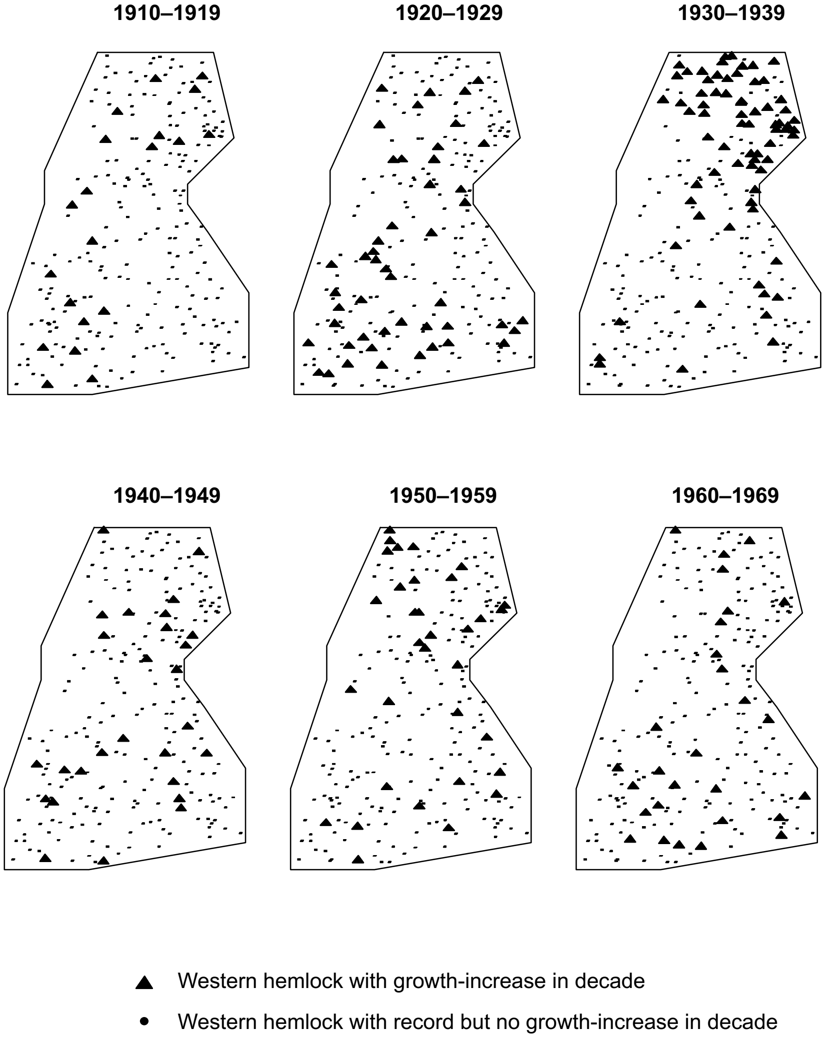
Discussion

Reconstructed disturbances

This study shows that during its five-century lifetime, the Yellowjacket stand experienced at least three medium-sized or larger (>0.8 ha) disturbances to the canopy, occurring in, or shortly prior to, the late 1500s, the 1760s, and the 1930s. The inference of canopy disturbances at these times was based on the pulses of western hemlock growth-increases (see Methods). The sizes of these disturbances within the plot are estimated to be 3.3 ha for the late 1500s disturbance (the whole plot), 1.5 ha for the 1760s disturbance, and 0.8 ha for the 1930s disturbance. Each of these disturbances would have additionally affected the canopy over an unknown area beyond the edge of the plot. We conclude that each of these disturbances likely thinned but did not clear the canopy over the affected areas, based on (*i*) the lack of Douglas-fir regeneration following these disturbances, (*ii*) the knowledge that Douglas-fir can establish on mesic sites in gaps >0.075 ha (Spies and Franklin 1989; Spies et al. 1990), yet no Douglas-fir established after any of the disturbances, and (*iii*) the distribution of Douglas-fir still living in 1992 (Fig. 8). These Douglas-fir, which established long before and survived all three of the disturbances, are located throughout the affected areas.

The three reconstructed canopy disturbances span much of the life of the stand. It is likely that over this long time span, the causes of the disturbances varied; however, they cannot be determined from the data, particularly for the two oldest disturbances. Potential causes would include insects, wind, ice storms, or disease. Judging from the absence of fire scars

Fig. 5. Locations of western hemlock 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 western hemlock with records for these decades.



1910–1919

1920–1929

1930–1939

1940–1949

1950–1959

1960–1969

and charred bark, fire was not a likely agent for any of the canopy disturbances. The multiple western hemlock growth-increases in the 1920s were likely unrelated to the 1930s disturbance, as the trees in which these occurred were distributed throughout the plot, with a concentration in the SW. It is possible that something occurred in the 1920s to cause growth-increases in the western hemlock. However, these responses did not meet the criteria used here to distinguish a definitive canopy disturbance. Although the 1930s and the 1920s had more growth-increases than the decades examined near the other two pulses, this difference may simply reflect the fact that the number of trees with records decrease as one goes back in time.

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, thus, were capable of leaving credible evidence, even after centuries. Additional, less evident, canopy and non-canopy disturbances likely occurred. Eighty percent (619) of the western hemlock growth-increases were relatively individual events, not related to 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.

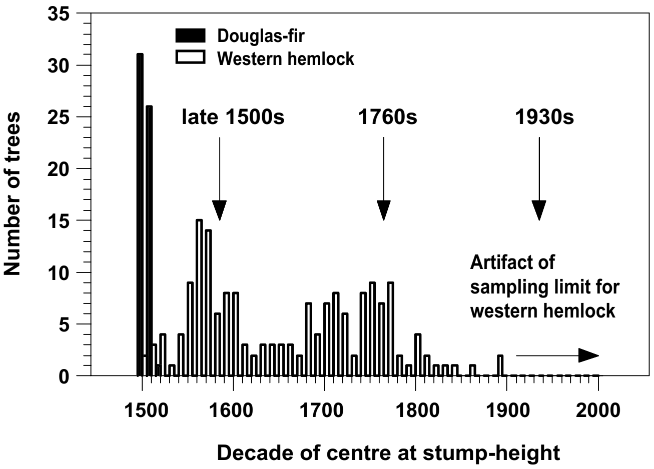
Pulses of other types of sudden changes in ringwidth (i.e., Douglas-fir growth-increases and sudden decreases in the ringwidths of western hemlock or Douglas-fir) were observed in the samples and evaluated but are not reported in this paper, because they did not contribute to the interpretation of the canopy disturbances. However, they may represent other kinds of disturbances (Winter 2000).

Establishment and growth in relation to identified canopy disturbances

Douglas-fir

Following a catastrophic disturbance (likely fire) in ca. 1500 or earlier, the site was rapidly colonized by an estimated 800 trees/ha, mostly Douglas-fir or Douglas-fir mixed

Fig. 6. Establishment history for all Douglas-fir (n = 58) and western hemlock (≥40 cm DBH, n = 175) with stump-height centre dates, whether live or dead in 1992. The decreasing numbers of establishment dates after ca. 1850 is an artifact of the 40-cm minimum DBH limit for sampling of western hemlock. The arrows mark the times of the 3 pulses of western hemlock growth-increases and, hence, the approximate times of the reconstructed canopy disturbances.



with other fast-growing species (Winter 2000; Winter et al. 2002). By 1992, only ca. 14/ha of the Douglas-fir remained alive. Although the amount of thinning of the pioneer trees was substantial over the life of the stand, the thinning never created canopy gaps large enough to allow further Douglas-fir establishment. Some of the thinning was brought about by the three reconstructed 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.

Western hemlock

Over the life of the stand, many western hemlock likely established that died too long ago or at too small a size to leave a record. Hence, the following descriptions are for only those western hemlock that survived long enough to leave a record. The sampled western hemlock established continuously throughout much of the life of the stand, with fewer than 10 establishing in most decades. The broad peak of establishment in ca. 1540–1609 may have been due at least in part to the late-1500s canopy disturbance. This suggestion is consistent with the similar, plotwide distribution for western hemlock growth-increases in the 1590s compared with that for establishment in the late 1500s. However, other possibilities cannot be ruled out.

The canopy disturbance of the 1760s may have resulted in some western hemlock establishment. Although there is no prominent peak of increased western hemlock establishment in or close to the 1760s, there is some overlap between the spatial distribution of western hemlock that established 1760–1779 compared with the spatial distribution of growth-increases in the 1760s.

Because of the minimum limit for sampling western hemlock (40 cm DBH), we could not directly assess the effect of the 1930s canopy disturbance on establishment. This lower limit resulted in an artificially low level of establishment identified after ca 1850. However, in the general area of the 1930s canopy disturbance, there is a cluster of 57 of the smallest size class sampled in 1992 (40–79 cm DBH; Fig. 8). At a causal glance, the spatial distribution of this cluster had the appearance of a cohort that may have originated following the 1930s canopy disturbances. However, these trees actually established over a wide range of dates (1580–1897) with none originating after 1930. 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 in part to synchronous increased growth due to the 1930s disturbance. It was found that of the 57 trees in this cluster, 40 (70%) responded with growth-increases to the 1930s disturbance. Some of this group was also in the area of the 1760s canopy disturbance, and 12 (21%) of these 57 trees responded to the 1760s disturbance with growth-increases. Eight (14%) responded to both disturbances, and 13 (23%) responded to neither.

The above considerations suggest that the effects of the canopy disturbances on western hemlock establishment were minimally detectable or uncertain. This is not surprising because, as noted by Lorimer and Frelich (1989) age distributions of shade-tolerant trees “may bear no meaningful relationship to disturbance history because disturbance is not a prerequisite for germination in most shade-tolerant species”. The successful establishment of western hemlock likely involves cumulative interactions among many factors, including understory light conditions, seedbed conditions, presence of woody debris, and competition. Regardless of the lack of a strong effect on western hemlock establishment, the canopy disturbances did have strong effects on the growth of western hemlock. 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). Most of the sampled western hemlock, which were canopy trees in 1992, established in the understory and reached the canopy with the help of one or more growth-increases. Some of the growth-increases were due to the three reconstructed canopy disturbances. Many others were more isolated events, either because of smaller canopy events or other causes such as events in the understory, isolated branch falls, or random variations.

Summary

A few main generalizations can be made about the 3 reconstructed canopy disturbances.

(1) These disturbances spanned the life of the stand, occurring at ages of ca. 80–90, 250, 430 years. Other smaller canopy disturbances likely occurred also, such as might occur because of competitive interactions.
(2) These three canopy disturbances thinned but did not clear the canopy over medium-sized or larger (>0.8 ha) areas.
(3) They did not promote regeneration of the shade-intolerant Douglas-fir.
(4) Western hemlock of all sampled sizes, many in the understory, responded to the canopy disturbances with growth-increases, thus increasing vertical stratification.

Fig. 7. Locations of sampled western hemlock that established (at stump-height) during 4 intervals: 1500–1609, 1610–1679, 1680–1779, and 1780–1897. These intervals correspond to the broad intervals of higher and lower amounts of successful western hemlock establishment (Fig. 6). Locations are highlighted with a box for trees that established 1580–1609, i.e., at or shortly following (by ≤10 years) the late 1500s pulse of western hemlock growth-increases, and those that established 1760–1779, i.e., at or shortly following the 1760s pulse. The lack of any establishment after 1897 is an artifact of the sampling limit for western hemlock. Because of this limit, no establishment was reconstructed following the 1930s pulse. Also shown for each of the 4 intervals are the locations of sampled western hemlock with centres that did not date to the period.

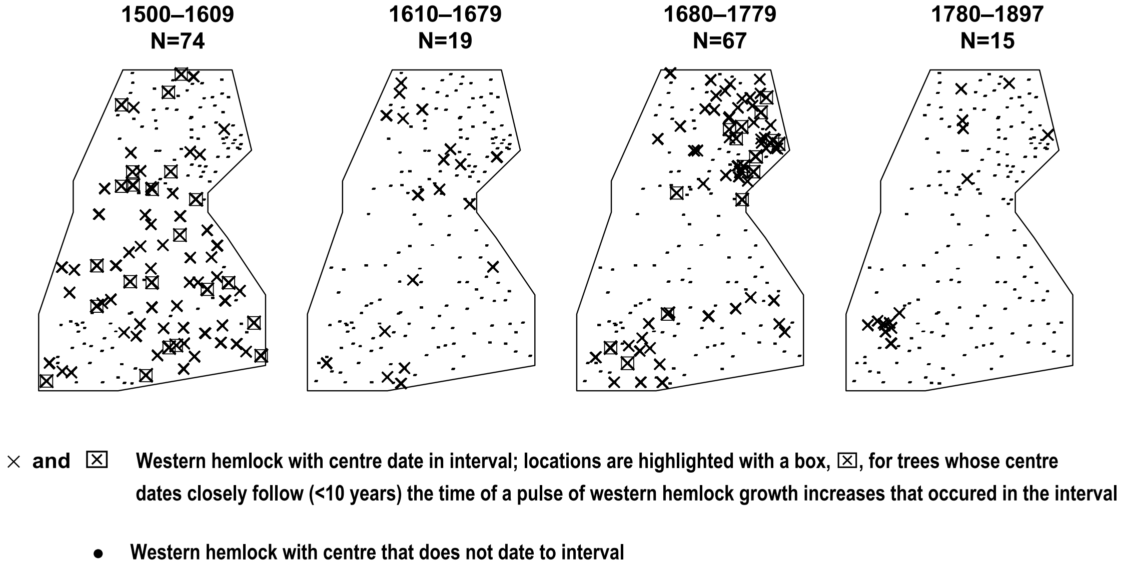
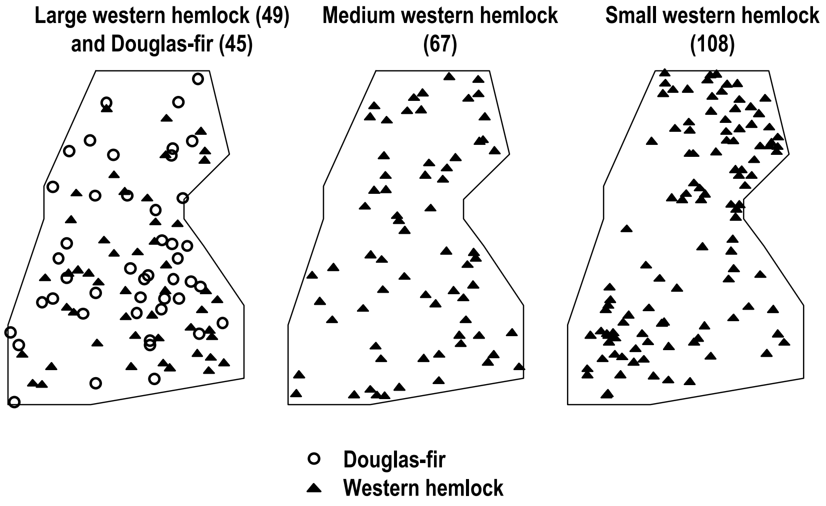


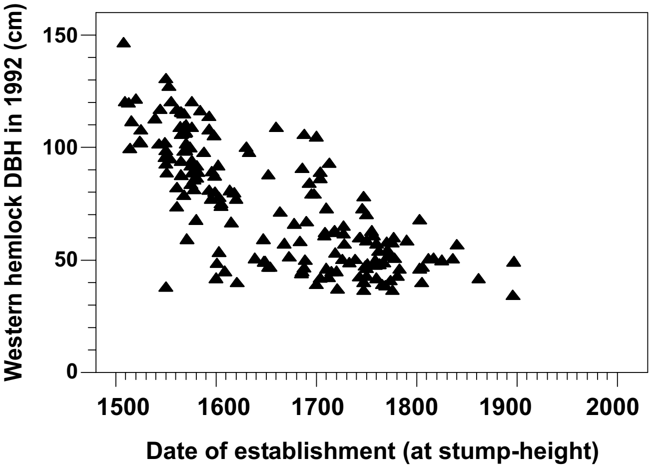
Fig. 8. Locations of sampled live western hemlock and Douglas-fir by 1992 DBH size classes. Western hemlock DBH size classes are as follows: small, 40–69 cm; medium, 70–99 cm; and large, ≥100 cm. The locations of all Douglas-fir are included in the map showing the large western hemlock.



These characteristics of the canopy disturbances at Yellowjacket may not be directly applicable to other forest ecosystem types. Although tree-fall gaps are common to almost all forests, the particulars (e.g., ages, sizes, intensity, tree responses) are likely to vary (e.g., Denslow and Spies 1990). For example, the structure and consequences of gaps will depend on many factors, including tree species involved, tree height and latitude, prevailing disturbance regimes, understory characteristics, and seedbed requirements of saplings. However, the methods used at Yellowjacket to reconstruct medium-sized canopy disturbances are applicable to any forest type. Many disturbance reconstructions in other forest types have mostly focused on small- and large-sized disturbances.

The reconstruction of canopy disturbances at Yellowjacket necessarily dealt only with trees. There are many other important effects of canopy disturbances we could not directly reconstruct. However, based on previous work in current small-sized gaps, some impacts of canopy disturbances are known to include release of resources, i.e., light and nutrients; alteration of microclimate; establishment and (or) release of trees, hence influence on the population dynamics of trees; understory growth; and creation of snags, logs, and rootwads (e.g., Spies et al. 1990; McComb et al. 1993; Van

Fig. 9. Western hemlock 1992 DBH versus date of establishment at stump-height (n = 175). The DBHs were measured on the live western hemlock ≥40 cm DBH in 1992 (12 western hemlock slightly <40 cm DBH were sampled and included in the data set). The establishment dates are the centre dates at stump-height.



Pelt and Franklin 1999; Gray and Spies 1996, 1997). Snags provide essential habitat for many species of vertebrates and invertebrates. Logs provide long-term sources of energy and nutrients, sites for nitrogen fixation, physical stability, essential habitat for many plant and animal species, and seedbed sites.

Because of these many effects, canopy disturbances can create patches that differ from the adjacent forest, producing a high degree of spatial patterning, i.e., horizontal heterogeneity (Franklin et al. 2002). Douglas-fir stands typically initiated following catastrophic disturbances and likely each started as an extensive patch of uniform and even-aged trees. Over time, canopy disturbances can break up the large uniform patch into multiple structural units, thus evolving the stand into one that is both horizontally and vertically diverse with a high level of niche diversity. An example of such disturbance-induced patchiness could be seen at Yellowjacket in the area of the 1930s canopy disturbance. The forest in this patch stood out for its relatively high densities of small western hemlock, and its relatively low densities of Douglas-fir and large western hemlock. This patch was also characterized by its large accumulations of coarse woody debris and abundant western hemlock regeneration, particularly on the many large logs and rootwads.

In the Pacific Northwest, with the increased emphasis on maintaining and developing old-growth stands, researchers and managers are asking whether and what silvicultural interventions may be needed to promote modern young stands to eventually develop old-growth structures (e.g., McComb et al. 1993; DeBell et al. 1997; Tappeiner et al. 1997; Aubry et al. 1999). Although many young stands, especially typical natural young stands, may not require silvicultural interventions (Winter 2000; Winter et al. 2002), for others, especially plantations, active management may be appropriate for increasing structural diversity. It has been suggested that for such cases, development and disturbances in natural stands can serve as models for management (e.g., McComb et al. 1993). The results of the current study adds to our menu of available models to aid in the design of restoration strategies, with the caveat that no single model should be used to guide management across large areas of forest. For example, the results support the practice of variable density thinning, which is being carried out in some stands in the region. In this approach, different areas in a stand are thinned to varying degrees, and some areas are not thinned at all. Such a practice would help to create structurally differing patches and hence horizontal spatial heterogeneity, much as canopy disturbances would. For some cases, the sizes of the patches could be guided by the Yellowjacket reconstruction. The reconstruction results also suggest that in cases where a restored stand is to mimic a natural stand similar to Yellowjacket, the thinned patches should not be heavily thinned nor viewed as “clearcuts”, the matrix surrounding the patches should be only lightly thinned or not thinned at all, and Douglas-fir should not be promoted to regenerate in the thinned areas. Instead, western hemlock already in the understory should be allowed to respond with increased growth, eventually contributing to both vertical and horizontal heterogeneity. Other silvicultural activities could be guided by what we have learned from currently disturbed areas. Above all, structural complexity and heterogeneity should be promoted within and between stands.

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References

Agee, J.K. 1991. Fire history of Douglas-fir forests in the Pacific Northwest. *In* Wildlife and vegetation of unmanaged Douglas-fir forests. *Edited by* L.F. Ruggiero, K.B. Aubry, A.B. Carey, and M.H. Huff. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-285. pp. 25–33.

Aubry, K.B., Amaranthus, M.P., Halpern, C.B., White, J.D., Woodard, B.L., Peterson, C.E., Lagoudakis, C.A., and Horton, A.J. 1999. Evaluating the effects of varying levels and patterns of green-tree retention: experimental design of the DEMO study. Northwest Sci. **73**(Spec. Issue): 12–26.

Burns, R.M., and Honkala, B.H. (*Technical coordinators*). 1990. Silvics of North America. Vol. 1. Conifers. U.S. Dep. Agric. Agric. Handb. 654.

Canham, C.D. 1985. Suppression and release during canopy recruitment in *Acer saccharum*. Bull. Torrey Bot. Club, **112**: 134–145.

Canham, C.D. 1990. Suppression and release during canopy recruitment in *Fagus grandifolia*. Bull. Torrey Bot. Club, **117**: 1–7.

Cho, D., and Boener, R.E.J. 1995. Dendrochronological analysis of the canopy history of two Ohio old-growth forests. Vegetatio, **120**: 173–183.

Cook, E.R. 1987. On the disaggregation of tree-ring series for environmental studies. *In* Proceedings of the International Symposium on Ecological Aspects of Tree-Ring Analysis, 17–21 Aug. 1986, Tarrytown, N.Y. pp. 522–542.

DeBell, D.S., Curtis, R.O., Harrington, C.A. and Tappeiner, J.C. 1997. Shaping stand development through silvicultural practices. *In* Creating a forestry for the 21st century. *Edited by* K.A. Kohm and J.F. Franklin. Island Press, Washington, D.C. pp. 141–149.

Denslow, J.S., and Spies, T. 1990. Canopy gaps in forest ecosystems: an introduction. Can. J. For. Res. **20**: 619.

Ferguson, C.W. 1970. Concepts and techniques of dendrochronology. *In* Scientific methods in medieval archaeology. *Edited by* R. Berger. University of California Press, Los Angeles, Calif. pp. 183–200.

Forest Ecosystem Management Assessment Team (FEMAT). 1993. Forest ecosystem management: an ecological, economic, and social assessment. Joint publication of the United States Department of Agriculture: Forest Service; United States Department of Commerce: National Oceanic and Atmospheric Administration and National Marine Fisheries Service; United States Department of the Interior: Bureau of Land Management, Fish and Wildlife Service, and National Park Service; and United States Environmental Protection Agency, Washington, D.C.

Franklin, J.F., and DeBell, D.S. 1988. Thirty-six years of tree population change in an old-growth *Pseudotsuga–Tsuga* forest. Can. J. For. Res. **18**: 633–639.

Franklin, J.F., and Dyrness, C.T. 1973. Natural vegetation of Oregon and Washington. USDA For. Serv. Gen. Tech. Rep. PNW-8.

Franklin, J.F., and Hemstrom, M.A. 1981. Aspects of succession in the coniferous forests of the Pacific Northwest. *In* Forest succession: concepts and applications. *Edited by* D. West, D. Botkin, and H. Shuggart. Springer-Verlag, New York. pp. 212–229.

Franklin, J.F., and Waring, R.H. 1980. Distinctive features of the Northwestern coniferous forest: Development, structure, and function. *In* Forests: Fresh Perspectives from Ecosystem Analysis. Proceedings of the 40th Annual Biological Colloquium, Corvallis, Oreg. *Edited by* R.H. Waring. Oregon State University Press, Corvallis, Oreg. pp. 59–86.

Franklin, J.F., Cromack, K., Jr., Denison, W., McKee, A., Maser, C., Sedell, J., Swanson F., and Juday, G. 1981. Ecological characteristics of old-growth Douglas-fir forests. USDA For. Serv. Gen. Tech. Rep. PNW-118.

Franklin, J.F., Spies, T.A., VanPelt, R., Carey, A.B., Thornburgh, D.A., Berg, D.R., Lindenmayer, D.B., Harmon, M.E., Keeton, W.S., Shaw, D.C., Bible, K., and Chen, J. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. For. Ecol. Manage. **155**: 399–423.

Freeman, E.A. 1997. The effects of data quality on spatial statistics. M.S. thesis, University of Washington, Seattle, Wash.

Fritts, H.C. 1976. Tree rings and climate. Academic Press, New York.

Glitzenstein, J.S., Harcombe, P.A., and Streng, D.R. 1986. Disturbance, succession, and maintenance of species diversity in an East Texas forest. Ecol. Monogr. **56**: 243–258.

Gray, A.N., and Spies, T.A. 1996. Gap size, within-gap position and canopy structure effects on conifer seedling establishment. J. Ecol. **84**: 635–645.

Gray, A.N., and Spies, T.A. 1997. Microsite controls on tree seedling establishment in conifer forest canopy gaps. Ecology, **78**: 2458–2473.

Holmes, R.L., Adams, R.K. and Fritts, H.C. 1986. Quality control of crossdating and measuring: a users manual for program COFECHA. *In* Tree-ring chronologies of western North America: California, eastern Oregon and northern Great Basin. Laboratory of Tree-Ring Research, University of Arizona, Tucson, Ariz. pp. 41–49.

Lorimer, C.G. 1980. Age structure and disturbance history of a southern Appalachian virgin forest. Ecology, **61**: 1169–1184.

Lorimer, C.G. 1985. Methodological considerations in the analysis of forest disturbance history. Can. J. For. Res. **15**: 200–213.

Lorimer, C.G., and Frelich, L.E. 1989. A methodology for estimating canopy disturbance frequency and intensity in dense temperate forests. Can. J. For. Res. **19**: 651–663.

Marcot, B.G., Holthausen, R.S., Teply, J. and Carrier, W.D. 1991. Old-growth inventories: status, definitions, and visions for the future. *In* Wildlife and vegetation of unmanaged Douglas-fir forests. *Edited by* L.F. Ruggiero, K.B. Aubry, A.B. Carey, and M.H. Huff. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-285. pp. 47–60.

McComb, W.C., Spies, T.A., and Emmingham, W.H. 1993. Douglas-fir forests: managing for timber and mature-forest habitat. J. For. **91**: 31–42.

Morrison, P.H., and Swanson, F.J. 1990. Fire history and pattern in a Cascade Range landscape. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-254.

Nowacki, G.J., and Abrams, M.D. 1997. Radial-growth averaging criteria for reconstructing disturbance histories from presettlement-origin oaks. Ecol. Monogr. **67**: 225–249.

Oliver, C.D., and Larson, B.C. 1990. Forest stand dynamics. McGraw-Hill, Inc. New York.

Payette, S., Filion, L., and Delwaide, A. 1990. Disturbance regime of a cold temperate forest as deduced from tree-ring patterns: the Tantare Ecological Reserve, Quebec. Can. J. For. Res. **20**: 1228–1241.

Runkle, J.R. 1982. Patterns of disturbance in some old-growth mesic forests of eastern North America. Ecology, **63**: 1533–1546.

Spies, T.A., and Franklin, J.F. 1989. Gap characteristics and vegetation response in coniferous forests of the Pacific Northwest. Ecology, **70**: 543–545.

Spies, T.A., and Franklin, J.F. 1991. The structure of natural young, mature, and old-growth Douglas-fir forests in Oregon and Washington. *In* Wildlife and vegetation of unmanaged Douglas-fir forests. *Edited by* L.F. Ruggiero, K.B. Aubry, A.B. Carey, and M.H. Huff. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-285. pp. 91–109.

Spies, T.A., Franklin, J.F., and Klopsch, M. 1990. Canopy gaps in Douglas-fir forests of the Cascade Mountains. Can. J. For. Res. **20**: 649–658.

Stewart, G.H. 1986*a*. Population dynamics of a montane conifer forest, western Cascade Range, Oregon, USA. Ecology, **67**: 534–544.

Stewart, G.H. 1986*b*. Forest development in canopy openings in old-growth *Pseudotsuga* forests of the western Cascade Range, Oregon. Can. J. For. Res. **16**: 558–568.

Stokes, M.A., and Smiley, T.L. 1968. An introduction to tree-ring dating. University of Chicago Press, Chicago, Ill.

Tappeiner, J.C., Huffman, D., Marshall, D., Spies, T.A., and Bailey, J.D. 1997. Density, ages, and growth rates in old-growth and young-growth forests in coastal Oregon. Can. J. For. Res. **27**: 638–648.

Thomas, J.W. 1991. Research on wildlife in old-growth forests: setting the stage. *In* Wildlife and vegetation of unmanaged Douglas-fir forests. *Edited by* L.F. Ruggiero, K.B. Aubry, A.B. Carey, and M.H. Huff. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-285. pp. 1–4.

Thomas, J.W. 1997. Foreword. *In* Creating a forestry for the 21st century. *Edited by* K.A. Kohm and J.F. Franklin. Island Press, Washington, D.C. pp. ix–xii.

Thomas, J.W., Raphael, M.G., Anthony, R.G., Forsman, E.D., Reeves, H., Sedell, J.R., and Solis, D.M. 1993. Viability assessments and management considerations for species associated with late-successional and old-growth forests of the Pacific Northwest. The report of the scientific analysis team. USDA Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, Oreg.

Van Pelt, R. 1995. Understory tree responses to canopy gaps in old-growth Douglas-fir forests of the Pacific Northwest. Ph.D. dissertation, University of Washington, Seattle, Wash.

Van Pelt, R., and Franklin, J.F. 1999. Response of understory trees to experimental gaps in old-growth Douglas-fir forests. Ecol. Appl. **9**: 504–512.

Winter, L.E. 2000. Five centuries of structural development in an old-growth Douglas-fir stand in the Pacific Northwest: a reconstruction from tree-ring records. Ph.D. dissertation, University of Washington, Seattle, Wash.

Winter, L.E., Brubaker, L.B., Franklin, J.F., Miller, E.A., and DeWitt, D.Q. 2002. Initiation of an old-growth Douglas-fir stand in the Pacific Northwest: a reconstruction from tree-ring records. Can. J. For. Res. **32**: 1039–1056.

Yamaguchi, D.K. 1991. A simple method for cross-dating increment cores from living trees. Can. J. For. Res. **21**: 414–416.