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FOREST AGE STRUCTURE AND DEVELOPMENT FOLLOWING WILDFIRES IN THE WESTERN OLYMPIC MOUNTAINS, WASHINGTON[1]

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Abstract. Fire is an important disturbance agent influencing forest composition and structure in Pacific Northwest ecosystems. I examined the effects of a long fire-return interval on forest development, composition, and tree age structure for a post-fire sere on the west slope of the moist Olympic Mountains. Similar sites that burned in 1978, 1961, 1870, 1799, and circa 1465 were selected. Tree cores and size charactersitics were collected from two randomly located 0.25-ha plots at each site. Fires usually burned catastrophically, killing most overstory vegetation. Pioneer tree species were Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*); western hemlock assumed numerical dominance early in the sere. Forest reestablishment after fire was slow, taking $\geq$50 yr to complete establishment of shade-intolerant Douglas-fir. Understory establishment of western hemlock increased 150 yr after fire, although conditions that enhance its long-term survival may occur $\approx$300 yr or more after fire. Establishment of western hemlocks existent at the 1465 fire site peaked $\approx$365–424 yr after the fire; individuals establishing 150–300 yr after the fire occurred much less frequently. Fire exclusion would shift the replacement sequence toward a wet, very-low-frequency fire regime, favoring western hemlock over Douglas-fir.

Key words: age class; Douglas-fir; fire ecology; fire effects; forest reestablishment; forest structure; forest succession; old-growth forests; Olympic National Park, Washington; sere; stand age characteristics; western hemlock.

INTRODUCTION

Ecosystem dynamics in the Pacific Northwest are closely tied to natural fire regimes (Agee 1981). Fire type, intensity, size, and return interval are fundamental to species distributions, ecological succession, community composition and structure, and landscape patterns and processes in this region. Natural resource managers are challenged and mandated by law to preserve and perpetuate natural processes such as fire in national parks and wilderness areas (sensu Leopold et al. 1963). Recent policy shifts in public land multiple-use management call for developing and implementing plans focused on sustaining ecosystem properties and processes (Kessler et al. 1992). Modeling natural disturbance patterns, such as fire, is the nucleus of landscape-level planning guides currently being prepared by managers in the Pacific Northwest (Diaz and Apostol 1992).

In the Pacific Northwest the distribution of many conifer species (Frothingham 1909, Clements 1920, Munger 1940) and dynamics of forest communities (e.g., Hemstrom and Franklin 1982, Agee and Smith 1984, Agee 1991, Brubaker 1991) are closely linked to recurring fires. Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), two long-lived coniferous species, occur together across a broad range of environmental conditions where fires have burned in western Washington and Oregon (Isaac 1940, Munger 1940, Bailey and Poulton 1968, Fonda and Bliss 1969, Dyrness 1973, Stewart 1986, Halpern 1987, Teensma 1987, Spies et al. 1988, Morrison and Swanson 1990, Agee 1991, Spies and Franklin 1991). In this area, Douglas-fir is a good competitor with herbs and shrubs that establish quickly after fire; it reproduces almost exclusively on recently burned landscapes, except for gap-phase reproduction on very dry sites (e.g., Means 1982). Western hemlock is considerably more shade tolerant than Douglas-fir; its seedlings are usually found beneath a tree canopy (e.g., Stewart 1988), where it germinates on a wide variety of moist substrates (Harmon 1987, Packee 1990). In general, live biomass of western hemlock accrues more rapidly on wet than dry sites.[3]

Douglas-fir usually outnumbers shade-tolerant western hemlock and western redcedar (*Thuja plicata*

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Donn) after fire (Franklin and Dyrness 1973). It loses its numerical dominance later in the sere, for example, ≈70–110 yr after fire in the relatively moist central Washington Cascades (Munger 1940). However, live biomass of Douglas-fir usually will exceed that of all other species for the first 600–700 yr after fire,[3] and may live for 1200 yr in the absence of catastrophic fire (Franklin and DeBell 1988).

Tree reestablishment after fire can be a slow process in the montane forests of the Cascade Mountains (Franklin and Hemstrom 1981, Hemstrom and Franklin 1982, Means 1982, Stewart 1986). Peak tree establishment of shade-intolerant species may occur as late as 20–50 yr after the fire and continue at lower levels for 30–100 yr more. As the sere develops, stand structure becomes complex and changes relatively fast until ≈400–500 yr after fire (Spies and Franklin 1991).

Historically, stand structure studies have emphasized the attributes of size rather than age (Knowles and Grant 1983). Diameter distributions tend to be more uniform, broader and flatter, and less likely to be dependent on stand history and geographic location, than the sharp-curved peaks of the age distributions (Whipple and Dix 1979). Marked differences between species on the same site have been reported in the central Oregon Cascades where diameters of Douglas-fir were more highly correlated with age than were those of western hemlock (Stewart 1986).

The major objective of this study was to identify stand structure and age characteristics of forest development following fire in the moist, long-lived western hemlock–Douglas-fir forests of the western Olympic Mountains. Infrequent, high-intensity fires characterize the fire regime of this area (Agee 1993). Regional fire return interval is ≈600 yr for forests dominated by western hemlock (Fahnestock and Agee 1983). Several general questions were examined: What effect might a long fire-return interval have on forest development and composition? What characteristics of forest structure change during succession? How is forest structure related to tree age?

STUDY AREA

The climate of the Olympic Mountains, located in the northwest corner of Washington State (Fig. 1), is maritime with cool year-round temperatures. The remote west slope is estimated to receive >250 cm of precipitation annually (e.g., Franklin and Dyrness 1973), most of which falls from October through April. Winter precipitation below 600 m elevation is mostly rain, up to 1400 m a snow/rain zone exists, and above 1400 m snow predominates (Phillips 1963). During the summer months, when fires occur, the weather is drier with lower humidity and less precipitation (Huff and Agee 1980, Pickford et al. 1980).

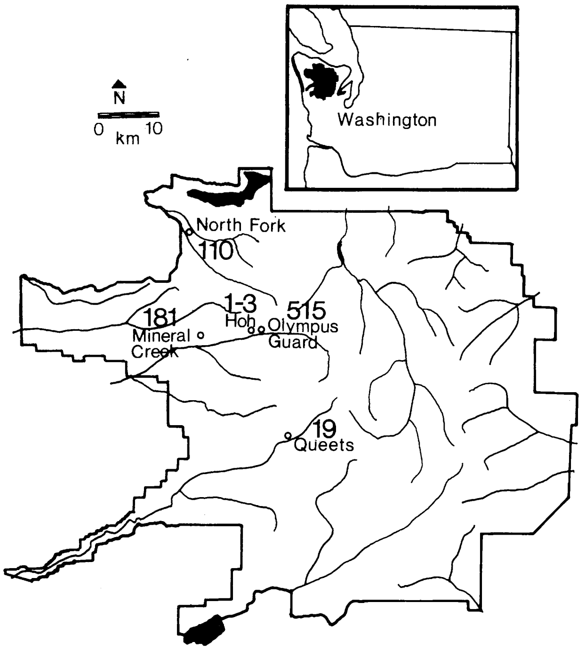

FIG. 1. Location and age (in years) of the fires of the five study areas in the lower montane zone in the western portion of Olympic National Park (Washington, USA).

The study region is located in the western portion of Olympic National Park (Fig. 1). It includes five major watersheds, Soleduck, Bogachiel, Hoh, Queets, and Quinault, each of which flow westward toward the Pacific Ocean. Within the study region, montane forests are typically found along steep, glacially carved valley walls. Only montane forests where western hemlock and Douglas-fir predominate were considered as potential study sites. The montane vegetation zone can be divided into two parts—lower and upper—according to elevation, topographic position, and vegetation composition. Generally, the lower zone is below 1000 m, where snow does not remain on the forest floor all winter, except in the coolest locations; this lower zone is the main focus of this study. In dry to mesic environments, the lower zone is dominated by Douglas-fir and western hemlock; in wet and cool environments western hemlock and Pacific silver fir (*Abies amabilis* (Dougl.) Forbes) prevail.

The most common vegetation type on south-facing slopes is *Tsuga heterophylla–Pseudotsuga menziesii/ Polystichum munitum* Kaulf. Presl (Fonda and Bliss 1969, Franklin and Dyrness 1973). Here, western hemlock and Douglas-fir comprise 80–90% of the total tree density and basal area (Fonda and Bliss 1969, Agee and Huff 1980, Agee and Huff 1987). Western redcedar is widely distributed in this type, but rarely comprises >10% of the total basal area or density. The shrub and herb layer is poorly developed beneath tree canopies. Mosses cover most of the forest floor. Swordfern (*Polystichum munitum*) is the most important herbaceous species.

Fire behavior in the lower montane zone is characterized by high-intensity burning in the understory, with flames that sporadically spread into the tree canopy. Tree mortality from heat scorch and root mortality is far more common than canopy consumption (Agee and Huff 1980). Intense heat produced while the understory is burning reaches high into the tree canopy, scorching the needles and fine branches. Douglas-fir, with its thick bark and canopy far above the forest floor, survives more often than other montane tree species; however, few survive the intense heat scorch. Survivors rarely live beyond 2–3 yr after the fire, except a few scattered in areas of low-intensity burning and areas of discontinuous fuels, or near ravines or seeps that did not burn at all. These cone-bearing survivors undoubtedly play an important role in forest reestablishment.

METHODS

Reconnaissance and site selection

Information on the historical role of fire in the montane zone of the western portion of Olympic National Park was collected as part of the site selection process. The study region was surveyed using aerial photographs and small aircraft. To locate past fires, I searched for textural differences in the canopy. Most, and likely all, fires within the study region that were >10 ha within the last ≈250 yr could be located this way. Each was field verified except in very remote areas.

My comprehensive search for fires in the western portion of Olympic National Park provided these insights: large tracts of late-seral forests predominated; few fires have burned over the last 250 yr; burns <175 yr old were small in size, usually <1000 ha; charcoal fragments of fires occurring 5 to 10 or more centuries ago were prolific in upper soil profiles beneath most mesic and dry western hemlock–Douglas-fir forests; evidence of surface fires or multiple burns was not found; and large catastrophic fires were widespread ≈300 yr ago and especially between 500 and 750 yr ago—similar to patterns found outside the park (Henderson et al. 1989).

This extensive approach provided a framework to develop and evaluate site selection criteria (below). A variety of burned sites from 1 to ≈750 yr old were visited. Fire scars and shade-intolerant tree species that establish after fire were cored to roughly determine the time since the last fire; if a fire site was selected as a study site, a more intensive approach (see *Fire age,* below) was used.

Five study sites were selected to represent a chronosequence of seral development (sensu Oliver 1981, Oliver and Larson 1990): (1) years 1 and 3 of [i.e., after] the 1978 Hoh Fire (early stand initiation stage), (2) year 19 of the 1961 Queets Fire (stand initiation stage), (3) year 110 of the 1870 North Fork Fire (stem exclusion stage), (4) year 181 of the 1799 Mineral Creek Fire (understory re-initiation stage), and (5) year ≈515 of the ≈1465 Olympus Guard Fire (old-growth stage) (see Figs. 1 and 2). The study sites lacked major windthrow and had similar environmental features, namely (1) south-facing slopes, (2) estimated 250–400 cm annual precipitation, (3) 430–610 m elevation, (4) 40–65% slope, (5) canopy dominance of western hemlock and Douglas-fir, and (6) swordfern as a prominent ground-cover plant. All study sites were of fires 150–600 ha in size, with trees older than 300 yr when burned, and where overstory mortality was extensive. This could not be verified for the ≈1465 fire, however; the 400-ha Hoh Fire reburned a portion of this fire.

Fire age

Fire scars and historical records (since 1916) were used to date the fire age of each study site except the ≈1465 fire, where fire scar material was lacking. Age of the early post-fire invaders (Douglas-fir) was used to determine the 1465 estimate. Estimates for tree ages ranged from 450 to 540 yr. Based on the best cores collected in 1980, the oldest pioneers were 500–520 yr old.

Design and field sampling

A 50 × 50 m grid pattern was blazed for ≈8 ha within each study area to survey bird populations (see Huff 1984, Huff et al. 1985). Two randomly chosen, 0.25-ha permanent macroplots were established within this grid without corrections for slope. The macroplots were 100–200 m and 250–400 m from the fire perimeter, respectively. These spatial controls were initiated to reduce sampling biases from variable fire sizes. Fire-edge effects were assumed to be minor beyond 100 m.

Four 12.5-m^2 tree-regeneration plots were established in each macroplot to measure all small trees >1 m in height but <5.5 cm in diameter at breast height (dbh). Nested within each 12.5-m^2 plot was a 3.1-m^2 plot to measure all trees and seedlings <1 m height. Regeneration was measured annually for 3 yr following the 1978 Hoh Fire.

Each macroplot was divided into 25 100-m^2 subplots to measure trees ≥5.5 cm dbh (and coarse woody debris; see Agee and Huff 1987). Each tree was identified with a number-coded aluminum tag, measured for height, dbh, species, and dominance class (dominant, codominant, intermediate, and suppressed; see Smith 1986). If multiple stems originated from one root stock (e.g., vine maple *Acer circinatum* (Pursh)), each individual stem ≥5.5 cm dbh was treated as one tree.

Tree cores were extracted from all live trees at the 110-, 181-, and 515-yr old site and stored in number-coded straws to be examined at a later date. If necessary, multiple corings were made to reach the center of each tree. The height of core extraction, core diameter, and bark thickness (large trees only) were measured. The presence or absence of rotten wood was noted for each tree. A tree core was not collected if a tree's xylem was decayed more than 20%. If the pres-

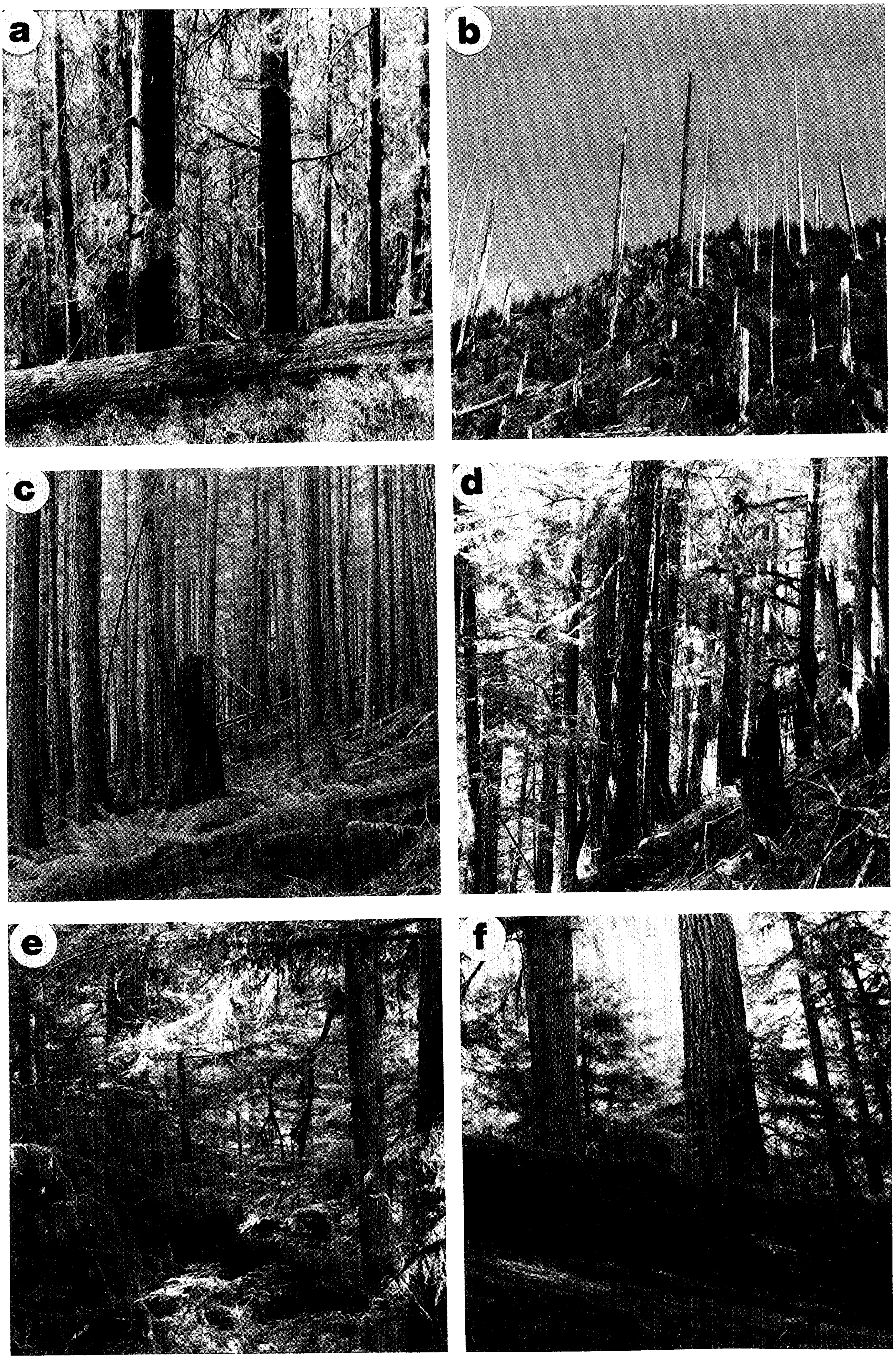
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TABLE 1. Densities (trees/ha) of live understory and overstory trees, by height and size classes and by species, at the five study areas in the lower montane zone of the western portion of Olympic National Park (Washington, USA).

	Stand age (yr after fire)						
Tree class	1	2	3	19	110	181	515
1st-yr seedlings	73 606	20 291	0	398	1194	344 560	335 409
Western hemlock	60 679	14 721	0	0	1194	341 377	333 817
Douglas-fir	13 527	4377	0	398	0	0	1194
Other species	0	1193	0	0	0	3183	398
Understory trees*							
>0.0–0.1 m	0	1591	8356	398	2388	85 942	22 678
Western hemlock	0	0	3581	0	2388	82 758	22 678
Douglas-fir	0	1193	4777	398	0	398	0
Other species	0	398	0	0	0	2786	0
>0.1–1.0 m	0	0	0	4377	796	7559	5172
Western hemlock	0	0	0	1592	796	7559	5172
Douglas-fir	0	0	0	796	0	0	0
Other species	0	0	0	1989†	0	0	0
>1.0 m	0	0	0	1394	100	199	1593
Western hemlock	0	0	0	1294	100	199	1593
Douglas-fir	0	0	0	0	0	0	0
Other species	0	0	0	100	0	0	0
Overstory trees‡	6	4	0	234	700	566	468
Western hemlock	0	0	0	112	466	308	390
Douglas-fir	6	4	0	104	224	130	24
Other species	0	0	0	18	10	128†	54§

* <5.5 cm dbh and 1st-yr seedlings excluded.
† *Thuja plicata.*
‡ ≥5.5 cm dbh.
§ 96% is *Acer circinatum.*

ence of rot impaired tree age determination, the age was estimated by methods outlined below.

Determining tree age and analysis

Tree cores were mounted on wooden holders, sanded, and rings counted using a binocular dissecting scope. Tree cores that displayed a center pith were aged first, then experience gained from examining these cores was used to derive ages for core specimens lacking a center pith.

After tree-ring counts, the age from ground level to the point of core extraction (usually 20–100 cm above the ground) was estimated using least-squares regression. These estimates were obtained by measuring height and age for different species at several sample sites (Huff 1984). Using an array of known height measurements (*x*), the number of years to core height, the dependent variable (*y*), was predicted. The years to core height were added to the ring count to ascertain the total age of each tree.

Western hemlock and Douglas-fir diameters were arranged by size and age classes for the 110-, 181-, and 515-yr-old sites. Only a few trees at the 19-yr-old site were tall enough to measure dbh; this site and the 1–3 yr old site were not used for size and age analysis. The association between diameter and age by species (western hemlock and Douglas-fir), crown class, and time since burn were measured using least-squares regression.

RESULTS

Successional characteristics

The 1978 Hoh Fire caused extensive tree mortality (see Fig. 2a). Density and basal area of standing dead trees (snags) in year 1 was 176 trees/ha and 95.1 m^2/ha, respectively. Eighty-eight percent of the snags were western hemlock. Only three Douglas-firs within the macroplots survived the fire; by 1981 these trees had died. Herbs became abundant in years 2 and 3 as *Lactuca muralis* (L.) Fresen. and *Senecio sylvaticus* L. dominated. Seedling establishment was highest the 1st yr after the Hoh Fire; by year 3, no new seedlings established (Table 1). By year 3 the species composition of seedlings was 43% western hemlock and 57% Douglas-fir.

The 1961 Queets Fire, like the Hoh Fire, caused extensive tree mortality. A large proportion of fire-killed trees had fallen to the ground by year 19 (see Agee and Huff 1987). Snag density was 27 trees/ha;

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FIG. 2. 1980 photographs of the fire study areas in the lower montane zone, Olympic National Park. (a) 1978 Hoh Fire: year 2, (b) 1961 Queets Fire: year 19, (c) 1870 North Fork Fire: year 110, (d) 1799 Mineral Creek Fire: year 181, and (e) and (f) circa 1465 Olympus Guard Fire: year ≈515.

basal area was 26.6 m²/ha. A few widely scattered survivors were present, however none were in the macroplots. Tree regeneration was well distributed throughout most of the fire (Fig. 2b); western hemlock, and to a lesser extent Douglas-fir and western redcedar, were the most abundant tree species (Table 1). Most trees were <5.5 cm dbh. Of the 1224 trees examined, 51% were browsed by ungulates. Western redcedar was browsed more often, 86%, than Douglas-fir or western hemlock, 34 and 31%, respectively.

The 110-yr-old study site was characterized by tall trees with long clear boles, a thick or continuous crown canopy layer, and a sparse or poorly developed understory (Fig. 2c). A high density of overstory trees (≥5.5 cm dbh) and low-density understory trees (<5.5 cm dbh) were present (Table 1). Density of western hemlock was higher than that of Douglas-fir in both the overstory and understory. Overstory tree basal area was 82 m²/ha, 60% of which was Douglas-fir. Western hemlock was the only understory species.

The 181-yr-old site had fewer overstory trees and substantially more understory trees compared to the 110-yr-old study site (Table 1 and Fig. 2d). Western hemlock numerically dominated the overstory layer with 2.3 times more trees than Douglas-fir. The total tree basal area, 83 m²/ha, was similar to the 110-yr-old study site. Over half of the basal area was Douglas-fir. Ninety-nine percent of the trees in the understory layer were western hemlock.

The 515-yr-old study site had stand characteristics typical of an old-growth Douglas-fir/western hemlock forest (sensu Franklin et al. 1981, Franklin and Spies 1991): tall and large trees, multilayered crown canopy, wide range of tree sizes, and large pieces of woody debris on the forest floor (see Agee and Huff 1987) (Fig 2e and f). At 390 trees/ha, western hemlock dominated the overstory. The density of Douglas-fir was low, with only 24 trees/ha. However, Douglas-fir accounted for 43% of the total basal area of 85 m²/ha. Western hemlock was the only understory tree species; density within the tall understory (>1.0 m and <5.5 cm dbh) was higher here than at the 110- and 181-yr-old study sites (Table 1).

Tree crown stratification after canopy closure

Douglas-fir was the most common tree species in the upper tree canopy or the dominant crown class at the 110- and 181-yr-old sites (Table 2). At the 515-yr-old site a few scattered individuals of western hemlock and Douglas-fir formed an emergent dominant crown class above a codominant canopy layer of western hemlock. Western hemlock was the most common species in the codominant, intermediate, and suppressed crown classes at all three study sites (Table 2).

Diameter distributions

The shape of tree diameter distributions resembled a normal distribution for Douglas-fir and a negative exponential distribution for western hemlock (Fig. 3). The inability of Douglas-fir to survive and establish beneath a forest canopy is shown by its poor representation in the small-diameter size classes at the 110- and 181-yr-old study sites and its absence at the 515-yr-old site. The shade-tolerant western hemlock was represented in nearly all the diameter classes, but most were 6–25 cm dbh.

TABLE 2. Percentage of overstory trees by species within each dominance category for the combined five study areas in Olympic National Park.

Dominance category	Species	Stand age (yr after fire) 110	181	515
Dominant	Douglas-fir	77	85	50
	Western hemlock	23	9	50
	Other	0	6	0
Codominant	Douglas-fir	40	55	0
	Western hemlock	60	37	100
	Other	0	8	0
Intermediate	Douglas-fir	14	5	0
	Western hemlock	84	66	100
	Other	2	29	0
Suppressed	Douglas-fir	2	0	0
	Western hemlock	95	69	90
	Other	3	31	10

Age-class distributions

Age-class distributions of overstory trees indicated that western hemlock and Douglas-fir were both pioneers after fire (Fig. 4). Reestablishment of Douglas-fir, the only shade-intolerant species, lasted for ≈35 and 50 yr at the 110- and 181-yr-old sites, respectively. Western hemlock reestablishment lasted longer than Douglas-fir, although once Douglas-fir reestablishment was complete, additional establishment of western hemlock was low. After 100 yr post-fire, western hemlock establishment occurred sporadically.

At the 110-yr-old site, western hemlock numerically dominated every age class, especially the first 20 yr after the fire (Fig. 4). More than 80% of the live trees sampled became established during this period. A substantial pulse of regeneration, nearly one third, established 11–15 yr after the fire (1876–1880; Fig. 4). The establishment of western hemlock declined noticeably after 1905. Between 1921 and 1940 few trees established.

At the 181-yr-old site, post-fire tree reestablishment was slower and peaked later than at the 110-yr-old site (Fig. 4). The peak periods of total tree establishment were 1–10 and 31–50 yr after the fire (Fig. 4). Douglas-fir establishment was highest in age classes 1–10 and 31–40 yr. Establishment of Douglas-fir occurred up to 75 yr after the fire, but few after year 50. Western hemlock was slow to establish; its most prolific period was 31–50 yr after the fire. Western hemlock estab-

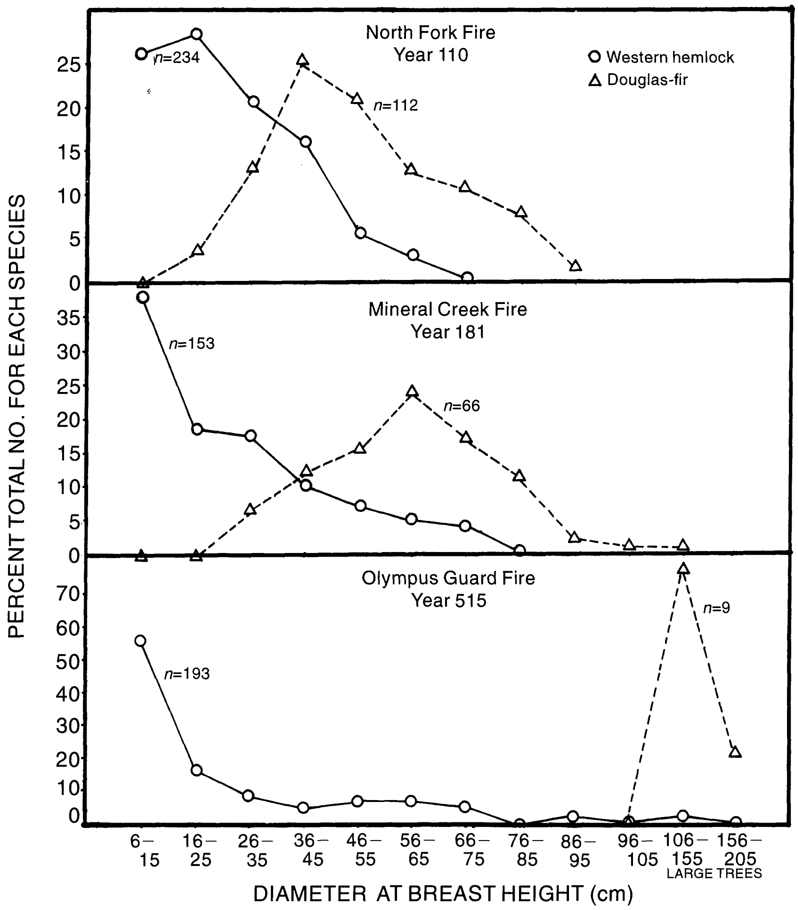

FIG. 3. Diameters of live Douglas-fir and western hemlock, by size class, at three of the study areas.

lishment decreased considerably after 1890, about 90 yr after the fire.

Douglas-fir reestablishment lasted 75 yr at the 515-yr-old site (Fig. 4), or perhaps longer, if the estimate of 1465 is too late as the date of the fire. Western hemlocks establishing 150–300 yr after the fire (215–365 yr old) occurred infrequently throughout the study site (Fig. 4). A substantial pulse of western hemlock establishment started about 1770, ≈300 yr after the fire. It lasted for ≈180 yr and subsided by 1950. Peak establishment occurred from 1830 to 1889, ≈365–424 yr after the fire.

The age distribution of trees at the 515-yr-old study site was prominently skewed toward younger age classes (Fig. 4). The overstory consisted of trees primarily <100 yr old, and only a few trees established within the first 300 yr after the fire. Twenty-five percent of all overstory trees established during just a 30-yr period from 1860 to 1889. Despite a wide size distribution of trees and a multilayered canopy appearance, this old-growth forest was numerically dominated by relatively young western hemlocks.

Age–diameter relationships

In general, tree diameter correlated poorly with tree age (Fig. 5); the strength of the associations was higher for western hemlock than Douglas-fir and increased with stand age. Using a subset of only dominant Douglas-firs or only dominant and codominant western hemlocks did not improve the strength of the relationship with any of the study sites except at the 515-yr-old site for western hemlock ($r^2 = 0.69$, $n = 26$).

DISCUSSION

Fire patterns

Fire is the primary disturbance agent within forests codominated by Douglas-fir and western hemlock, but fire occurrence and size and environmental conditions vary widely throughout their distribution (e.g., Hemstrom and Franklin 1982, Spies and Franklin 1988, Agee 1991). However, the function of fire in these forest ecosystems is less clear in wet environments, such as the temperate "rainforests" of the western Olympic Mountains, than in drier environments. In the western portion of Olympic National Park, fires burn infrequently; few burned over the last 2–3 centuries and only three relatively small lightning fires have burned >15 ha since 1900. Cool summer temperatures, relatively high precipitation and humidity, and low frequency of lightning storms account for the low fire

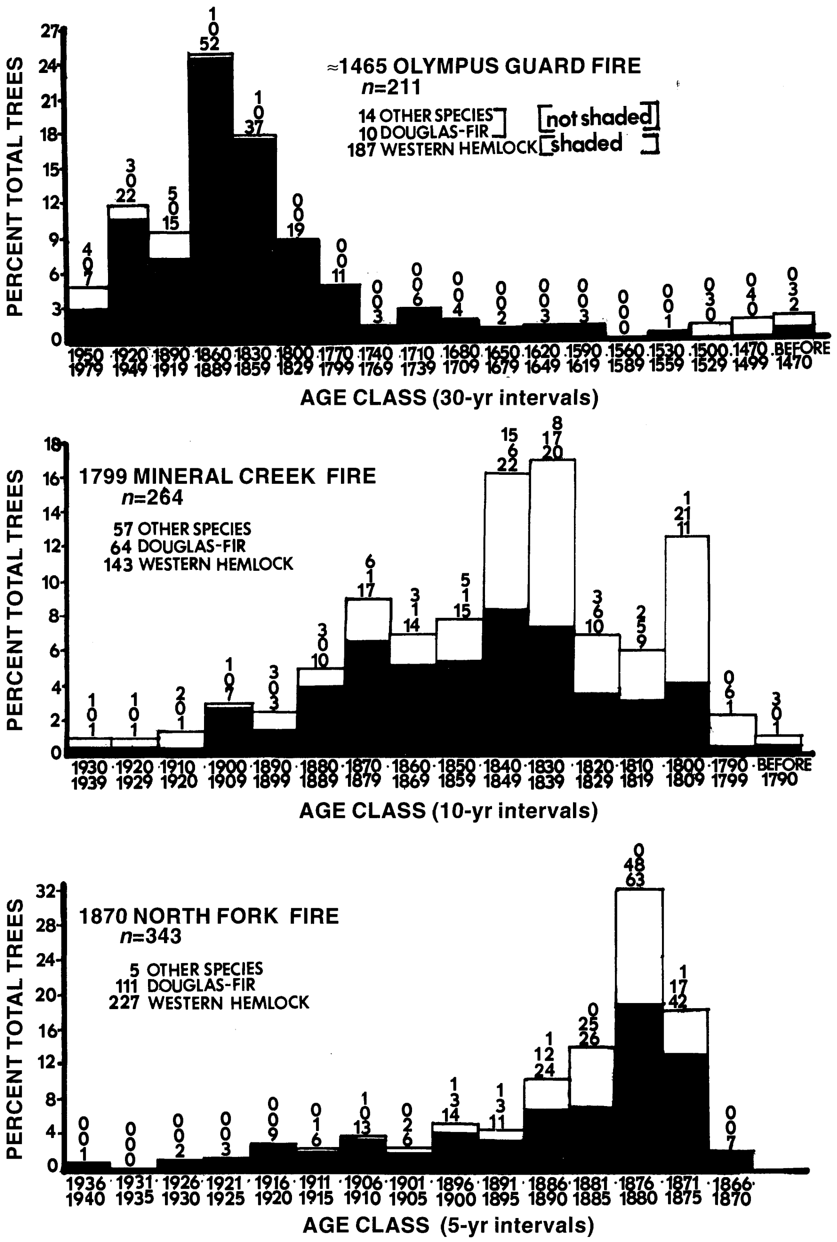

FIG. 4. Percentage of trees, by age class, in 1980 (Olympus Guard and Mineral Creek Fires) and 1981 (North Fork Fire). Time of regeneration is shown along the *x* axis.

frequency (Agee 1991). Because of its remote, rugged, and steep terrain, fire suppression efforts have not been effective (Agee and Flewelling 1983).

The ubiquity of Douglas-fir in the western Olympic Mountains (see Fonda and Bliss 1969, Henderson et al. 1989) suggests that fire has burned repeatedly in this area for thousands of years. Relatively recent charcoal fragments and widespread areas of stand ages that date to ≈300–500 to 750 yr ago suggest that large areas within the Park burned centuries ago, a sharp contrast to its present old-forest condition.

Agee and Huff (1987) estimated that early and late-seral western hemlock–Douglas-fir forests have high potential for surface fires. Late-seral forests also have a high likelihood of crown fire, with a multilayered, all-sized stand structure that links surface with canopy fuels. I suspect that the large expanse of old forests within the montane zone of the western Olympic Mountains offers fuel conditions predisposed for large catastrophic fire events. However, the likelihood of such fires occurring would be only during conditions of very extreme drought and altered synoptic weather patterns (Agee 1991).

Fuel conditions that existed prior to the widespread

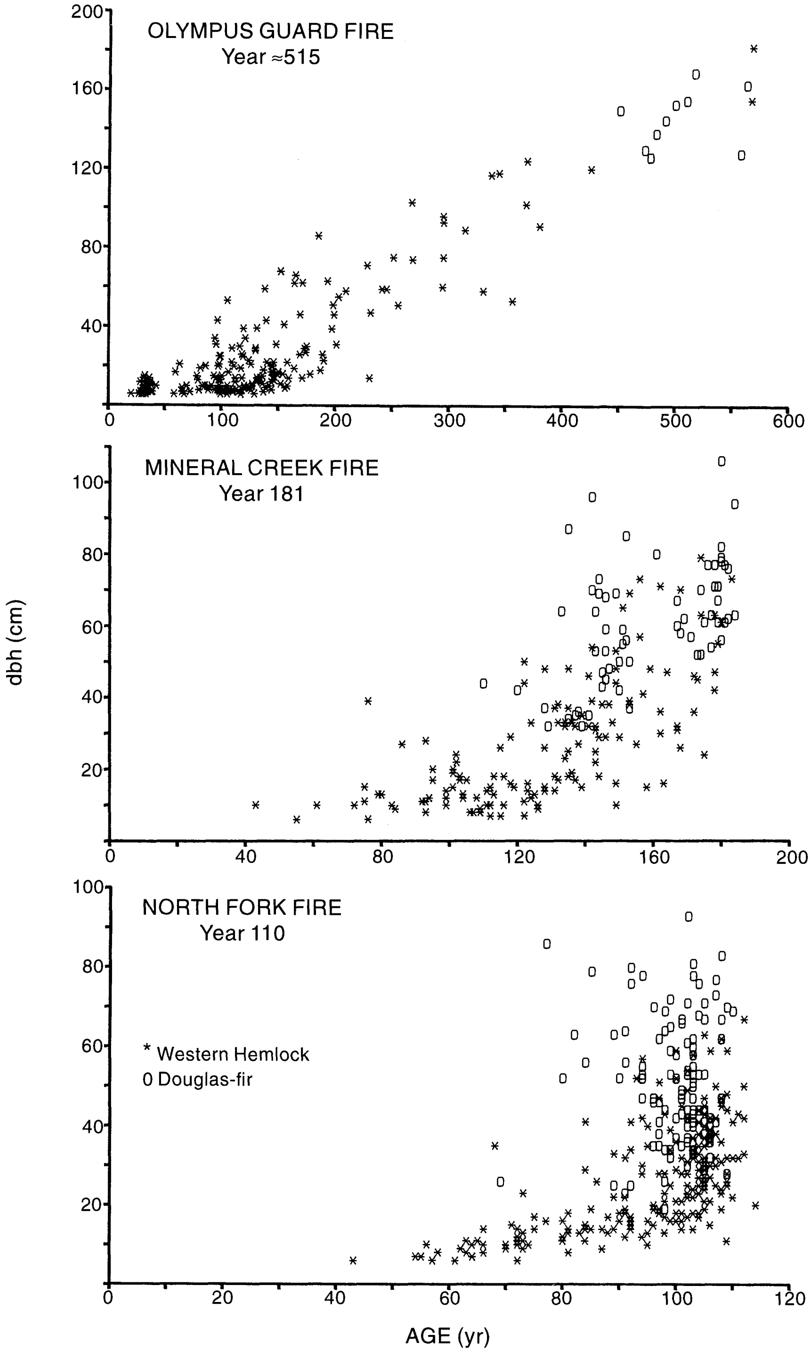

FIG. 5. Scatterplots of tree diameter vs. age for western hemlock and Douglas-fir at the 110-, 181-, and 515-yr-old sites. Squared correlation coefficients of diameter and age at the 110-, 181-, and 515-yr-old sites for Douglas-fir were $r^2 = 0.0$ ($n = 111$), 0.26 ($n = 65$), and 0.37 ($n = 8$), respectively, and for western hemlock were $r^2 = 0.40$ ($n = 226$), 0.46 ($n = 146$), and 0.68 ($n = 185$), respectively.

fires 4–7 centuries ago obviously are unknown. Yet, these fire events may have been cultivated by widespread changes in fuel structure during succession, suggesting a long, partly cyclic pattern of fire events operating at a large landscape scale. A landscape-level succession model driven primarily by extensive, cyclic fire events has been hypothesized for subalpine forests of Yellowstone National Park, where fuels capable of carrying a crown fire develop 300–400 yr after fire (Romme 1982). The massive 1988 Yellowstone fire event supported this hypothesis. Knowledge of the dates of old-growth forest establishment in the western

Olympic Mountains and elsewhere in the Douglas-fir region is so weak, however, that firm hypotheses about fire events operating at the landscape level are difficult to substantiate (Agee 1991).

Forest succession

Douglas-fir is the most important seral tree species after fire throughout most of the distribution of the western hemlock series in Washington and Oregon (Franklin and Dyrness 1973). Shrubs and herbs that dominate the post-fire environment eventually are overtopped by Douglas-fir saplings. Invasion of shade-tolerant western hemlock normally takes place as mortality begins to open up the canopy at 50–150 yr of age. Exceptions to this are found in cool and moist environments, such as the northern Washington Cascade Range and the west side of the Olympic Mountains, where western hemlock and western redcedar are major components from the beginning of the sere (Franklin and Dyrness 1973). Here, site conditions, fire intensity, fire-return interval, stand history, and many other factors interact with a moist macroclimate to produce stands with mixed tree-species composition early in the sere. Tree establishment after fire in the sere I examined consisted of two major species, western hemlock and Douglas-fir, and one minor one, western redcedar. Western hemlock was the most common species throughout the sere (Table 1).

Establishment of western hemlock and Douglas-fir appeared to be slow for the first 10 yr after fire at the 110- and 181-yr-old sites (Fig. 4) and the 19-yr-old site (Table 1; Douglas-fir in overstory and in understory: >1.0 m). Lack of seed and unfavorable establishment environment could have delayed tree establishment at these sites. Although seed was plentiful the first year after the 1978 Hoh Fire, where >70 000 tree seedlings/ha became established, few survived (Table 1). Seedling establishment decreased each year; by year 3, no new seedlings became established. The first decade after fire could be too moisture-limiting for most individual trees to survive the periods of low precipitation during the summer months (Huff 1984). Site amelioration that accompanies ecological succession, such as increased shade provided by herbs, shrubs, and downed woody material, could improve tree establishment. More intensive studies that examine the environmental conditions surrounding tree establishment and the direction of successional pathways (sensu Halpern 1988) after natural fires are needed in this region.

Most tree establishment during stand initiation occurred 11–50 yr after fire (Fig. 4). One or more peaks of major tree establishment occurred during this period, but varied among study sites. Waves of tree reestablishment that occur several decades after a fire can be associated with the appearance of new seed sources from trees that established early and reached seed-bearing age (sensu Agee and Smith 1984). Douglas-fir and western hemlock reach sexual maturity at about 15 and 25 yr, respectively (Hermann and Lavender 1990, Packee 1990). Evidence of this regeneration process was observed at the 19-yr-old site where the oldest saplings were producing seeds. Additional tree establishment is likely at this site based on establishment patterns observed at the older study sites and space for further tree establishment is available (see Fig. 2b).

After establishment of Douglas-fir peaked at about 20–50 yr, it decreased slowly over a period of 20–30 yr. Individual tree crowns probably began to crowd each other about 40–75 yr after fire, making conditions less favorable for Douglas-fir regeneration. The last few Douglas-firs probably became established in small openings that essentially remained unoccupied by trees for several decades.

Western hemlock establishment patterns resembled those of Douglas-fir, except that western hemlock continued to establish at low levels for many decades after Douglas-fir establishment ceased (Fig. 4). Later in the sere, understory establishment of western hemlock occurred at a higher frequency. This establishment probably occurs sporadically or in pulses and varies considerably within and among sites depending on local conditions and stand history. Based on tree establishment observed at the 181-yr-old site (Table 1) and other similar-aged stands in the western Olympic Mountains, the first distinct increase of western hemlock establishment may occur sometime between 150 and 300 yr after fire.

Long-term survival of western hemlocks that establish in the understory is poorly understood for this vegetation type. At the 515-yr-old site, western hemlocks that established 150–300 yr after the fire were encountered infrequently (36 trees/ha) (Fig. 4: ≈1465 fire). This suggests that understory establishment at 150–300 yr after fire was poorly developed at this site or that trees established during this period were not long lived. Understory establishment that took place at 150–300 yr after fire probably was associated with light gaps in the canopy. At this stage of succession, canopy gaps are small and are usually formed by just one tree dying (Spies et al. 1990). A gap formed this way should close relatively rapidly. Trees that establish beneath small canopy gaps may require subsequent gap openings to reach even the lower portions of the main canopy. Without additional openings, western hemlocks that colonize small gaps are likely to be severely suppressed; most likely they will die at a relatively young age, long before they reach the canopy. A few severely suppressed hemlocks were observed to live 150–200 yr at the 515-yr-old site (Fig. 5), yet these individuals appear to be rare.

The most significant pulses of understory establishment of western hemlock should occur when canopy gaps become more common and persistent. Spies et al. (1990) found that regeneration of western hemlock typically was more common in gaps than beneath tree canopies, and that in older stands (>200 yr old) the time since formation of a canopy gap was more closely associated with hemlock establishment than was gap size. Mean gap size, however, was about 4 times larger in older forests (usually formed by mortality of two or more trees) than younger ones (100–150 yr old). Logically, gap size and longevity are related. Hence, optimal survival for regeneration of western hemlock is probably beneath large, long-lasting gaps, with suitable log substrates (Harmon and Franklin 1989).

Conditions that enhance long-term survival of understory-established western hemlocks may occur later in the sere (>300 yr). As represented by live trees growing at the 515-yr-old site, a large pulse of understory establishment occurred ≈365–424 yr after the fire (Fig. 4). Important changes in the canopy layer and the suitability of log substrates for establishment probably developed just prior to and during this period. Western hemlocks that established early in the sere would have reached the end of their normal life span at ≈400 yr. It is possible that the 1800s was a period when many 300–400 yr old trees, especially the western hemlock pioneers, gradually died. The remains of many large Douglas-firs and western hemlocks were amply distributed throughout the study site as well-decayed coarse woody debris (see Agee and Huff 1987), although any connection of these logs to mortality occurring in the 1800s could not be made. The amount of large woody debris beneath canopy gaps also may enhance hemlock establishment by providing more substrates for establishment. If so, older Douglas-fir–western hemlock forests have substantially more large-log biomass than forests 80–200 yr old (Agee and Huff 1987, Spies et al. 1988, Spies and Franklin 1991).

Fire replacement sequence

The fire-return interval for the western hemlock–Douglas-fir forests in the western Olympic Mountains is long, given that so little of the landscape has burned over the last 250 yr. It probably exceeds 400 yr, but is within the typical life-span of the oldest Douglas-firs—about 700–800 yr. If fires occur within this interval, the probable replacement sequence will more or less repeat itself under similar climatic conditions. However, if fire occurs later, Douglas-fir, which rarely establishes in late-seral forests in this region, would become rare or locally extinct. Fires at this stage would likely result in a new forest dominated by western hemlock, although examples of this are rare since most of the montane zone in the western portion of Olympic National Park appears to have burned regularly over the last 800 yr. One example, however, is the 1890 Hee Haw Fire, located on a northwest slope in the Queets Valley. Here, Douglas-fir was a minor stand component after fire as a post-fire stand of nearly pure western hemlock developed.

Applying tree size to age

Tree size is still functionally used as an indicator of tree age, even though the concept has been regularly refuted for western conifers (e.g., Knowles and Grant 1983, Stuart 1983, Stewart 1986). Because of time and costs, ages of the oldest seral cohorts (i.e., time since last major disturbance) often are determined by extracting cores of only a few of the largest trees. Yet, a small sample of the largest trees can lead to erroneous conclusions. At the 110-yr-old site, for example, the three oldest trees of the 111 Douglas-firs sampled ranked 19th, 17th, and 105th in diameter size. It is unlikely that these, the oldest trees, would have been selected with a small sample.

To ensure that the oldest living trees are located during site characterization (e.g., during evaluations to determine stand age), it is imperative to obtain an adequate sample of trees with different diameters, while emphasizing trees with the largest diameters. The sample size necessary to determine forest age, for example, will depend on the time available for coring trees, the level of accuracy desired, the variability of tree ages, and the time since last burned. A sample of the 25 largest Douglas-firs at the 181- and 110-yr-old fires showed that only 7 and 3 trees, respectively, would have approximated stand age within ±3 yr.

Management considerations

To exclude fire from natural processes causes subtle, eventually substantial changes to plant and animal populations by increasing the distribution of late-successional species and structure (Marsden 1983). In western hemlock–Douglas-fir forests of the western Olympic Mountains, long-term fire exclusion would favor western hemlock over Douglas-fir (Dale et al. 1986), shifting the replacement sequence toward a wet, very-low-frequency fire regime (see Agee 1991). Douglas-fir, a key component of live and dead forest structure inherent to these systems, would dwindle in numbers over time from fire exclusion. In order to maintain the important seral characteristics of these forests, resource managers would need to implement a variety of process-oriented tools for managing vegetation (Agee and Huff 1986), including prescribed catastrophic fires.

Maintaining a dynamic landscape of stand age-class distributions and varied stand structures formed by natural disturbance patterns is a desired managed condition in park and wilderness settings (Kilgore 1990). Sustaining ecosystem properties and processes by maintaining and/or approximating natural disturbance patterns, including fire, poses serious challenges and opportunities to resource managers. Because wildfires in parks and wilderness areas present certain risks to society in and outside these areas, some level of fire exclusion is unavoidable by management. Developing plans to achieve and/or approximate conditions of a natural fire regime while excluding some fires requires a much deeper understanding of fire processes in ecological systems than is customarily available to decision-makers. A thorough ecological characterization is needed of a planning area that includes determining landscape patterns and range of stand-level structures (e.g., tree sizes and ages) and species composition associated with wildland fires.

The results of this study, including the comprehensive site-selection surveys, that can be applied to management of western hemlock–Douglas-fir forests in the western Olympic Mountains are: (1) relatively few fires burned over the last 250 yr, indicating that a long fire-return interval of several centuries or more exists; (2) the largest fires tend to be small, 100 to 600 ha, although more research is needed to determine the size of fires that burned >300 yr ago and the implications of that information for this fire regime; (3) fires typically cause high tree mortality while individual trees or groups of trees survive fire in areas that are topographically moist and/or isolated by discontinuous fuel structure; (4) tree species composition early in the sere is dominated by both Douglas-fir and western hemlock; (5) Douglas-fir appears to require fire disturbances for establishment; (6) western hemlock tends to be numerically dominant throughout the sere; (7) tree reestablishment after fire spans several decades, which may have many long-term effects on stand structure, including wide distribution of tree sizes and vertical layering, depth, and complexity of tree canopies; and (8) understory establishment of western hemlock tends to increase 150 yr after fire.

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