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SUBALPINE TREE REESTABLISHMENT AFTER FIRE IN THE OLYMPIC MOUNTAINS, WASHINGTON[1]

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Abstract. Rates of subalpine tree reestablishment were measured on the 1978 Hoh burn (3 yr old), the 1924 Mount Wilder burn (55 yr old), and the 1891 High Divide burn (88 yr old) in Olympic National Park, Washington, USA. All three sites were *Abies lasiocarpa/Tsuga mertensiana* forest at the time of burning; *Vaccinium* spp. were dominant after the fire. Tree establishment rates were higher on burned sites during periods with generally above-average to average spring/summer precipitation than during below-average periods. Highest rates of tree establishment occurred close to fire edges. Current species composition on the older burns closely reflects the composition of residual trees. Drought resistance of the residual tree species may interact with climate to affect establishment rates. *Tsuga mertensiana* establishes best during wet periods; *Abies lasiocarpa, Pseudotsuga menziesii,* and *Pinus monticola* establish well during normal periods.

These patterns are quite different from tree invasion into heather (*Phyllodoce/Cassiope*) meadows, which occurred during a fairly discrete 1920–1940 regional drought when extended snow-free periods apparently existed in these meadows.

Key words: Abies lasiocarpa; *fire effects; meadow invasion; Pacific Northwest; subalpine forests;* Tsuga mertensiana.

INTRODUCTION

Subalpine forest environments are generally difficult sites for tree establishment. Disturbance by fire or other factors may result in forest openings that remain a century or more, as forest succession may be much slower in subalpine than in montane forests (e.g., Peet 1978, 1981).

Fire-climate interactions are important in predicting the nature and rate of forest succession after disturbance. Fire removes the existing tree canopy and may limit the postfire seed source. Even if seed is available, climatic conditions after the fire may determine whether the forest regenerates immediately or slowly. The forest-tundra ecotone provides a northern analog. During widespread warming trends, forests have moved northerly and upslope. During cooling trends, mature forests disturbed by fire have reverted to tundra (Bryson et al. 1965). In the Rocky Mountains, burned subalpine forest has reverted to alpine tundra (Stahelin 1943) or ribbon forest (Billings 1969) on certain flat areas or gentle slopes.

On cool, wet subalpine sites in the Pacific Northwest, regional drying trends have been associated with tree establishment in normally open meadows. Trees usually occur in scattered clumps on favorable microsites (Lowery 1972); the surrounding meadows with late snowmelt have growing seasons too short for tree establishment. Longer snow-free periods associated with a regional drought in 1920–1940 were accompanied by a massive tree invasion in these meadows (Brink 1959, Fonda and Bliss 1969, Franklin et al. 1971). This "window" for forest establishment did not continue, and many meadows contain stunted regeneration 40–60 yr old that may eventually shrink the extent of subalpine meadows in the region.

Forest fires are an important factor in the creation of new subalpine meadows in the Olympic Mountains (Kuramoto and Bliss 1970), usually on drier, warmer sites. Once burned, these sites are slowly reinvaded by trees (Henderson 1973). Light to moderate use of these meadows by native or exotic animals may accelerate the trend, while heavy use will retard forest establishment (Dunwiddie 1977, Vale 1981).

The present study was concerned with identifying which subalpine plant communities are most flammable, how long fire-created meadows persist, and to what degree the reforestation process is predictable. This information was needed to evaluate the impact of allowing some naturally occurring fires to burn in Olympic National Park. These objectives were met by observing fire behavior on recent fires and evaluating climate and seed source effects on reforestation over time on three burns in the park.

STUDY AREA

Three primary study sites were established in the subalpine zone of the Olympic Mountains of Washington on south-facing burned slopes near 1400–1500 m elevation (Fig. 1). The first area was the Hoh fire, which burned 67 ha of subalpine forest in 1978 (Agee and Huff 1980). The second area was the 55-yr-old, 100-ha Mount Wilder fire (1924) in the Elwha River headwaters, and the third was the 88-yr-old, 55-ha

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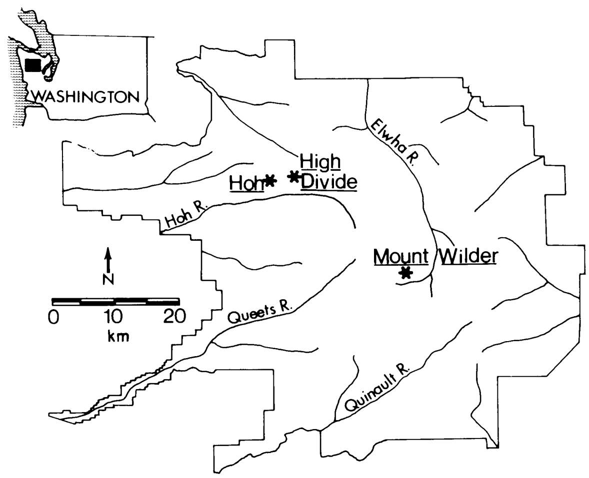

FIG. 1. Location of study sites in Olympic National Park.

High Divide fire (1891) in the Hoh River drainage. The Mount Wilder fire was dated from old fire records (Pickford et al. 1980), and the High Divide fire was identified from historical forest survey maps (Dodwell and Rixon 1902) and dated from a fire scar at the burn edge.

All study sites have similar geologic substrates. Parent material is interbedded slate-sandstone-schist of Eocene age (Tabor and Cady 1978). Slopes exceed 60% and have southeast to southwest aspects. Soils are rocky, coarse-textured entisols with little profile development.

Climate on the Olympic Peninsula is generally characterized by relatively mild, wet winters and cool, dry summers. The mountains provide an effective barrier against the moist winter storms generally travelling from the southwest, creating a steep precipitation gradient from the southwest to the northeast mountains. Annual precipitation on Mount Olympus is estimated to exceed 500 cm/yr, while lowland areas in the northeastern rainshadow receive $\approx$40 cm (Kuramoto and Bliss 1970). Precipitation at the Hoh and High Divide fire sites is estimated at $\approx$400 cm/yr, while the Mount Wilder site receives an estimated 300 cm/yr. Much of the winter precipitation falls as snow, but these steep south-facing slopes are among the first subalpine sites to be free of snow in late spring.

The High Divide, Mount Wilder, and Hoh sites (Fig. 2) are adjacent to *Tsuga mertensiana–Abies lasiocarpa* forest with varying amounts of *Abies amabilis* and *Chamaecyparis nootkatensis* (plant nomenclature follows Hitchcock and Cronquist [1973]). *Pseudotsuga menziesii* and *Pinus monticola* are occasionally found along the lower margins of the subalpine zone.

The understory of the High Divide fire site is dominated by *Vaccinium deliciosum* and *Lupinus latifolius* with various grasses and sedges. Plants cover 78% of the ground surface. The Mount Wilder understory was dominated by bare ground (40–50% cover), *Vaccinium membranaceum,* and *Xerophyllum tenax. Lupinus latifolius* and *Anaphalis margaritacea* were also abundant. The understory at the Hoh fire site is undergoing considerable change at present. Nonflowering *Carex* spp. and a tentatively identified *Arnica* sp. are most frequently encountered, but total plant cover is $<$10%. Both *V. deliciosum* and *V. membranaceum,* as well as *L. latifolius,* are present at the site.

The Hoh and High Divide sites appear to be more mesic than the Mount Wilder site. At Mount Wilder, the absence of *V. deliciosum* and the presence of *X. tenax* and *A. margaritacea* suggest that this site is drier than the corresponding sites to the west (del Moral and Watson 1978).

METHODS

One 50 × 50 m plot was randomly established in the central portion of the High Divide fire and separated into 10 × 10 m cells. All trees, including seedlings, were identified by cell location, species, and height. Age was determined by increment coring either at the base, or at a minimal height above the base; any tree that could not be cored was aged by harvesting the tree and cutting a basal disc. Shrub and herbaceous cover on the 50 × 50 m plot was sampled along 10-m line transects randomly located along five stratified lines parallel to the slope contour (Buell and Cantlon 1950).

Sampling procedures were identical at Mount Wilder, except that two 50 × 50 m plots were randomly established in the central "open" portion of the burned area and two "edge" plots were randomly located within 200 m of unburned forest. The 200-m distance was selected as a boundary between the "edge" and "open" plots due to the substantial decline in seedfall in openings further than 125 m from clear-cut edges for *Tsuga mertensiana* (Franklin and Smith 1974) and probably for its heavier seeded associated species, too.

The Hoh fire regeneration was sampled with reconnaissance methods. Seedling establishment was monitored with 1 m radius plots in year 1 (1979) and year 3 (1981), but substantial browsing, wallowing, and trampling of the area by native Roosevelt elk (*Cervus elaphus roosevelti* Merriam) and exotic mountain goats (*Oreamnos americanus* Blainville, introduced into the Olympic Mountains in the 1920s) resulted in the destruction of precise sampling points. A 30 × 50 m permanent plot was established for future reference.

One 2.2 × 30 m belt transect was placed perpendicular to the forest edge into an unburned heath-dominated meadow on a bench near the High Divide fire. This meadow showed no evidence of fire for at least the past century or two. Both *Phyllodoce empetriformis* and *Cassiope mertensiana* occur in such meadows, which are hereafter referred to as heather meadows. Tree invasion apparently unrelated to fire was occurring on this 15% south-facing slope. All trees within the transect were aged.

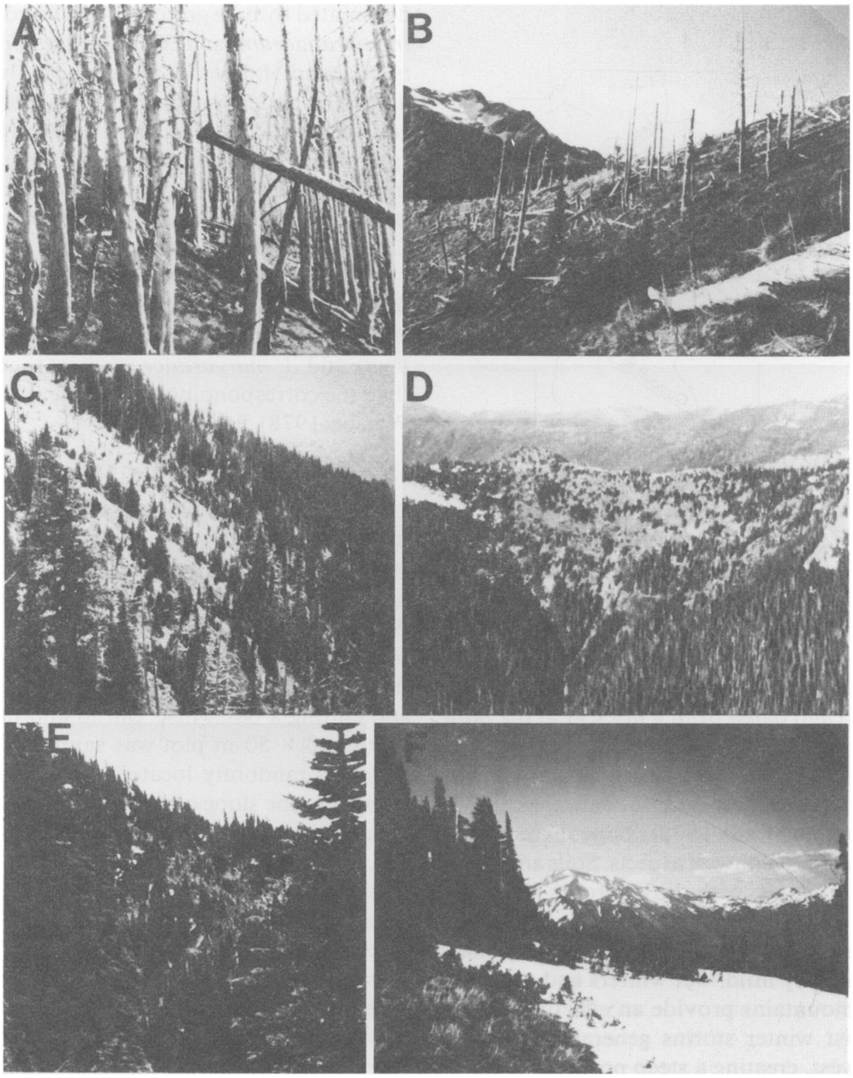

FIG. 2. A. The Hoh fire site 3 yr after the fire. Tree bark is almost completely exfoliated. B. The central portions of the 1924 Mount Wilder fire, with larger regeneration clustered around down logs. C. Edge of Mount Wilder fire, with more regeneration than in central areas of fire. D. The 1891 High Divide fire is in the center, with the *Phyllodoce* meadow on the snow-covered bench to the left. E. Closer view of High Divide fire, showing considerable regeneration in the open areas apparent in (D). F. Character of *Tsuga mertensiana* invasion into the *Phyllodoce* meadow.

All tree core and disc samples were returned to the laboratory, sanded, and counted under a dissecting microscope. Tree ages are accurate to ± 2 yr at best, with generally higher precision in the younger specimens. Sources of error include occasional missing rings, uncertainty in determining the exact location of the tree base, and some estimation of age from tree core height to the tree base on larger specimens.

Selection of appropriate time intervals to analyze general climatic trends was subjective. There are no regularly operating weather stations with long periods of record at subalpine sites in the Olympic Mountains. Annual totals may mask short-term phenomena that affect seedling survival. Regional dendrochronological records were selected for defining climatic intervals (Brubaker 1980). Principal component analysis using records across Washington associated regional tree growth anomaly patterns with climatic variation. The amplitudes of tree-growth eigenvector I correlated with spring-summer rainfall in both eastern and western Washington. Positive amplitudes imply above-average and negative values below-average growing-season rainfall.

The eigenvector I amplitudes from Brubaker (1980) were used to create short-interval and long-interval classifications defining dry, normal, and wet spring/summer conditions (Table 1). The short-interval climate periods were identified as dry if three consecutive

TABLE 1. Climate period classes derived from tree ring eigenvectors. Climate period denotes relative spring/summer precipitation.

Short interval		Long interval	
Years	Climate period	Years	Climate period
1895–1899	Normal	1897–1919	Wet
1900–1909	Wet	1920–1939	Dry
1910–1911	Normal	1940–1958	Wet
1912–1917	Wet	1959–1972	Normal
1918–1921	Normal	1973–1979	Dry
1922–1927	Dry		
1928	Normal		
1929–1933	Dry		
1934	Normal		
1935–1937	Dry		
1938–1940	Normal		
1941–1948	Wet		
1949–1952	Normal		
1953–1958	Wet		
1959–1972	Normal		
1973–1979	Dry		

years had negative amplitudes and at least two of those exceeded -0.5. Wet periods were similarly defined using positive amplitudes. Other years were grouped into normal periods. The long-interval climate periods were identified as dry or wet in the same manner. With the exception of a long normal period, 1959–1972, all other normal periods were very short (≤ 4 yr) and therefore were halved and assigned to the adjacent wet or dry period. Given the uncertainties in actual dates of tree establishment, definition of more precise climatic intervals was not justified.

The effects on regeneration of general climatic patterns, distance to edge, and presence of nearby seed source were analyzed, using standard analysis of variance (ANOVA) and covariance (ANOCOV) techniques. The objective of all analyses was to separate the variance in the establishment rates associated with seed source from that due to general climate. The High Divide tree establishment data were analyzed, using a one-way ANOCOV, with the tree establishment per year over the interval defined as the dependent variable, the short-interval climatic period (three levels) used as the independent variable, and number of trees on the plot exceeding 20 yr of age at the beginning of the interval as an initial-stocking covariate.

At Mount Wilder the effect on regeneration of plot distance from the fire edge and climate was tested by ANOVA, using tree establishment per year over the interval as the dependent variable, with distance from edge (two levels: open and edge) and broad climate periods (dry and normal/wet) as independent variables. A second analysis of the Mount Wilder data was designed to test the effect of immediately adjacent stocking on annual tree establishment rate within each of the nine central 10×10 m subplots within the two edge plots. A two-way ANOCOV was used, with the two plots as blocks, broad climate period (dry, normal, wet) as the independent variable, and stocking of trees older than 20 yr at the beginning of the climate period in the subplot and in all surrounding subplots as the covariate.

All analyses required transformations of the dependent variable to meet the analysis assumptions. No transformation was successful in meeting the homogeneity of variance assumption on the Mount Wilder edge plot analysis, and results should be interpreted cautiously.

RESULTS

Characteristics of subalpine fires

Large fires in the subalpine areas of the Olympic Mountains usually occur in drought years, after several weeks of dry summer weather, with ignition from a lightning storm, and in the presence of an east wind synoptic weather pattern that lowers relative humidity (Huff and Agee 1980, Pickford et al. 1980). The 1978 Hoh fire and the 1981 Chimney Peak fire (5 km southeast of the Mount Wilder fire) burned under such conditions. Fire behavior tends to be erratic and unpredictable. The Hoh fire burned, with a crown fire, primarily through forested areas and tree clumps, skipping over subalpine meadows with less dead fuel and also skipping those meadow edges invaded by small trees. The Chimney Peak fire burned both forested areas and substantial areas of heather meadows, including some heather meadows being invaded by small trees. The only plant community that completely escaped burning was the late-snowmelt *Carex nigricans* community growing in the bottoms of microtopographic basins. In areas that did burn, most trees were killed; along the margins of burns, some trees survived the fire.

Although no descriptions of the Mount Wilder and High Divide fires exist, both burned in drought years, with substantial to complete tree mortality within the fire boundaries.

Fires of the last century in montane and subalpine areas of the west-central Olympic Mountains, as identified from park fire records, aerial photos, and ground observations, have occurred primarily on south to west aspects exceeding 40% slope.

Tree establishment rates

Total tree density on sites ranging from 3 to 88 yr old is quite variable, with patterns being more clearly defined at older sites. Regeneration at the Hoh fire averaged 955 1-yr seedlings/ha of *Abies amabilis* in 1979; total density increased to 1592 by 1981 (year 3). The 1981 seedlings were 1st- and 2nd-yr seedlings; apparent mortality of the 1979 seedlings suggests that tree reestablishment may be a slow process. None of the seedlings appears to be well established, although occasional *Pseudotsuga menziesii* seedlings outside of

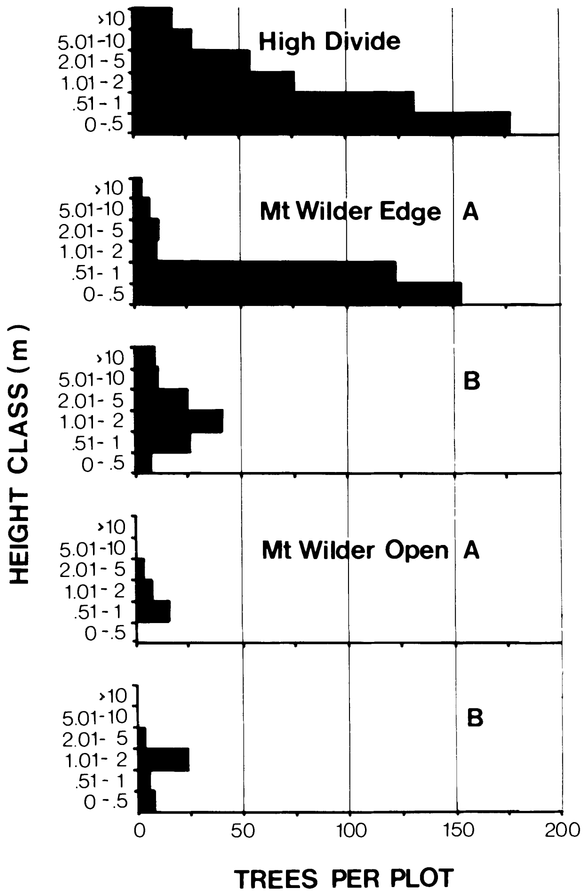

FIG. 3. Vertical structure of current forest vegetation at Mount Wilder and High Divide fires. Plots are 0.25 ha.

the survey plots appear to be growing well. Although *Abies lasiocarpa* and *Tsuga mertensiana* were present before the fire, both have failed to reinvade the site immediately.

At the 55-yr-old Mount Wilder site (1924), edge plots contained 480 and 1248 trees/ha, and open plots had 60 and 84 trees/ha. The majority of trees on these plots are <5 m tall (Fig. 3). No trees in open plots exceed 10 cm diameter at breast height (dbh), while 92 trees/ha exceed this diameter in the edge plots. All of these plots retain a meadow-like appearance after 55 yr, although the presence of snags and logs clearly indicates that these sites were once well forested.

The High Divide site (1891) has the best developed forest. Total density is 1948 trees/ha, and over 400 trees/ha exceed 5 m height (Fig. 3). Although 216 trees/ha exceed 10 cm dbh, this site is still quite open (Fig. 2) and will not become closed forest for at least several more decades.

The rate of tree reestablishment over time appears to be a site-specific process. The number of trees established in a particular year varies considerably within the Mount Wilder sites (Fig. 4), between the Mount Wilder and High Divide (Fig. 5) sites, and between the burned sites and the unburned heather meadow near High Divide (Fig. 6). The dominant species at both High Divide and Mount Wilder Edge A is *Abies lasiocarpa,* but the years of peak establishment differ. The peak at High Divide was 1955–1965, while at Mount Wilder Edge A the peak was 1968–1972. The Mount Wilder Edge B plot is dominated by *Tsuga mertensiana,* with some *Pseudotsuga menziesii* and *Pinus monticola* and no major peaks in establishment rates. The Mount Wilder Open plots have so few trees that even when these plots are graphed together no trends are apparent; the dominant tree here is *Pinus monticola.* In the Mount Wilder vicinity, *Pinus monticola* is heavily infested with white pine blister rust (*Cronartium ribicola*), and few of the trees on the plots are expected to survive more than a few decades. Particularly on the open plots, this exotic disease may delay natural tree restocking. The heather meadow invasion shows a pattern quite different from the other sites. *Tsuga mertensiana* is the only species invading. The peak years for tree establishment were 1930–1950; little invasion occurred on this site before 1920 or after 1960.

Effect of seed source and climate

Postfire tree establishment has not been uniform in space or time. A simple geographical analysis (Fig. 7) shows immediate postfire spatial pattern and subsequent increases in tree density over time. At the High Divide plot all of the residual stocking after the fire occurred in the lower 20 m; this portion of the plot is most heavily stocked today. With the exception of the Mount Wilder Edge A plot, the Mount Wilder plots have tended to increase tree density most in and around areas where trees survived the fire or where trees initially were established after the fire.

Where residual trees occurred at High Divide or the edge plots at Mount Wilder, present species composition closely parallels residual species composition (Table 2).

Three statistical analyses were done to determine the effect of seed source and climate on tree establishment. The one-way ANOCOV at High Divide (Table 3) failed to indicate that tree establishment per year is significantly related to climate period, owing to high within-cell variance. The initial-stocking covariate was significant, once the variance due to a significant interaction between climate period and the initial-stocking covariate was removed. The significant interaction meant that during dry-climate periods, initial stocking of trees older than 20 yr was not significantly related to tree establishment. However, during normal and wet periods, there was a significant positive relationship between initial stocking on the plot and tree establishment.

Seed source and climate were significantly related to

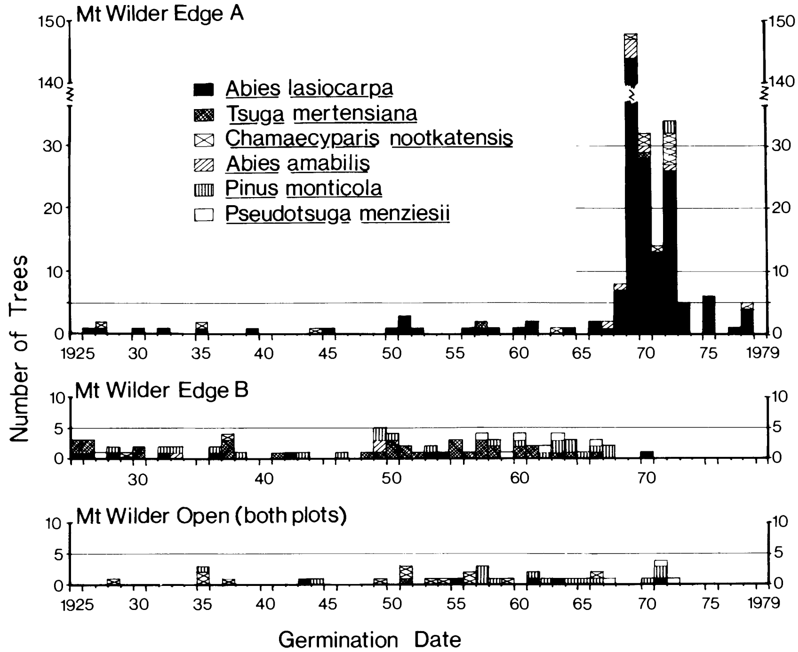

FIG. 4. Tree establishment rates at the Mount Wilder fire by year. Plots are 0.25 ha.

tree establishment at Mount Wilder. The two-way ANOVA using as main effects climate period and distance to edge (Table 4) indicated tree establishment differed significantly between climate periods and by distance to edge of fire. Tree establishment during normal and wet periods was several times that during dry-climate periods; the higher rates of establishment in the edge plots are obvious in Figs. 3, 4, and 7.

Within the two edge plots at Mount Wilder, the effect of broad climate period, block (plot), and initial stocking on tree establishment rates was analyzed, using a two-way ANOCOV on the nine central 10 × 10 m subplots of each 50 × 50 m plot. The analysis was restricted to the central subplots so that the initial-stocking covariate could be calculated as the sum of the selected subplot initial stocking plus that of all immediately adjacent subplots. Climate period, block (plot), and interaction effects (Table 5) were significant, suggesting that the climate effect differed on each plot. Tree establishment per year on the Edge A plot was significantly more during normal years and significantly less during wet years than on the Edge B plot. Dry years again resulted in very little tree survival on either plot.

Tree invasion into the short-growing-season heather meadow peaked at the end of the apparent regional 1920–1940 drought (Keen 1937, Governor's Ad Hoc Committee 1977) in the Pacific Northwest (Fig. 6). The bell-shaped distribution, if assumed to be normal, has a mean establishment date of 1939, with 95% of the establishment between 1920 and 1960. Consistently lower snowpacks in the 1920–1940 period may have

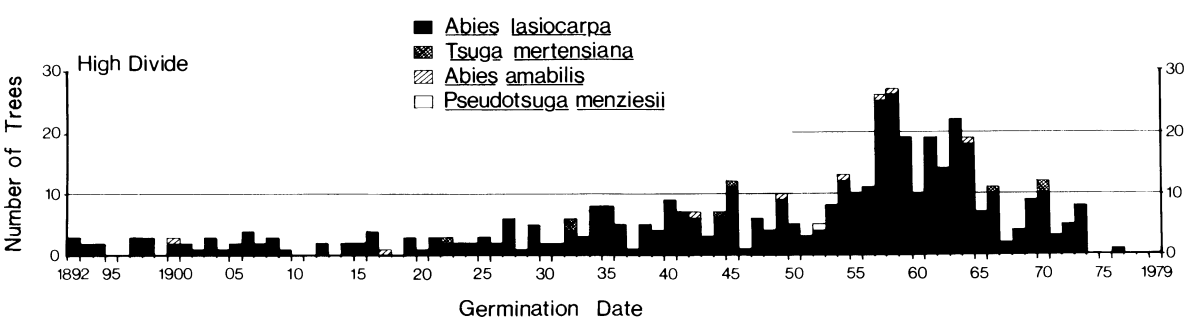

FIG. 5. Tree establishment rates at the High Divide fire by year. Plot is 0.25 ha.

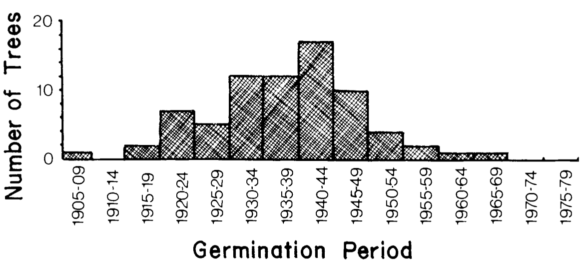

FIG. 6. Tree invasion into *Phyllodoce* meadow near High Divide. All trees are *Tsuga mertensiana* on this 66-m^2 belt transect.

created longer growing seasons, allowing substantial tree invasion; many glaciers of the Olympic and Cascade Mountains were shrinking rapidly during this period (Hubley 1956, Heusser 1957). The continuation of establishment into the succeeding wet climatic period (1940–1958) is difficult to explain. Apparently the 1973–1979 dry period was not long enough to initiate another wave of tree invasion into these meadows.

The periodicity of cone crops, once trees of cone-bearing age are present, affects the availability of seed.

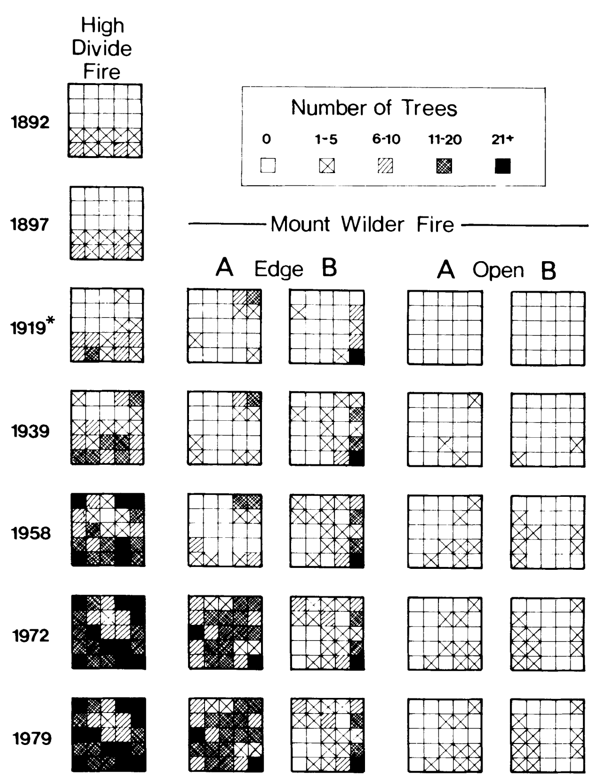

FIG. 7. Spatial pattern of tree establishment after fire. The large squares are 50 × 50 m divided into 10 × 10 m cells. The 1919 tree density at Mount Wilder (*) is pre-1924 density that survived the fire, not actual 1919 density.

TABLE 2. Correspondence between residual species composition after fire and present species composition.

Species	High Divide (residuals < 1891) Residual	High Divide 1979	Mount Wilder edge plots (residuals < 1924) Plot A Residual	Plot A 1979	Plot B Residual	Plot B 1979
	Percent of trees					
Abies lasiocarpa	100	96.6	87.9	90.8	28.6	18.1
Tsuga mertensiana	0	1.6	0	0.6	67.3	53.5
Abies amabilis	0		0	2.2	0	2.4
Chamaecyparis nootkatensis	0	0	12.1	5.8	4.1	3.1
Pinus monticola	0	0	0	0.6	0	17.3
Pseudotsuga menziesii	0	0.2	0	0	0	5.6

Abies lasiocarpa typically has a 3–6 yr interval between good cone crops, and Franklin et al. (1971) hypothesized this might be responsible for the short-term pulses of establishment of this species into normally snow-maintained meadows at Mount Rainier. The two plots that had significant amounts of *Abies lasiocarpa* both show limited recent association with assumed good seed years. Using the 1968 bumper cone crop in Washington (Franklin et al. 1971) and thus 1969 as a base establishment year, the Mount Wilder Edge A plot has relative regeneration peaks in 1978, 1975, 1972, 1969, and 1966, all multiples of three years before and after 1969. Earlier years do not show an association. The High Divide site shows little correlation after 1969, but does show relative peaks in 1966 and 1963. While cone crop periodicity for *Abies lasiocarpa* may contribute to tree establishment, given that seed trees are present and climatic conditions are amenable, the association in this case cannot be strongly demonstrated.

DISCUSSION

The burned study sites appear to lie in the dry to mesic portion of the environmental gradients that are found in subalpine forest habitats in the Olympic

TABLE 3. Tree establishment per year by climate period for High Divide plot (0.25 ha). * $P < .05$; ** $P < .01$.

Climate period: Dry	Normal	Wet
2.84	4.79	6.43

Source of variation	df	Mean square	F
Main effect—climate	2	0.394	1.74
Covariate—stocking	1	1.461	6.46*
Interaction	2	1.764	7.81**
Error	10	0.226	
Total	15		

TABLE 4. Tree establishment per year per 0.25 ha for Mount Wilder open and edge plots by climate interval. * $P < .05$.

	Climate period		
	Dry	Normal/wet	
Open plots	0.063	0.483	
Edge plots	1.070	5.338	
Source of variation	df	Mean square	F
Main effect—climate	1	19.503	7.39*
Main effect—location	1	15.002	5.68*
Interaction	1	0.507	0.19
Error	12	2.639	
Total	15		

Mountains. The Hoh and High Divide sites are nested within the western, wet portion of the subalpine forest zone, but the southerly aspect and steep slopes make these sites warmer, drier, and apparently more flammable than adjacent sites on other aspects or more gentle slopes. These adjacent sites have fewer *Abies lasiocarpa* and more *Tsuga mertensiana* and *Abies amabilis*, suggesting shorter and more moist growing seasons (Fonda and Bliss 1969, Franklin and Dyrness 1973). Even so, there is little geographical distance between the relatively dry, warm subalpine study sites and nonforested areas where late snowmelt prevents closed forests.

The south-facing heather meadow near High Divide, because of its bench-like physiography, has an environment similar to nonforested, north-facing slopes in the adjacent Seven Lakes Basin. During 1979, it was largely snow covered (Fig. 2) in July, while the adjacent steep-sloped burned area was snow-free. Short growing seasons and low moisture stress are characteristic of heather meadows (Olmsted 1975, Edwards 1980).

Mount Wilder, unlike the Hoh–High Divide area, has one range of roughly 2000 m high mountains between it and the path of major winter storms. The vegetation appears to indicate a slightly drier site than the Hoh–High Divide area. While *Pinus monticola* and *Pseudotsuga menziesii* are present in low numbers, the presence of *Tsuga mertensiana* and *Abies amabilis* suggests the Mount Wilder site is at the moist end of the relatively dry *Abies lasiocarpa* type of Fonda and Bliss (1969). As precipitation decreases to the northeast, the *Abies lasiocarpa* type, characterized by *Abies lasiocarpa* and *Pinus contorta,* becomes widespread.

TABLE 5. Tree establishment per year on central subplots (0.01 ha) of Mount Wilder edge plots by climate period. *** $P < .001$.

Block	Climate period		
	Dry	Normal	Wet
Edge plot A	0.096	1.025	0
Edge plot B	0.006	0.062	0.058
Source of variation	df	Mean square	F
Main effect—climate	2	0.677	50.46***
Main effect—plot	1	0.574	42.77***
Interaction	2	0.589	43.92***
Covariate—stocking	1	0.033	2.48
Error	47	0.013	
Total	53		

Recent tree invasion into subalpine heather meadows which appear to have been herb or shrub communities for several centuries is not related to fire. As shown by this study and others in the Pacific Northwest (Brink 1959, Fonda and Bliss 1969, Franklin et al. 1971), these once stable, snow-dominated meadows have been invaded by a pronounced wave of tree regeneration, primarily *Abies lasiocarpa* or *Tsuga mertensiana.* Although size-class data might characterize the invasion as continuous, age-class data in these studies have shown a 25-yr period (1920–1945) during which almost all of the invasion occurred. This period was associated with longer snow-free growing seasons, which for two decades created conditions generally suitable for tree establishment. Fonda and Bliss (1969) identified a 1953–1960 age-class in the northeastern Olympics, one that was not present at the other Pacific Northwest sites or in the west-central Olympic Mountain sites of this study. Heather meadows appear to be the most heavily invaded, while later snowmelt communities, such as *Carex nigricans* communities (Kuramoto and Bliss 1970), have not experienced tree invasion.

The interaction of fire with these tree-invaded heather meadows has not been clearly established. In the North Cascades of Washington, Douglas and Ballard (1971) reported that a krummholz community with *Vaccinium* and *Phyllodoce* burned in 1940 had not been invaded by trees after 20 yr; rather, *Vaccinium deliciosum* had become the dominant shrub on burned areas. The 1978 Hoh fire did not burn heather-dominated communities which contained invading trees, although the fire did skip to islands of scattered tree clumps where higher fuel loads existed. The 1981 Chimney Peak fire did burn across some heather meadows, including those with recent tree invasion. Ten sample trees from these meadows all became established between 1920 and 1940. Fire has clearly inhibited tree dominance by killing the invading cohort of trees, but there is no evidence to indicate if tree invasion reoccurs on these marginal forest sites after they are burned.

Subalpine forests that burn are usually transformed into *Vaccinium* meadows in which trees reestablish slowly. Fonda and Bliss (1969) characterize subalpine forests as dense, with 750 trees/ha exceeding 10 cm diameter at breast height. None of the study sites approaches this stocking level 55–90 yr after burning. Minore and Dubrasich (1981) defined adequate stocking for commercial forests at ≈600 trees/ha; the High Divide site was 50 yr old before it reached this stocking level, and only the Edge A plot at Mount Wilder, after 45 yr, had reached that level. Restocking of burned subalpine forests is not a continuous process in space or time. Regeneration tends to be clumped and reflects the species composition of residual trees. Burned areas with no residual trees after the fire may remain treeless meadows for a century or more.

In this study, climate has been shown to be associated with significantly different rates of tree establishment; much higher establishment on these relatively dry slopes occurs with normal to above-average growing-season moisture. Below-average spring/summer precipitation is likely associated with critical moisture stress for the current-year seedlings and significant mortality of both current-year and other recently established trees.

The physiological adaptations of different tree species may also influence the rate of tree reestablishment after fire. The relative drought tolerance, as seedlings, of the major species, in increasing order, is (Lowery 1972, Minore 1979): *Tsuga mertensiana, Abies lasiocarpa, Pinus monticola,* and *Pseudotsuga menziesii.* At Mount Wilder, where all four species were present, *Tsuga mertensiana* tended to have higher proportions of regeneration during wet periods; the others had highest proportions during normal periods. None had highest proportions during dry periods.

The High Divide and Mount Wilder Edge A plots show a 40–70 yr lag time before the maximum regeneration pulse occurred. Periods of apparently suitable moisture regime occurred earlier but were not accompanied by substantial tree regeneration. Part of this lag is due to the time required for trees that established early to mature and to produce seed; there is a significant relationship between tree establishment and number of trees older than 20 yr in the immediate vicinity. Other factors may include the ameliorating effect of fallen snags and the impact of elk browsing. Snags on burned subalpine sites may stand for decades, due to rapid bark exfoliation, case hardening of the sapwood, and rocky sites into which tree roots are wedged. Visual inspection of the study sites suggests that the conversion of snags to down logs may exceed the 20–30 yr conversion period commonly observed in lower montane Olympic forests; after 50 yr, the conversion process is only partially complete. After falling they may reduce snow creep and create barriers to elk use. Such protected microsites may buffer surface temperature extremes and may also slightly delay snowmelt, creating more optimal environments for seedling survival.

Conclusion

Fires in the west-central subalpine Olympic Mountains occur mainly on steep, south-facing slopes. Communities observed most likely to burn are, in decreasing order: closed *Tsuga mertensiana/Abies lasiocarpa* forest, heather meadows with tree invasion, heather meadows without tree invasion, and *Carex nigricans* basins. This order appears to parallel a summer moisture stress gradient.

Tree regeneration after fire is only partially correlated with time since disturbance. Tree establishment in burned areas is higher during normal to wet growing seasons than during dry growing seasons. Areas near the edge of the fire or where survivor trees are present have higher establishment rates than areas farther removed from seed sources. Given favorable climate and availability of seed, regeneration may also depend on the relative drought resistance of the seed source species and on periodicity of seed crops.

A lag time of 40–50 yr before substantial natural regeneration occurs may be related to maturation of early invading trees, dynamics of down-log accumulation, and possibly elk browsing.

Our understanding of subalpine tree establishment patterns is complicated because shrub or herb communities are well developed on both ends of commonly encountered environmental gradients; mesic conditions appear most suitable for tree establishment. The influence of a given climatic trend on forest regeneration depends on whether a site moves towards or away from the mesic state. On cold, wet sites, a dry-warm trend may create conditions amenable to tree establishment (Franklin et al. 1971), while the same trend on an already dry-warm site may produce stresses unsuitable for tree establishment (Kuramoto and Bliss 1970).

Reforestation of the 1891 and 1924 burns suggests tree establishment is largely unpredictable after subalpine fires. While it is possible to go back in time and show associations among climate, seed source, and tree reestablishment, it is not possible to predict future climate and, therefore, future tree reestablishment trends.

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