

SPATIAL CONTROLS OF HISTORICAL FIRE REGIMES: A MULTISCALE EXAMPLE FROM THE INTERIOR WEST, USA

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Abstract. Our objective was to infer the controls of spatial variation in historical fire regimes. We reconstructed a multicentury history of fire frequency, size, season, and severity from fire scars and establishment dates of 1426 trees sampled on grids in four watersheds (~64 plots, over ~1620 ha each) representative of the Blue Mountains, Oregon and Washington, USA. The influence of regional climate, a top-down control, was inferred from among-watershed variation in fire regimes, while the influence of local topography, a bottom-up control, was inferred from within-watershed variation. Before about 1900, fire regimes varied among and within watersheds, suggesting that both top-down and bottom-up controls were important. At the regional scale, dry forests (dominated by ponderosa pine), burned twice as frequently and earlier in the growing season in southern watersheds than in northern watersheds, consistent with longer and drier fire seasons to the south. Mesic forests (dominated by subalpine fir or grand fir) probably also burned more frequently to the south. At the local scale, fire frequency varied with different parameters of topography in watersheds with steep terrain, but not in the watershed with gentle terrain. Frequency varied with aspect in watersheds where topographic facets are separated by significant barriers to fire spread, but not in watersheds where such facets interfinger without fire barriers. Frequency varied with elevation where elevation and aspect interact to create gradients in snow-cover duration and also where steep talus interrupts fuel continuity. Frequency did not vary with slope within any watershed. The presence of both regional-scale and local-scale variation in the Blue Mountains suggests that top-down and bottom-up controls were both important and acted simultaneously to influence fire regimes in the past. However, an abrupt decline in fire frequency around 1900 was much greater than any regional or local variation in the previous several centuries and indicates that 20th-century fire regimes in these watersheds were dramatically affected by additional controls such as livestock grazing and fire suppression. Our results demonstrate the usefulness of examining spatial variation in historical fire regimes across scales as a means for inferring their controls.

Key words: *bottom-up; climate; dendrochronology; fire history; landscape ecology; local scale; Oregon; regional scale; top-down; topography; Washington.*

INTRODUCTION

Historical fire regimes and their controls varied across a wide range of spatial scales in western North America (e.g., Tande 1979, Hemstrom and Franklin 1982, Payette et al. 1989, Swetnam and Baisan 1996, Wright 1996, Taylor and Skinner 1998). This variation was the result of complex interactions of the controls of fire across a similarly wide range of scales. Such controls can be broadly classified as top-down or bottom-up (Lertzman and Fall 1998). Processes acting on fire at coarse spatial scales exert top-down control. For example, regional climate can influence fire regimes directly because moisture in the air and soil affects the moisture content of fuel, and thus the probability that it will ignite. Regional climate also indirectly affects fire regimes by influencing coarse-scale spatial variation in forest composition and structure, which in turn

influences fuel size, amount, and arrangement. In contrast, factors that vary at fine spatial scales, such as topography, may exert bottom-up control on fire regimes. For example, local-scale variation in topography can affect the moisture content of fuel by influencing microclimate, and can further affect fire regimes by influencing fuel continuity (Tande 1979, Hemstrom and Franklin 1982, Wright 1996, Taylor and Skinner 1998). The relative influence of top-down and bottom-up processes on past fires can be inferred by comparing patterns of variation in fire regimes at regional and local spatial scales. To infer such processes, fire regimes must be examined at the same spatial scales over which those processes operated (Ricklefs 1987, Urban et al. 1987, Wiens 1989, Allen and Hoekstra 1991, Levin 1992, Lertzman and Fall 1998). If top-down controls were important, we would expect historical fire regimes to vary at regional scales, whereas if bottom-up controls were important, we would expect them to vary at local scales.

The Blue Mountains of northeastern Oregon and southeastern Washington are well situated for exam-

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ining historical fire regimes and the multiscale factors that controlled them, because both top-down and bottom-up controls operate in this region. Fire regimes summarize the predominant characteristics of fires occurring over time in a given ecosystem, including how often they burn (frequency), how large they are (size), when during the year they burn (season) and their effects on vegetation (severity). Top-down control is exerted on such fire regimes by regional-scale climate variation. The Cascade Range and Columbia River Gorge to the west affect atmospheric circulation, causing climate to vary regionally (50–250 km) across the Blue Mountains. Precipitation is higher, snow cover persists longer, and lightning may be less frequent in the northern Blue Mountains than in the southern portion of this region. Operating within the regional climate gradient, bottom-up control is exerted by complex variations in local (0.5–10 km) topography and vegetation. Northerly slopes receive less direct solar radiation and have lower temperature and higher relative humidity than do southerly slopes. These spatial variations in microclimate affect the distribution of forest types at the local scale. Forests on northerly slopes and at high elevations are dominated by grand fir (*Abies grandis* (Dougl.) Lindl.) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.; Johnson and Simon 1987, Johnson and Clausnitzer 1992). These mesic forests historically sustained moderate- to high-severity fire regimes, in which some or all of the overstory trees are killed, due to their long crowns and thin bark. In contrast, southerly slopes and low elevations support ponderosa pine (*Pinus ponderosa* Dougl. ex Loud.) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests. These dry forests historically sustained low-severity fires, in which most overstory trees are not killed, due to their high crowns and thick bark.

The Blue Mountains are also a good place to examine historical fire regimes because a well-preserved, multicentury proxy record of fire can be reconstructed from tree rings there (Maruoka 1994). To understand spatial variation in fire regimes that is due to spatial variation in climate, topography, and vegetation, fire regimes must be examined during periods when their controls were not undergoing major changes through time, such as the dramatic change in land use that occurred in the Blue Mountains at the end of the nineteenth century. Fortunately, the tree ring record of fire in the Blue Mountains predates this period of change by several centuries.

Our objective was to understand the relative influence of top-down and bottom-up controls of spatial variation in historical fire regimes in forests representative of the Blue Mountains, by examining those regimes at the same scales at which the controls operated. Specifically, we compiled a spatially explicit, multicentury history of fire regimes from tree rings, by reconstructing the occurrence, size, season, and severity of past fires, using fire scars and the establishment dates

of postfire cohorts, sampled on a ~1620-ha grid of ~64 plots in each of four watersheds. We assessed regional-scale variation in fire regimes by comparing fire frequency, size, and season among the four sampled watersheds in forests of similar composition. We assessed local-scale variation by comparing fire frequency and severity across topographic settings and forest types within each watershed.

STUDY AREA

The climate of the Blue Mountains is generally continental, with low annual precipitation, most of which falls during the winter as snow (mean = 446 mm, 1985–1996; EarthInfo 1990, Mock 1996). Winters are cold and summers warm (mean for 1895–1991 for January = -3.2°C , for July = 18.8°C ; NOAA 1997). Within the region, climate varies at both regional and local spatial scales (Bryson and Hare 1974, Mock 1996). At the regional scale, precipitation is higher in the northern portion than in the southern portion of the study area. Both annual and summer precipitation are significantly correlated with latitude for stations at comparable elevation (Spearman rank correlation, $r = 0.73$ and 0.70 , respectively, $P < 0.01$, Heyerdahl 1997). This gradient in precipitation is due in part to the penetration of westerly Pacific air through the Cascade Range via the Columbia River Gorge (Fig. 1), which brings moist air across the northern, but not across the southern Blue Mountains (Mock 1996). This regional gradient in precipitation is partly responsible for more persistent snow packs in the northern Blue Mountains. Snow cover duration is significantly correlated with latitude ($r = 0.75$, $P < 0.01$; Natural Resources Conservation Service 1997). Lightning storms were slightly more frequent in the southern Blue Mountains during the late 1920s (Morris 1934), although dry summer lightning storms are common throughout the region (Morris 1934, Rorig and Ferguson 1999). At the local scale, steep gradients in elevation and abrupt changes in aspect cause microclimate to vary dramatically over short distances. The study area spans the latitude ($\sim 45^{\circ}\text{N}$) where aspect has the greatest influence on the input of annual solar radiation. In steep terrain (50% slope) at this latitude, southerly slopes receive twice the direct solar energy that northerly slopes receive (Holland and Steyn 1975). Consequently, southerly slopes have higher surface temperature and lower relative humidity than do northerly slopes at comparable elevation.

The potential vegetation of the Blue Mountains has been classified based on the species of trees, shrubs, and herbs that would dominate in the absence of disturbance (Johnson and Simon 1987, Johnson and Clausnitzer 1992). These plant associations vary along a gradient of moisture and other factors. For this study, we divided plant associations into two broad groups, mesic and dry forest. Mesic forest includes all associations potentially dominated by subalpine fir, and moist associations potentially dominated by grand fir

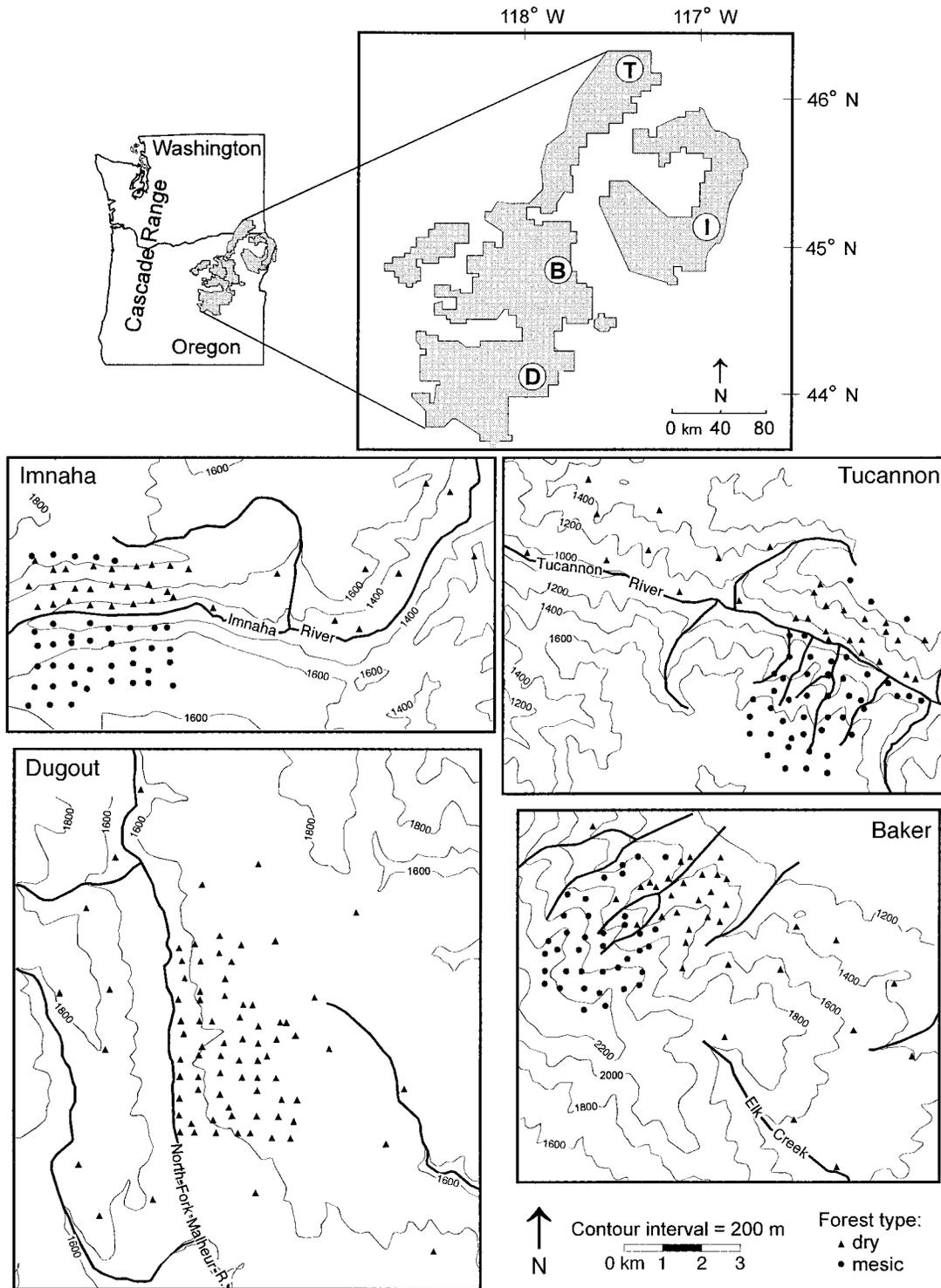


FIG. 1. The Blue Mountains of Oregon and Washington, showing the location of the four sampled watersheds (T = Tucannon, I = Imnaha, B = Baker, and D = Dugout) and the locations of sampled plots within each watershed, by forest type (dry vs. mesic). The Columbia River flows through the Cascade Range along the border between Oregon and Washington. Shaded areas are managed by the U.S. Forest Service.

TABLE 1. Number of plots by plant association, watershed, and evidence of fire.

Plant association		Watershed†				Evidence of fire	
Common name	Scientific name	T	I	B	D	Age cohorts	Fire scars
Mesic forest associations							
Subalpine fir/fool's huckleberry	<i>Abies lasiocarpa/Menziesia ferruginea</i>	3	3	...
Subalpine fir/big huckleberry	<i>A. lasiocarpa/Vaccinium membranaceum</i>	9	1	4	...	14	...
Subalpine fir/grouse huckleberry	<i>A. lasiocarpa/Vaccinium scoparium</i>	12	...	12	...
Subalpine fir/elk sedge	<i>A. lasiocarpa/Carex geyeri</i>	1	...	4	...	5	...
Grand fir/Pacific yew/twinflower	<i>A. grandis/Taxus brevifolia/Linnaea borealis</i>	3	3	...
Grand fir/queen's cup beadlily	<i>A. grandis/Clintonia uniflora</i>	2	2	4	...
Grand fir/twinflower	<i>A. grandis/Linnaea borealis</i>	4	...	4	...	6	2
Grand fir/big huckleberry	<i>A. grandis/Vaccinium membranaceum</i>	14	24	7	...	43	2
Grand fir/Columbia brome	<i>A. grandis/Bromus vulgaris</i>	2	...	2	...	4	...
Grand fir/birchleaf spiraea	<i>A. grandis/Spiraea betulifolia</i>	5	5	...
Dry forest associations							
Grand fir/pinegrass	<i>A. grandis/Calamagrostis rubescens</i>	4	9	5	11	10	19
Grand fir/elk sedge	<i>A. grandis/Carex geyeri</i>	...	2	1	3	...	6
Douglas-fir/pinegrass	<i>Pseudotsuga menziesii/Calamagrostis rubescens</i>	19	30	21	44	3	111
Douglas-fir/elk sedge	<i>P. menziesii/Carex geyeri</i>	3	1	4	11	...	19
Ponderosa pine/pinegrass	<i>P. ponderosa/Calamagrostis rubescens</i>	1	2	...	9	...	12
Ponderosa pine/elk sedge	<i>P. ponderosa/Carex geyeri</i>	1	...	1	2	...	4
Total		71	71	65	80	112	175

Notes: Only associations found at more than two plots are shown (95% of the 303 plots sampled). The plant associations are ordered from those growing in mesic to those growing in dry environments (top to bottom).

† Watershed abbreviations: T, Tucannon; I, Imnaha; B, Baker; D, Dugout.

(Table 1). Dry forest includes the remaining associations, all those potentially dominated by Douglas-fir and ponderosa pine, and the dry associations potentially dominated by grand fir. Most mesic forests in the sampled watersheds are currently dominated by grand fir, subalpine fir, or lodgepole pine (*Pinus contorta* Dougl. ex Loud.). In contrast, dry forests are typically dominated by ponderosa pine with some Douglas-fir or grand fir.

The Blue Mountains encompass several small mountain ranges in northeastern Oregon and southeastern Washington (Fig. 1). We sampled four topographically unique watersheds in this region. The sampled area at each of the northern watersheds, Tucannon and Imnaha, covers steep slopes on both sides of roughly east–west trending river valleys. Elevations at Tucannon range from 1000 to 1800 m, sampled slopes average 47%, and all aspects are well represented (Fig. 2). Imnaha is higher in elevation (1300–1900 m), slopes are more gentle (28%) and aspects are limited to primarily north or south. Baker, one of the southern watersheds, lies on the northeastern face of the Elkhorn Mountains and abuts the southern edge of the broad Baker Valley. It has the greatest range in elevation of the four watersheds (1250–2300 m), intermediate slope steepness (40%), and all aspects except southwesterly ones are well represented. Dugout, also in the south, has gentle landforms. This watershed has the smallest elevation range (1400–1800 m), the gentlest slopes (16%) of the four watersheds, and is dominated by westerly aspects.

Each watershed can be divided into contiguous areas

of relatively homogeneous slope and aspect, known as topographic facets (Daly et al. 1994). The northern watersheds, and Dugout, to the south, are relatively smooth topographically. Hence the sampled areas include few facets, separated by rivers in each watershed (Fig. 1). The topography of Baker is more complex. This watershed contains several deeply incised stream channels that separate a number of small topographic facets. Locally, plant associations occur on different topographic facets within the sampled watersheds. In the northern watersheds (Tucannon and Imnaha), most mesic forests occur on northerly and easterly slopes, while dry forests occur primarily on southerly and westerly slopes. At Baker, mesic forests occur above ~1500 m, while dry forests are found below ~1700 m. At the transition, forest types interfinger, with mesic forests limited to northerly and easterly slopes. At Dugout, dry forests occur on all aspects and at all elevations, but mesic forests are not present in the sampled portion of this watershed.

METHODS

Sampling scales

We examined historical fire regimes at regional and local scales in four watersheds distributed along 250 km of latitude in the Malheur, Wallowa-Whitman, and Umatilla National Forests (Fig. 1). In minimally harvested portions of each watershed, we selected a ~1620-ha sampling area to represent the range of topographic settings within that watershed. Each sam-

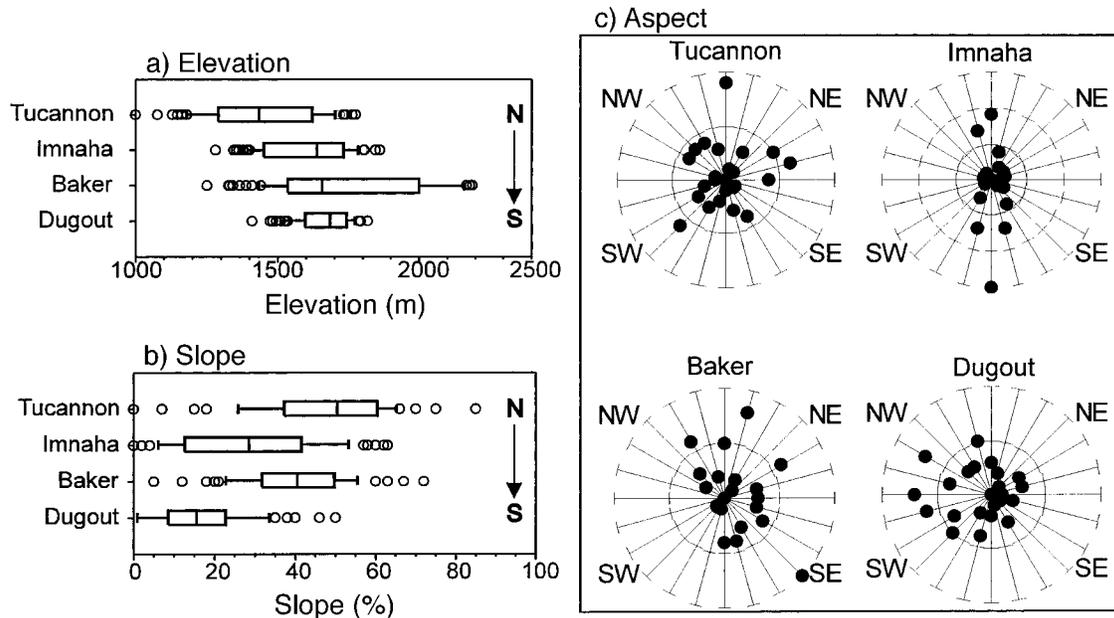


FIG. 2. Topographic distribution of sampled plots at the four watersheds. Aspect scale is from 0 plots at the center to 10 plots at the outside, except at Imnaha, where the outside is 15 plots.

pling area was divided into a grid of 64 cells (~25 ha each), and a ~1-ha plot was sampled near the center of each cell. Because many of the reconstructed fires intersected the boundaries of these sampling areas, we sampled an additional 10–19 plots, at a lower density, outside the grid in each watershed in order to reconstruct the size of large fires. This increased the size of the sampling areas to 2914–8585 ha (Table 2). To assess *regional* variation in fire regimes as indicators of top-down control, we compared fire frequency, size, and season in similar plant associations (dry forest) among the four sampled watersheds. To assess *local* variation in fire regimes within each watershed as indicators of bottom-up control, we compared fire frequency and severity in all plant associations (both mesic and dry forest) across the range of topographic settings present in each watershed.

Topography and forest composition

At each plot, we measured slope, aspect, elevation, latitude, and longitude. We also visually estimated the percentage cover of grass, forb, shrub, and tree species, and used this information with existing local keys to assign each plot to a plant association (Johnson and Simon 1987, Johnson and Clausnitzer 1992).

To evaluate the degree to which the topography of the sampled plots represents that of the Blue Mountains as a whole, we graphically compared the topography measured in the plots (elevation, aspect, and slope) to that of the Blue Mountains, derived from a digital elevation model (DEM, 90-m resolution). We categorized each topographic characteristic and computed the percentage of plots and land area for each category, as well as for all possible combinations of categories. We

TABLE 2. Size of sampling areas (18 904 ha total) and amount of fire evidence collected.

Watershed	Sampled area (ha)		Number of trees			Fire scar record		
	Mesic forest	Dry forest	Age cohort	Fire scar	No. Fire scars	Potential evidence of fire	Earliest year	Earliest reliable year
Tucannon	912	2 002	334	86	382	27	1487	1639
Imnaha	860	2 095	282	109	517	55	1480	1687
Baker	638	3 812	286	114	1258	104	1403	1646
Dugout	0	8 585	0	215	2156	130	1346	1629
Total	2410	16 494	902	524	4313	316		

Notes: In the column labeled “potential evidence of fire” we report the number of trees with abrupt increases or decreases in ring width. Earliest years are dates of first rings found at each watershed, while earliest reliable year is the first year for which at least 30% of plots with fire scars were susceptible to scarring. Numbers of trees are for the entire period of record. About half of the trees (55%) from which fire-scarred sections were removed were stumps, logs, or snags and more than one section was removed from roughly one-third of these.

eliminated area below 600 m and above 2500 m from the DEM (7% of total area) to restrict the comparison to areas likely to be forested (Johnson and Simon 1987). We compared the topographic distribution of the sampled plots to the distribution of land area derived from the DEM.

To evaluate the degree to which the forests of the sampled plots represent those of the Blue Mountains as a whole, we compared the current overstory composition of the plots we sampled to an assessment of the recent forest composition of the region, based on satellite imagery (Loveland et al. 1991, Burgan et al. 1997). For the satellite assessment, forests were assigned to one of eight categories, based on the overstory species that currently dominates: ponderosa pine, grand fir, Douglas-fir, lodgepole pine, western juniper (*Juniperus occidentalis* Hook.), aspen (*Populus tremuloides* Michx.), whitebark pine (*Pinus albicaulis* Engelm.), or a combined category for Englemann spruce (*Picea engelmannii* Parry ex Engelm.) and subalpine fir. We assigned each sampled plot to these same categories, based on the tree species currently dominating the plot, and compared the distribution of forest types of the sampled plots to the distribution of land area derived from the satellite data.

Evidence of fire

The type of evidence we used to reconstruct fire regimes varied among plots, depending on the severity of past fires. We used fire scars in stands that sustained low-severity fire regimes. Such fires can kill a portion of the cambium (McBride 1983). In subsequent years, new cambial cells grow over the damaged surface, forming fire scars, which we identified as a discontinuity, or gap in cells, within a ring or along a ring boundary followed by overlapping, curled rings. Low-severity fires can also cause abrupt increases or decreases in the width of annual rings following fire (Landsberg et al. 1984, Sutherland et al. 1991). However, because other factors can also cause abrupt changes in cambial growth (Brubaker 1978), we used such changes in a given sample as evidence of a low-severity fire only when it coincided with a fire scar in other samples. We used cohorts of early seral trees (western larch (*Larix occidentalis* Nutt.) and/or lodgepole pine) as evidence of fire in stands that sustained high- and moderate-severity fire regimes. High-severity fires kill most overstory trees in a stand while moderate-severity fires kill only a portion of overstory trees. The death of these trees creates openings for a cohort of early seral, shade-intolerant trees whose date of establishment approximates the year of the fire (Oliver and Larson 1990). Fires spread contiguously from a point of ignition so that postfire cohorts occur as patches of similarly aged trees, although these patches can overlap spatially, because moderate-severity fires do not kill all trees in a stand. In areas where such patches overlap, trees of different ages are present in the same stand.

Fire scars.—In plots containing fire-scarred trees, we used a chain saw to remove scarred sections from a mean of three of those stumps, short snags, logs, or living trees with the greatest number of well-preserved scars (range of 1–8 trees; Arno and Sneek 1977). We included scarred sections from four trees previously sampled in a 1-ha plot at Imnaha (Maruoka 1994). All sections were sanded until the cell structure was visible with a binocular microscope. We assigned calendar years to tree rings using a combination of visual cross-dating of ring widths and cross-correlation of measured ring-width series (Holmes 1983, Swetnam et al. 1985, Swetnam et al. 1995). Approximately 4% of the sections could not be crossdated and were excluded from further analyses.

To determine the calendar year of fire occurrence, we noted the year in which each scar formed. We also noted the position of the scar within the ring (earlywood, latewood, ring boundary, or unknown) as an indication of the season during which the fire burned. The season of cambial dormancy (i.e., the period represented by the ring boundary) spans two calendar years, from the time the cambium stops growing in the summer of one year until it resumes in the spring of the following year. For this study, we generally assigned ring-boundary scars to the *preceding* calendar year, because most modern fires in the Blue Mountains occur in the summer or fall (Avalos 1998), and there is no evidence in the past few centuries of changes in the seasonal timing of precipitation that might affect the seasonality of fire (Graumlich 1987). However, scars from a given fire can have a range of intra-annual positions because the timing of radial growth varies across the landscape (Fritts 1976) and because fires may burn for several months (Parsons and van Wagtendonk 1996). For four fires in our study, scars occurred in the earlywood of many trees but on the preceding ring boundary of some. We inferred that the scars in both positions were created by a single fire burning early in the growing season and therefore assigned the ring-boundary scars (34 scars) to the *following* calendar year, i.e., the same year as the earlywood scars. Scar position could not always be determined because rings are narrow, especially in the vicinity of scars, or because rot or insect galleries obscured scars.

The dates of fire scars and abrupt growth changes from all samples at a plot were combined into a single record of fire occurrence for that plot (~1 ha, Dieterich 1980). General features of fire frequency and size in each watershed were assessed using fire charts in which time lines represent composite fire histories for all the trees sampled in a plot, and crossbars on the time lines identify years with evidence of fire (Dieterich 1980, Grissino-Mayer 1995). We used the fire charts to visually assess three types of variation in fire regimes. First, we assessed variation in fire frequency through time by observing changes in the frequency of years

with evidence of fire (crossbars) *along* lines in the fire charts. Second, we assessed variation in fire frequency across space by observing variation in the frequency of fire evidence *among* lines. Third, we assessed changes in fire size by observing the number of plots (lines) with evidence of fire during the same year. For example, fires were larger during years when many plots showed evidence of fire than during years when only a few plots had such evidence.

Postfire cohorts.—In plots where cohorts of early seral species were present (western larch and/or lodgepole pine), we removed increment cores from 5 to 10 of the largest diameter living trees to determine establishment dates. Many plots had more than one size class of such trees. At these plots, we cored the largest individuals in each class. Trees were cored near the ground (mean height of 23 cm). We mounted the cores on wooden holders and sanded and crossdated them using the methods employed for fire-scarred sections. Those that did not crossdate (5%) were excluded from further analyses. To estimate establishment dates from the date of the innermost ring sampled, we applied one, and sometimes two corrections. First, for cores that did not intersect the pith (60%), we estimated the number of rings to the pith, based on the curvature of the innermost rings sampled (mean correction, 4 yr; Applequist 1958, Duncan 1989). Second, to account for the number of years it took for the tree to reach coring height, we subtracted one calendar year from the pith date for every 5 cm between ground level and coring height, based on a previous analysis of early height growth in the Blue Mountains (Maruoka 1994).

We identified postfire cohorts from the establishment dates and locations of cored trees using spatial autocorrelation and cluster analyses (Duncan and Stewart 1991). The estimated establishment dates of trees in postfire cohorts are not identical, because tree-ring determinations of such dates are not exact, and trees may establish in fire-created openings over a period of years (Oliver and Larsen 1990). Furthermore, moderate-severity fires kill only a portion of the trees in a stand so that trees from more than one postfire cohort sometimes coexist at a single plot. As a result, the structural legacy of an individual fire is not always obvious on air photos (Arno et al. 1995). To accommodate the range of establishment dates within individual cohorts and the potential spatial overlap of some cohorts, we statistically tested the establishment dates in each watershed for the presence of similarly aged patches of trees, using Moran's *I* as a measure of spatial autocorrelation (Legendre and Fortin 1989). An all-directional correlogram of Moran's *I* was constructed for 8–10 distance classes (500 m each) and tested for significance ($P < 0.01$) using a Bonferroni corrected significance level that accounts for multiple tests (P /number of distance classes; Oden 1984). The general shape of the correlogram indicates the spatial arrangement of tree ages within a watershed (Legendre and

Fortin 1989). Significant positive autocorrelation in short distance classes indicates that trees that are near one another are similar in age, while significant negative autocorrelation in long distance classes indicates that trees that are far apart are different in age. In combination, these two features indicate the presence of patches of similarly aged trees with differences in age among the patches, i.e., the presence of cohorts. Because a given postfire cohort includes a range of establishment dates, cohorts are identifiable only if the fires that created them are sufficiently separated in time or in space for clusters of similarly aged trees to be distinguishable. Therefore, failure to detect cohorts does not necessarily imply the absence of similarly aged patches of trees or a lack of fire, especially where early seral species are abundant. Rather, it may imply that fires occurred too frequently, or were too small and close together to be detectable from the ages and locations of trees in postfire cohorts.

In watersheds for which spatial autocorrelation indicated the presence of cohorts, we identified the trees belonging to individual cohorts by clustering trees based on their age and location (Gordon 1981, Duncan and Stewart 1991). We selected a level of similarity among trees that minimized both the number of cohorts and the range of establishment dates within those cohorts (roughly, less than 40 yr). We mapped the cohorts identified by clustering to verify that the trees in each cohort were in adjacent or nearly adjacent plots. Some of the cohorts established in similar years and were separated only by plots containing younger trees. For these cohorts, we assumed that a subsequent fire had killed the trees in the intervening plots, and so we combined them into a single cohort.

We used the establishment dates within each cohort to estimate the year of the fire that created the opening in which the cohort established. Initially, we assigned the earliest establishment date within each cohort as the year in which the fire occurred. When this initial estimate was similar to the year of an adjacent large, low-severity fire, we adjusted the year of occurrence so that it coincided with the year of the low-severity fire, because scar dates are more accurate than establishment dates (adjustments of 1–5 yr, mean of 3 yr). We assessed general features of the frequency and size of high- and moderate-severity fire regimes using fire charts, as described above for low-severity regimes.

Reconstructing fire regimes from evidence of fire

We reconstructed four parameters of fire regimes (frequency, season, size, and severity) from fire scars, abrupt changes in ring width, and the establishment dates of cohorts. We selected the period during which at least 30% of the plots within a watershed *could* show evidence of fire as the period with sufficient information to characterize fire regimes in that watershed. Plots could show evidence of fire if cohorts had established or the plots had trees that were susceptible to

scarring, i.e., had been previously scarred (Gill 1974, Romme 1980). *Frequency* was computed as the number of fire years for each plot (~1 ha), during the period with sufficient information that was common to all plots in the analysis, but before the period of dramatic land use change in the Blue Mountains (1687–1900 for dry forest plots, 1798–1900 for mesic forest plots). *Season* was determined for each scar as described above. *Size* was estimated within each watershed by mapping the evidence of fire for every year during which a cohort of early seral trees established and/or at least three trees were scarred. For each such year, we drew fire boundaries approximately halfway between plots with and without evidence of fire, or along a perennial stream, where present. Evidence of fire occurred in disjunct plots for some fire years (23%). For these years, if the evidence of fire was separated by more than three plots without evidence, or more than 1.5 km without a sampled plot, we assumed that more than one fire burned that year and so we drew separate fire boundaries around the disjunct groups of plots. During some fire years, the trees at some plots were too young to show evidence of fire, or the trees were not susceptible to scarring, and thus we considered these plots to be unsampled for that fire year. We truncated fire boundaries at the edges of the sampled areas. Fire size was computed as the area within each fire boundary. The fire boundaries we determined in this manner are similar to those we determined with automated methods that use Thiessen polygons and convex hulls. Fire sizes computed using these three methods were significantly and highly correlated at all watersheds ($r = 0.74\text{--}0.96$, $P < 0.01$, Heyerdahl 1997). *Severity* was inferred from the type of evidence of fire. Plots with fire scars historically sustained low-severity fire regimes, whereas plots with cohorts of early seral trees historically sustained fire regimes of moderate (>1 cohort), or high (a single cohort) severity.

Variation in fire regimes at regional and local scales

Temporal homogeneity of the record.—To ensure that the period chosen to characterize spatial variation in fire regimes was relatively homogeneous through time, we examined cumulative fire extent (annual area burned) and fire charts for evidence of centennial-scale changes in fire regimes. We computed a time series of cumulative extent as the running sum of annual area burned for the entire sampled area in each watershed from 1687 to 1994. If a similar extent burns with constant frequency, we would expect the time series of cumulative extent to be linear. We fit a regression line to this time series (1687–1900) using ordinary least squares, and checked for significant deviations from the regression line that would indicate long-term shifts in fire frequency, or the area burned per year. In addition, we visually examined the fire charts for each watershed for major shifts in fire frequency or size.

Regional variation (among watersheds) of fire re-

gimes in dry forest.—We assessed regional variation in fire regimes by comparing fire frequency, season, and size among the four sampled watersheds. Only the six dry forest plant associations were included in this analysis (Table 1). Regional variation in fire frequency was assessed using analysis of variance (ANOVA) to test whether mean frequency was the same for plots in all four watersheds. To meet the assumptions of ANOVA, we linearly transformed the number of fires per ~1-ha plot (1687–1900) using a monotonic function to normalize the sampled distribution and stabilize its variance (Eq. 2 with $\lambda = 0.5$ in Box and Cox 1964). Preliminary analysis showed no statistical interaction between watershed and plant association, indicating that within every watershed, fires were most frequent in ponderosa pine associations, least frequent in dry grand fir associations, and intermediate in those of Douglas-fir. Therefore, we pooled the plots in all dry forest plant associations within each watershed for the ANOVA. We conducted a post-ANOVA multiple range test to identify which watersheds had significantly different frequencies (Tukey's honestly significant difference, Zar 1984). Regional variation in fire season was assessed by comparing the distribution of scars by intra-annual position (earlywood, latewood or ring boundary) among watersheds. Regional variation in fire size was assessed by comparing the distribution of fires by size class among watersheds.

Local variation (within watersheds) of fire regimes in all forest types.—We assessed local variation in fire regimes separately within each watershed by correlating fire frequency with topographic variables, and examining the spatial patterns of fire severity with respect to topography. This analysis included all plant associations (both mesic and dry forest). We correlated the number of fires for each ~1-ha plot (1798–1900) with the elevation, aspect, and slope of that plot using a nonparametric test (Spearman rank correlation). Because aspect has an arbitrary zero (i.e., values near 0° are similar to those near 360°), we transformed it into a variable with low values for warm, dry aspects and high values for cool, moist aspects (0 on southwesterly slopes to 2 on northeasterly slopes; $A' = \cosine(45 - A) + 1$; Beers et al. 1966).

RESULTS

Topography and forest composition

The topography and vegetation of the 303 sampled plots are similar to that of the Blue Mountains as a whole. Most of the sampled plots and forested land area lie between 1000 and 2000 m, are distributed among all aspects, and have low to moderate slopes (<66% slope, Fig. 3a, b, c). No combinations of elevation, aspect, and slope were particularly over- or underrepresented in the sampled plots. The majority of plots and forested land area are currently dominated by ponderosa pine (~43%, Fig. 3d), Douglas-fir

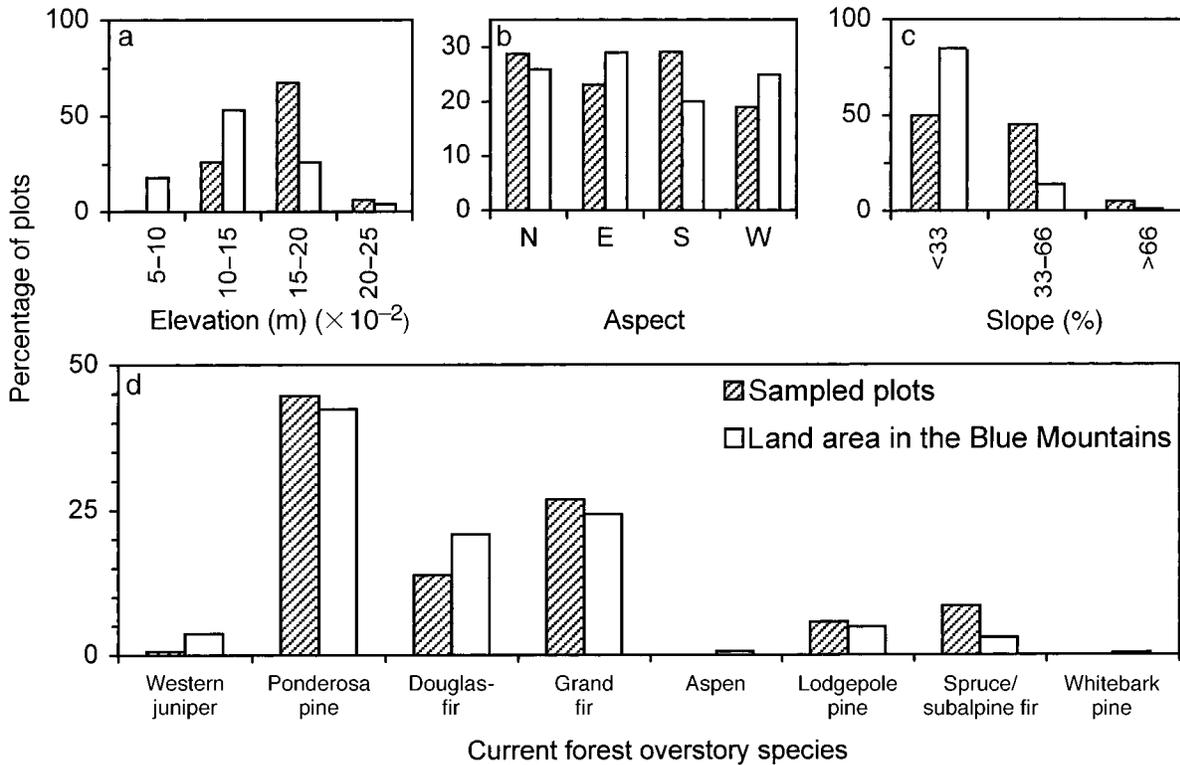


FIG. 3. Distribution by topography and current forest overstory for sampled plots and forested land in the Blue Mountains. Aspect classes are 90° wide, beginning with 46° for east (E). Land area for the Blue Mountains was derived from a digital elevation model for topography and from satellite data for current forest overstory. Note that elevations in panel (a) are given in hundreds of meters.

(~17%) or grand fir (~26%). Lodgepole pine, western juniper, and Englemann spruce/subalpine fir comprise most of the remaining plots and land area. Aspen or whitebark pine dominate a small area of the Blue Mountains (<1%), but none of the sampled plots are currently dominated by these species.

Evidence of fire

Trees with visible scars were present in all plots at Dugout, but in less than half the plots at Tucannon (38%), Imnaha (46%) and Baker (49%, Table 1). Almost all plots with fire-scarred trees were in dry forest plant associations (98%). We collected fire scars from 524 trees, most of which were ponderosa pine (98%), and half of which were dead when sampled (55%). Fire regimes can be reliably reconstructed from fire scars (i.e., 30% of plots in a watershed had trees that had been previously scarred) during the period 1687–1994 among all watersheds (Table 2). Within this period, 3659 fire scars and 261 abrupt changes in ring width corresponded to 121 separate calendar years (32–65 yr per watershed). During the majority of fire years at each watershed (77%), we reconstructed only a single fire. We were able to assign an intra-annual position to most of the scars (73%).

The establishment dates of early seral trees were an-

alyzed at Tucannon, Imnaha, and Baker, but not at Dugout, because western larch and lodgepole pine were not common in the sampled area in this watershed. Most plots with early seral trees were in mesic forest plant associations (88%, Table 1). At Tucannon and Imnaha, the northern watersheds, we estimated 616 establishment dates from roughly equal numbers of western larch and lodgepole pine trees (Table 2). The general shape of the correlograms indicate that trees within each watershed occur in similarly aged patches (Fig. 4). Namely, tree ages were significantly autocorrelated, both positively at short distances and negatively at long distances. The establishment dates clustered into four cohorts in both watersheds. Each cohort includes 16–192 trees (mean of 66) whose establishment dates differ by 14–42 yr (mean of 30). There is no temporal overlap in the establishment dates of trees assigned to different cohorts within either watershed, although some cohorts overlap spatially. The earliest establishment date within most cohorts is similar to the date of an adjacent low-severity fire. Therefore, we assigned the year of the low-severity fire as the year for the moderate- or high-severity fire that created the cohort (1774, 1888 at Tucannon; 1798, 1834, 1886 at Imnaha). Moderate-severity fires were less common at Tucannon than at Imnaha. At Tucannon, only a third of plots (33%) had

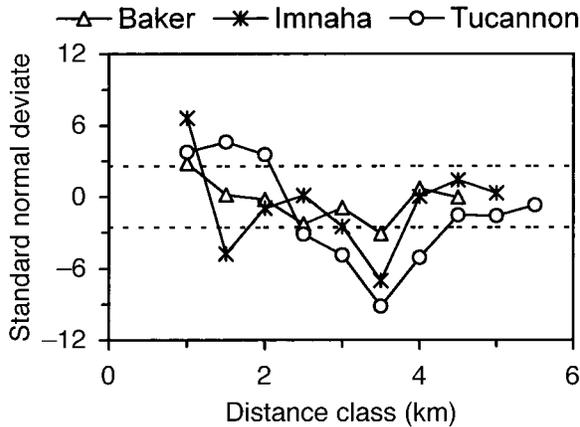


FIG. 4. Spatial correlogram of tree ages in mesic forests by watershed. The standard normal deviate of Moran's I is plotted. Values falling outside the envelope of the dotted lines are significant at the Bonferroni corrected level. Mesic forests did not occur at Dugout.

more than one cohort (Fig. 5a), whereas half the plots (52%) at Imnaha contained two or three cohorts (Fig. 5b). At Baker, in the south, we estimated 286 establishment dates from roughly equal numbers of western larch and lodgepole pine trees. However, unlike the northern watersheds, these establishment dates were not spatially autocorrelated in any distance class (Fig. 4), indicating that we could not detect similarly aged patches of trees and, consequently, could not identify postfire cohorts at this watershed. In light of the abundance of early seral trees in this watershed, the lack of identifiable cohorts does not imply that fires did not burn in the mesic forests in this watershed. Rather, moderate-severity fires probably burned frequently enough that the difference in establishment dates among the resulting cohorts is not detectable.

Variation in fire regimes at regional and local scales

Temporal homogeneity of the record.—There were no substantial centennial-scale changes in the reconstructed fire regimes before ~1900. Cumulative fire extent fit a straight line ($r_a^2 = 0.97-0.99$) from 1687 to 1900 in each watershed (Fig. 6). This lack of major shifts in fire regimes prior to 1900 is generally confirmed by a lack of major changes in fire frequency and size as shown by the fire charts, although there were fewer small fires at Dugout in the 1800s than before this time (Fig. 7). The decadal-scale variations obvious during this period in the fire charts and the plot of cumulative fire extent are likely due to temporal variation in precipitation (Heyerdahl 1997). The fire regimes in all four watersheds underwent a major shift ~1900. Only a few small fires burned in any of the watersheds after this time (Fig. 7). Consequently, we only analyzed spatial variation in fire regimes prior to 1900.

Regional variation (among watersheds) of fire re-

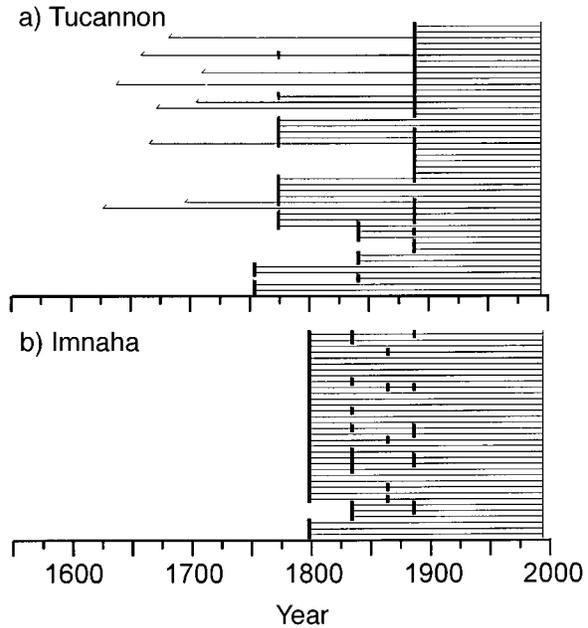


FIG. 5. Fire chart for mesic forest plots at Tucannon and Imnaha. Each horizontal line shows the composite tree-ring record at a single plot (~1 ha) through time. For each watershed, the lines are arranged roughly north (top) to south (bottom). Short vertical lines indicate the year of a fire, estimated from postfire cohorts of early seral species.

gimes in dry forest.—1. *Fire frequency.*—Fire frequency was significantly different among watersheds ($P < 0.01$), with fires more than twice as frequent at plots in the southern watersheds than in the northern watersheds (Fig. 8a). Plots to the south at Dugout and Baker experienced 15 and 13 fires on average (1687–

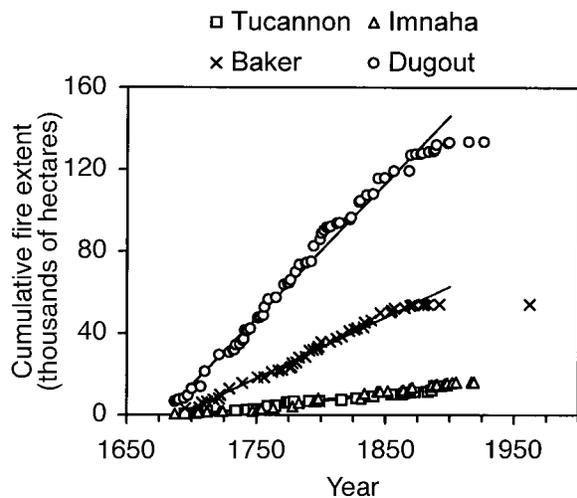


FIG. 6. Cumulative fire extent by watershed. Regression lines were determined using ordinary least squares from 1687 to 1900 ($r_a^2 = 0.97-0.99$). The slopes of the lines are partially dependent on sampling area size, which is not the same for all watersheds (Table 2).

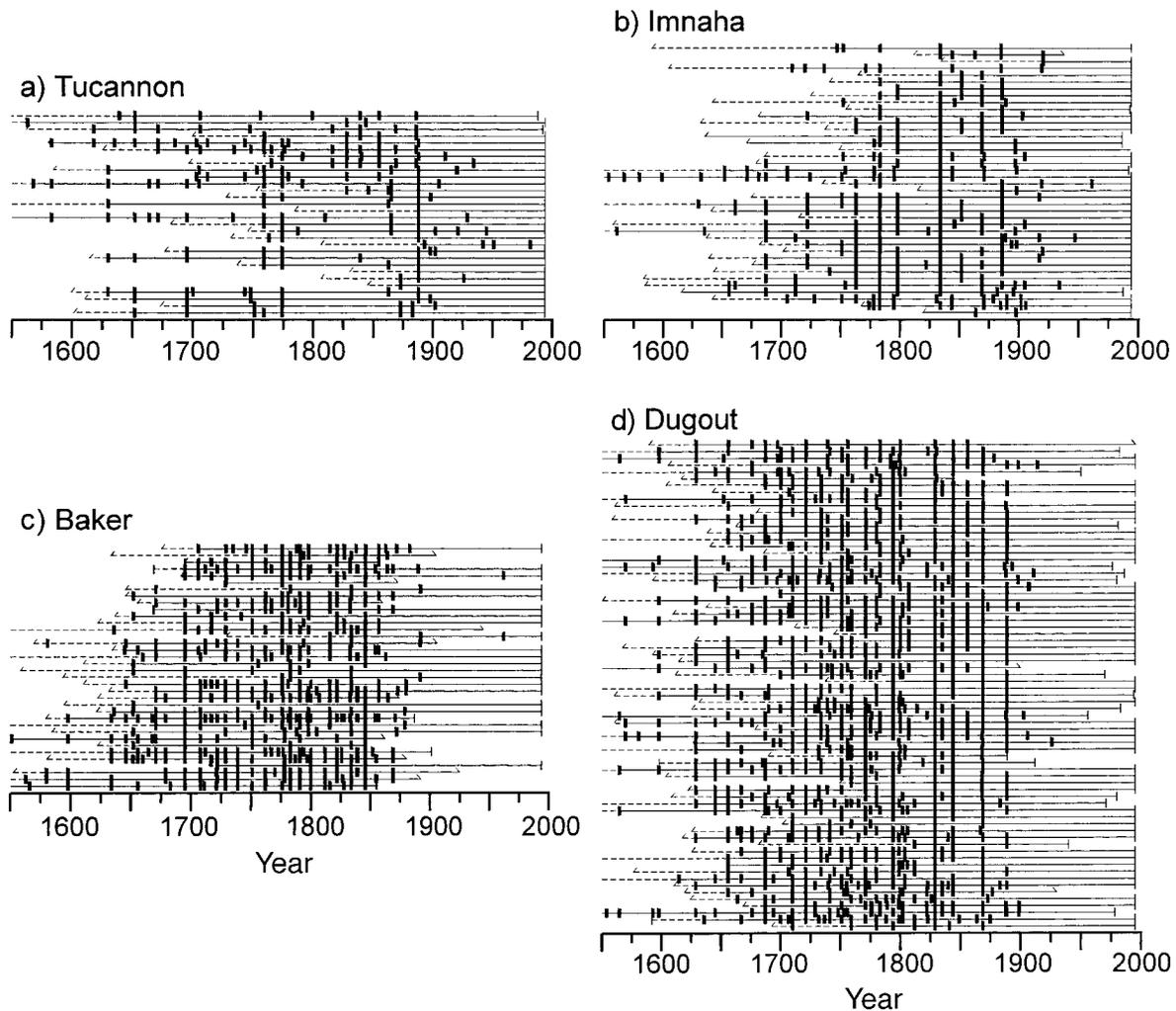


FIG. 7. Fire chart for dry forest plots at the northern (Tucannon and Imnaha) and southern (Baker and Dugout) watersheds. Each horizontal line shows the composite fire-scar record at a single sampling plot (~ 1 ha) through time. For each watershed, the lines are arranged roughly north (top) to south (bottom). A fire may have scarred more than one tree per plot. Vertical bars mark fire years. Dashed horizontal lines indicate years that preceded formation of the first scar on samples from that plot. Fine vertical lines at the beginning and end of each chronology mark pith or bark dates, while fine diagonal lines mark the earliest or latest ring dates for plots where pith or bark dates were not sampled.

1900), whereas plots to the north at Tucannon and Imnaha experienced only six. Furthermore, fire frequency differed between all pairs of watersheds except Baker and Dugout. Fire frequency varied more strongly with the location of a watershed (north vs. south, Fig. 8a) than with forest type (Fig. 8b). For example, at Dugout, in the south, a similar number of fires burned per plot in Douglas-fir and grand fir associations (~ 15), but less than half that number burned at plots in the same associations at Imnaha, in the north (7 and 3, respectively, Fig. 8c).

2. *Fire season*.—More fires burned during the growing season in the southern watersheds than in the northern watersheds (Fig. 9). Nearly half the scars (48%) formed in the early- or latewood in the south (Baker and Dugout), whereas only a few scars (8%) occurred

in these positions in the north (Tucannon and Imnaha). Furthermore, only the southern watersheds had years in which a majority of the scars occurred in the early- or latewood (12 fire years at Dugout and 9 fire years at Baker).

3. *Fire size*.—Most fires were small relative to the size of the sampled area (Fig. 10). Roughly half the fires at each watershed burned less than $\sim 10\%$ of the sampled area (< 296 ha at Tucannon and Imnaha, < 381 ha at Baker, and < 859 ha at Dugout). Nevertheless, large areas burned in some years. At Imnaha, Baker, and Dugout, the entire sampled area burned during at least one year, and at Tucannon, 70% of the sampled area burned during one year. During some fire years (23%, mostly at Dugout), the evidence of fire within a watershed was disjunct, so that we identified more than

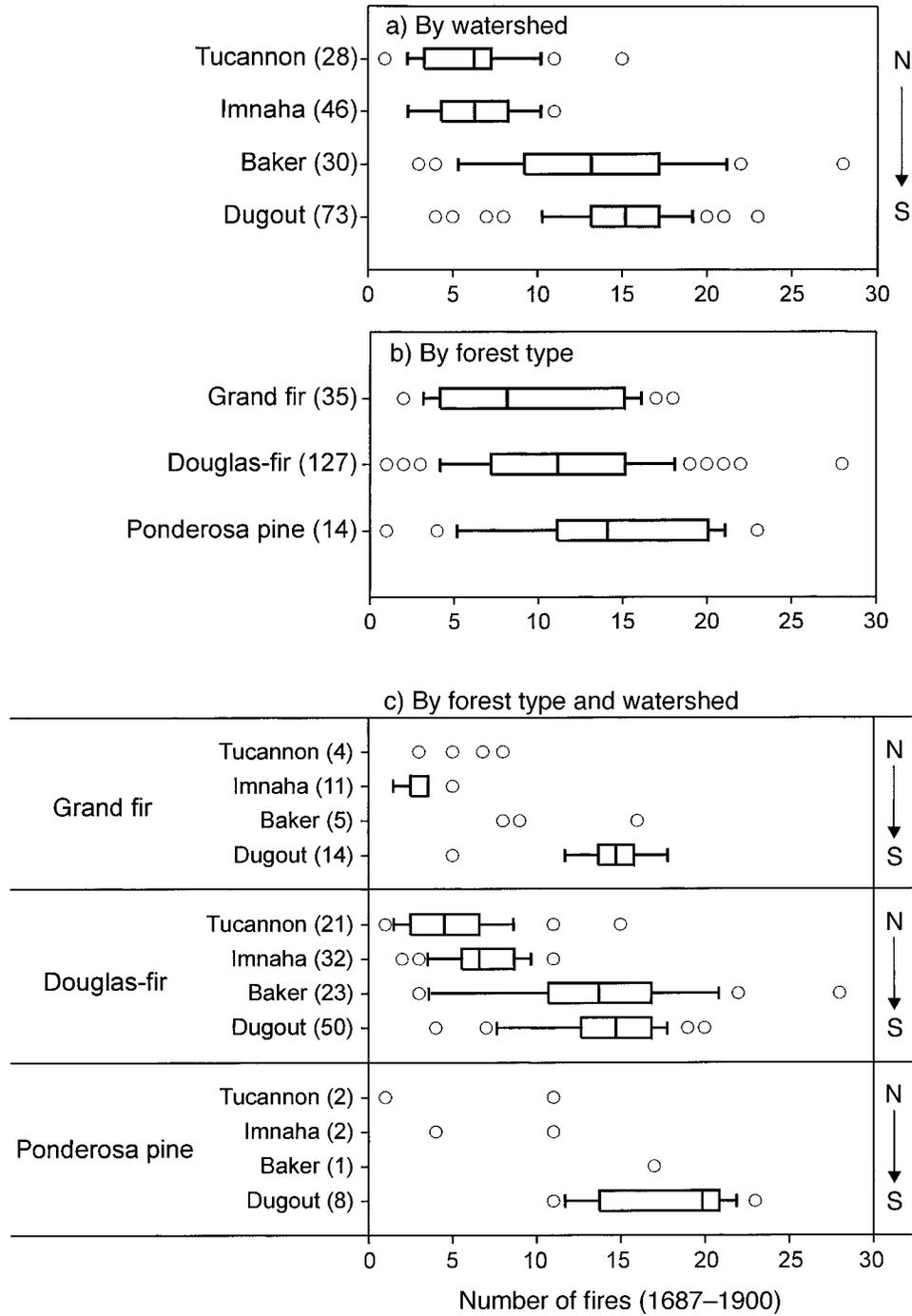


FIG. 8. Regional variation in fire frequency in dry forest (1687–1900). Frequency was computed for each plot (~1 ha) in the pinegrass and elk sedge associations of the grand fir, Douglas-fir, and ponderosa pine series. The boxes enclose the 25th to 75th percentiles; the whiskers enclose the 10th to 90th percentiles of the distribution of number of fires per plot. The vertical line across each box indicates the median, and all values falling outside the 10th to 90th percentiles are shown as circles. Where fewer than six plots were sampled in a forest type at a watershed, the number of fires is indicated by circles for all the plots that were sampled.

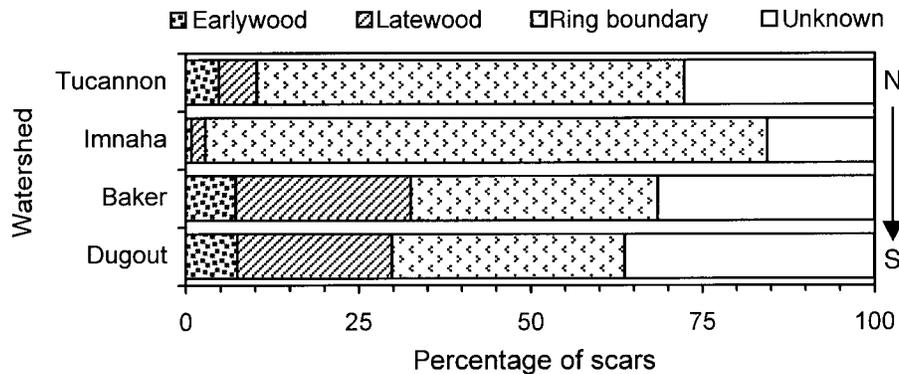


FIG. 9. Regional variation in fire season in dry forest (1687–1900). Intra-annular position of scars is shown as a percentage of total scars at each watershed.

one fire during a given year. In all watersheds, fire boundaries during most fire years (82%) intersected the edge of the sampled area, suggesting that the actual size of individual fires was larger than those we reconstructed. Although the general shape of the fire size distribution did not vary regionally, there were somewhat fewer large fires in the northern watersheds than in the southern watersheds (Fig. 10).

Local variation (within watersheds) of fire regimes in dry and mesic forest.—1. *Fire frequency.*—Frequency per plot varied with different parameters of topography (aspect, elevation, and slope) in each wa-

tershed (Fig. 11). Aspect was significantly correlated with frequency at Tucannon and Imnaha ($r = -0.56$ and -0.50 , respectively; $P < 0.01$), but not at Baker or Dugout. Fires were more frequent on southwesterly slopes than on northeasterly slopes at Tucannon (mean of 2 vs. 1 fires, 1798–1900) and Imnaha (3 vs. 2 fires). Elevation was significantly correlated with frequency at Tucannon and Baker ($r = -0.50$ and -0.59 , respectively; $P < 0.01$) but not at Imnaha or Dugout. Frequency was negatively correlated with elevation at Tucannon, indicating that fires were more frequent at low elevation than at high elevation, however, this re-

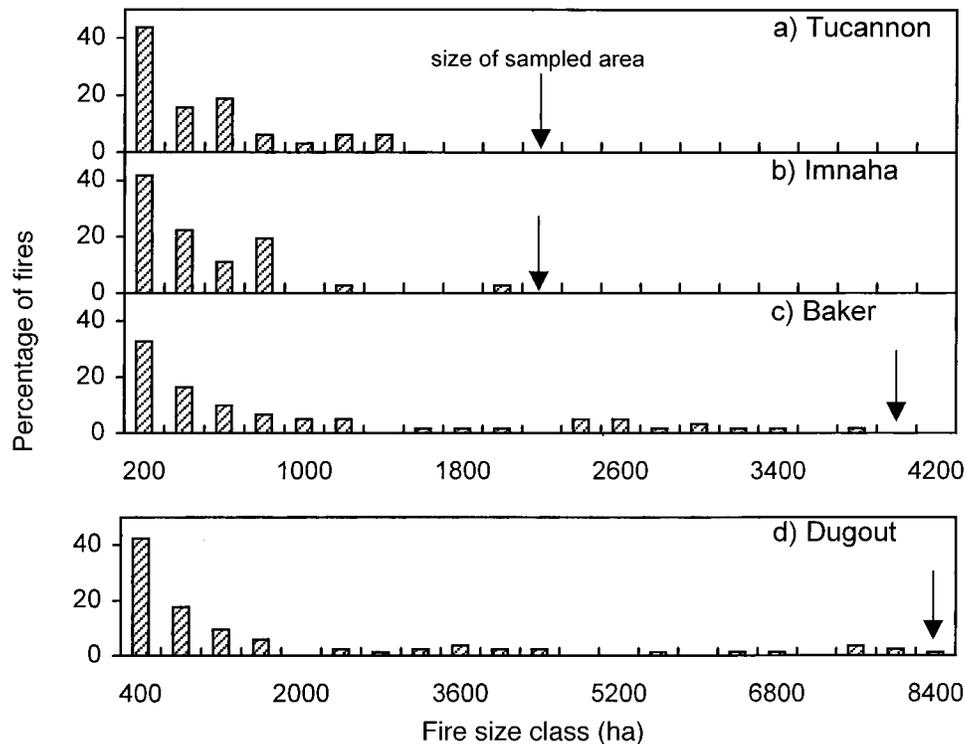


FIG. 10. Regional variation in fire size in dry forest (1687–1900). Size classes for Dugout are twice as large as the classes for the other three watersheds. The sizes of the sampling areas are indicated by arrows.

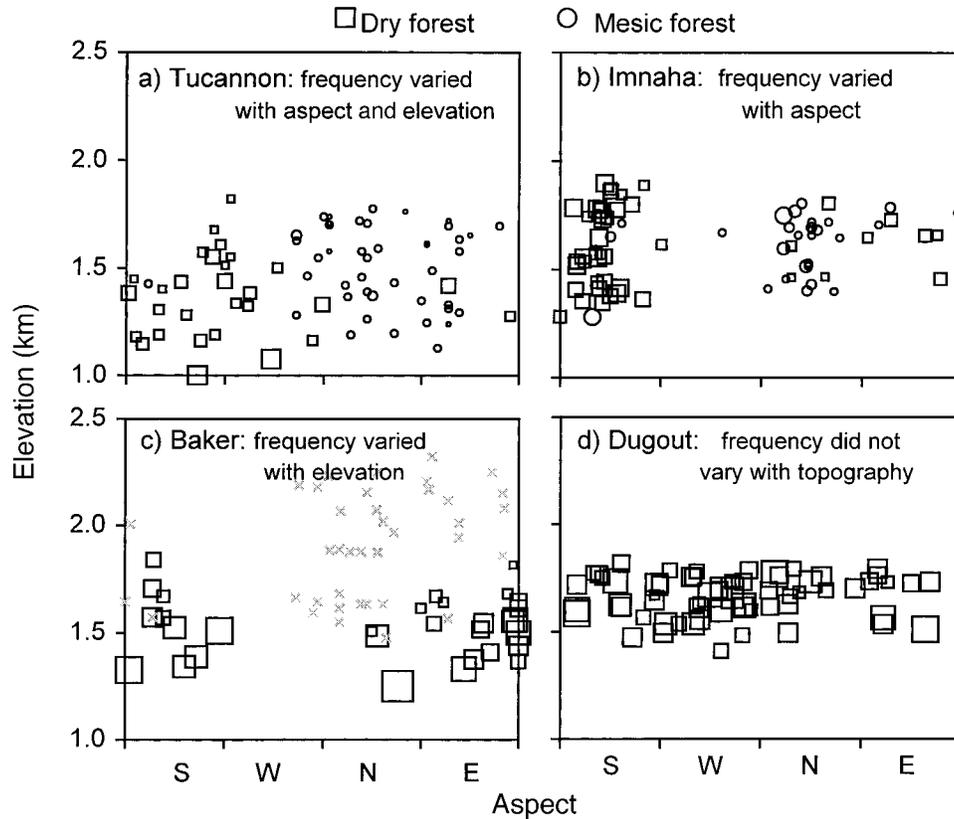


FIG. 11. Local variation in fire frequency in dry and mesic forest (1798–1900). Frequency was computed for each plot (~1 ha). The size of the symbols is proportional to the number of fires, with the smallest symbol representing no fires, and the largest representing 10 fires. At Baker, fire frequency could not be reconstructed from age cohorts, but gray x's of moderate size are plotted to show the topographic distribution of mesic forests at this watershed. Mesic forests were not found in the sampled area at Dugout.

relationship is only significant for dry forest plots. Fire frequency is not significantly correlated with elevation in mesic forests at this watershed. At Baker, fires were also more frequent at low elevations than at high elevations. Plots below 1545 m sustained a mean of 6 fires, plots above this sustained a mean of 4. Slope was not significantly correlated with fire frequency in any of the watersheds.

2. *Fire severity.*—Fire severity varied with topography and forest type at most watersheds. Severity varied with aspect at Tucannon and Imnaha, and with aspect and elevation at Baker, but did not vary at Dugout or with slope at any of the watersheds. At Tucannon and Imnaha, most plots (80–93%) with moderate- and high-severity fire regimes occur on north and east aspects, while most plots (86%) with low-severity regimes are on south and west aspects. At Baker, plots with low-severity fires occur on all sampled aspects but most (96%) are limited to low elevations (<1700 m), while most mesic plots (96%) occur above this elevation. Among the four watersheds, most mesic forest plots (96%) had obvious cohorts of early seral trees, implying that mesic forests historically sustained mod-

erate- or high-severity fire regimes. In contrast, most dry forest plots (92%) contained fire scars, implying that these forests historically sustained low-severity fire regimes.

DISCUSSION

Fire frequency varied both regionally and locally

Regional variation implies top-down controls.—Within dry forest types, fires burned more frequently in the southern than in the northern watersheds (Fig. 8). Latitudinal variations in summer precipitation, snow-cover duration, and perhaps, lightning strikes across the Blue Mountains are consistent with this regional variation in frequency, suggesting that frequency is at least partly controlled by top-down processes. These latitudinal variations in climate probably all contributed to lower fuel moisture contents and a higher probability that fires would ignite in the south than in the north. Lower summer precipitation to the south probably resulted in a similar regional gradient in fuel moisture (Schroeder and Buck 1970, Blackmarr 1972, Rothermel 1983) so that fires were more likely to ignite

and spread in the southern than in the northern watersheds. Similarly, the shorter snow-cover duration to the south probably resulted in longer periods during which fuels were sufficiently dry for fires to ignite and spread. Lastly, summer lightning strikes may have been more frequent in the southern than in the northern portion of the study area, which would have caused fires to ignite more frequently to the south. Our results may suggest that there was also a regional gradient in fire frequency in mesic forests. We were able to identify distinct cohorts of early seral trees in mesic forests at the northern watersheds, but not in mesic forests to the south at Baker. The lack of distinct cohorts at Baker is probably the result of fires occurring so frequently that the resulting postfire cohorts overlap in age, and are thus indistinguishable. This higher frequency in the south is consistent with the regional gradient in dry forest fire frequency and with the gradient in climate.

In addition to regional gradients in climate, variation in landforms across the Blue Mountains may also have contributed to the pattern of fire frequency by consistently facilitating or inhibiting the spread of individual fires (Swanson et al. 1988, Agee 1993, Swetnam and Baisan 1996). Both northern watersheds, Tucannon and Imnaha, are embedded in complex terrain where rivers, ridges, and barren rocky slopes interrupt the continuity of surface fuels, and may have limited fire spread and occurrence. In contrast, to the south, Dugout lies in an area of gentle topography and Baker is at the edge of a broad, flat valley. Consequently, fires that ignited outside the sampled watersheds may have spread more readily into the southern than into the northern watersheds, resulting in more frequent fires to the south.

In the Blue Mountains, forest composition and fire regimes are both driven partly by top-down processes such as climate. Spatial variation in the composition of mid- to late-successional forests in this region is strongly controlled by growing season temperature and precipitation (Ohmann and Spies 1998), while fire frequency varied with precipitation, lightning and snow-cover duration. However, forest composition and fire frequency did not vary at the same spatial scales, indicating that vegetation types occur over a range of environmental conditions that, while they produce forests of similar composition, cause variation in fire regimes. It also indicates that fire was not a primary driver of spatial variation in vegetation. This difference in the spatial scales of variation of vegetation and fire reinforce the idea that to understand the controls of fire regimes, we must reconstruct those regimes on the same scales at which the controls operated, which in the case of fire regimes in the Blue Mountains was climate rather than forest type (Ricklefs 1987, Urban et al. 1987, Wiens 1989, Allen and Hoekstra 1991, Levin 1992, Lertzman and Fall 1998).

Local variation implies bottom-up controls.—Fire frequency varied with topography within most watersheds, suggesting that there are bottom-up as well as

top-down controls of this parameter of fire regimes. These bottom-up controls include a combination of direct and indirect influences of topography on fuels. Frequency varied with different parameters of topography (aspect and/or elevation) in most of the sampled watersheds, indicating that we cannot understand local-scale spatial patterns in fire frequency solely by identifying the characteristics of individual topographic facets. To understand such patterns, we must also consider the size, juxtaposition, and fire barriers between topographic facets, because the influence of topography on fire regimes is not independent of the landscape matrix in which it is embedded (Heinselman 1973, Grimm 1984, Agee et al. 1990, Bergeron 1991).

1. *Aspect.*—Fire frequency varied with aspect in the two watersheds (Tucannon and Imnaha) that have large areas of differing aspects (northerly vs. southerly) separated by wide fire barriers. The difference in aspect between the topographic facets at these watersheds probably contributed to local variation in frequency directly by affecting fuel moisture, and indirectly by affecting fuel type. At the beginning of the fire season, steep slopes with south and west aspects are free of snow earlier in the year because they receive more direct solar energy and consequently have longer periods with dry, combustible fuels than do north and east aspects. Later in the fire season, aspect affects fuel moisture by controlling the input of direct solar radiation, which heats fuels and hence lowers fuel moisture (Hayes 1941, 1942, Countryman 1978). Forest type, hence fuel amount and arrangement, also varies with topography in these steep, topographically simple watersheds. Northerly slopes at Tucannon and Imnaha generally support Douglas-fir and grand fir forests that generate compact short-needled fuels which can inhibit fire spread (Agee et al. 1978). In contrast, southerly slopes generally support ponderosa pine forests that generate long-needled, well-aerated grassy surface fuels that facilitate the spread of surface fires (Agee et al. 1978). These local, topographically driven variations in fuel condition and type are consistent with the patterns of fire frequency we observed at Tucannon and Imnaha, where fires were more frequent on south and west aspects than on north and east aspects. In addition, the northerly and southerly slopes at these watersheds are separated by rivers that appear to have inhibited the spread of fires between them. In contrast, fire frequency did not vary with aspect at Baker. The influence of aspect on fire regimes at this watershed was modified by the size and arrangement of its topographic facets. Slopes of differing aspects interfinger at fine scales in the highly dissected terrain at Baker and are not separated by fire barriers, as they are at the northern watersheds (Fig. 1). Consequently, fires readily spread between facets, resulting in little variation of frequency with aspect. At Dugout, fire frequency did not vary with aspect, because the gentle slopes of this watershed result in only small differences in microclimate and

forest type among topographic facets. The input of solar energy does not vary much across space in gentle terrain at this latitude. For example, gentle northerly slopes characteristic of those at Dugout (17%) receive nearly as much solar energy (80%) as southerly ones. The lack of variation in fire frequency at Dugout is consistent with other studies in gentle terrain where historical fire regimes also did not vary with aspect or elevation (Engelmark 1987).

2. *Elevation.*—Elevation was correlated with fire frequency at Baker and on southerly slopes at Tucannon, with fires less frequent at high elevation (Fig. 11). Similar to the influence of aspect on fire frequency, elevation probably directly influenced frequency by affecting fuel moisture, and indirectly by affecting fuel type. Fuel moisture generally increases with elevation during the fire season (e.g., Hayes 1941, 1942). However, the range of elevation of most plots in the sampled watersheds is probably not large enough to cause summer fuel moisture gradients that would inhibit the spread of fires (Fig. 2a). Fuel type also varies with elevation. At Baker, the fuel beds of low-elevation ponderosa pine forests facilitate fire spread, in contrast with those of high-elevation forests of grand fir and Douglas-fir which inhibit fire spread, as discussed above. Frequency may also vary with elevation at this watershed due to variation in the effect of temperature on snow-cover duration. At this watershed, the gradient in temperature with elevation probably causes snow cover to melt sooner at low elevations than high elevations, resulting in a longer fire season at low elevations. This effect of temperature on snow-cover duration is most pronounced on northerly and easterly slopes where direct solar radiation is less important for melting snow than it is on southerly or westerly slopes. Consequently, we see this effect most strongly at Baker where north and east aspects dominate. At Tucannon, surface fuels are not continuous on the southerly slopes, but are interrupted by areas of sparsely vegetated talus. These interruptions in the spatial continuity of fuel probably inhibited the spread of some fires upslope, resulting in higher frequencies at low elevations than at high elevations. In contrast, the northerly slopes at Tucannon and all slopes at Imnaha generally have a continuous cover of surface fuels that probably facilitated the upslope spread of fires, contributing to the lack of variation in frequency on these slopes. This is consistent with fire regimes in northern California, where the frequency of surface fires also did not vary with elevation on slopes with continuous surface fuels (Taylor and Skinner 1998).

3. *Slope.*—Slope angle was not important in explaining spatial variation in fire frequency within the sampled watersheds. Slope affects the rate of spread and fire line intensity of individual fires, so that fires are more intense and spread faster on steep slopes than on gentle slopes (Albini 1976, Rothermel 1983). However, while slope affects short-term fire behavior, it

does not change the long-term likelihood of the occurrence of fire at a given point on the landscape, so that when viewed over centuries, the frequency of fire did not vary with slope in these watersheds.

Fire season varied regionally

Growing season fires were more common in the southern watersheds than in the northern watersheds (Fig. 9), suggesting that there were top-down controls of this parameter of fire regimes. Two possible causes for this pattern are regional variation in the timing of fire, and/or in the timing of cambial growth. Tree growth may have stopped synchronously across the Blue Mountains, while fires burned earlier in the year in the south, due to earlier snow melt and lower fire season precipitation to the south. Alternatively, fires may have burned at similar times throughout the Blue Mountains, but growth continued later into the year in the south. Consequently, fires burning simultaneously across the Blue Mountains could have created early- and latewood scars in the south, but scars on the ring boundary to the north. However, the first alternative seems more likely, because modern fires burn earlier in the year in the southern Blue Mountains (C. Avalos, *personal communication*).

Fire size did not vary regionally

In contrast to fire frequency and season, the distribution of fire sizes did not vary among watersheds (Fig. 10). However, because we did not detect the full range of fire sizes, we cannot conclude that regional-scale controls were not important for this parameter of fire regimes. Although most fires were small relative to the sampled area, many fires intersected the boundary of that area, so we probably did not detect the full extent of these fires. We probably also did not detect all of the very small fires because we sampled one plot per ~25 ha. However, we suspect that fires <25 ha were not common in the sampled areas because most fires burned more than one plot (73%). Overall, fire size in the Blue Mountains had a similar distribution to those in dry forests of the eastern Cascade Range of Washington, where most historical fires (1700–1900) were small relative to the size of the sampled area (30 000 ha). However, many fires intersected the boundary of the sampled area, so that fire sizes are probably underestimated for this study as well (Wright 1996). Variation in fire size in the Blue Mountains appears to be controlled more by temporal than by spatial variation in climate (Heyerdahl 1997).

Controls of modern fire regimes

Around 1900, fire frequency and size decreased abruptly in all watersheds (Fig. 7). The difference in frequency before and after 1900 is much greater than any regional or local variation in frequency we documented prior to this time in the Blue Mountains. Before 1900, over half the fires (60%) in the sampled water-

sheds burned >250 ha. These were large compared to many modern fires (U.S. Forest Service 1993). After this time, no fires greater than ~250 ha burned in any watershed. The initial decline in fire size and occurrence in the late 1800s was probably caused by a combination of above-average precipitation and domestic livestock grazing, and was clearly affected by fire suppression starting in the mid-1900s (Heyerdahl 1997). The number of Euro-Americans settling in the Blue Mountains increased substantially after the completion of the transcontinental railroad in 1884 (Schwantes 1989, Evans 1990, Robbins and Wolf 1994, Langston 1995). This increase was accompanied by an eight- to tenfold rise in the number of grazing animals (Irwin et al. 1994). Before this time, the Cayuse, Nez Percé, Paiute, Umatilla and Shoshone tribes inhabited the Blue Mountains region. They based their economies on hunting and gathering (Schwantes 1989) and may have ignited fires (Langston 1995). Disease dramatically reduced their populations well before the dramatic decline in fire frequency that we documented in the Blue Mountains (Schwantes 1989). Widespread timber harvesting began in the late 1800s (Robbins and Wolf 1994, Langston 1995). A fire suppression policy was implemented in the early 1900s, but was not effective in many areas until the 1940s (Pyne 1982).

As a consequence of excluding fire, spatial variation in climate, topography and vegetation no longer influences fire regimes as it did before ~1900, either regionally or locally. This dramatic change in fire frequency has profoundly affected forest composition and structure in the Blue Mountains, most notably in dry forests where grand fir and Douglas-fir trees have established in the understory of forests that were historically dominated by ponderosa pine (Maruoka 1994, Agee 1996). As a consequence, forests that were probably patchy at fine scales are now much more homogeneous (Agee 1998). These changes in forest composition and structure have shifted the fire regime of dry forests from frequent, low-severity fires to infrequent, high-severity fires that kill large areas of ponderosa pine trees that had survived numerous low-severity fires in previous centuries (Agee 1993, 1996). Such changes have also occurred in similar forest types throughout the interior of western North America where fire has been excluded for many decades (Weaver 1959, 1961, Cooper 1960, Mutch et al. 1993, Covington and Moore 1994, Agee 1996). Concern over this change in fire regimes in the Blue Mountains was one factor prompting the U.S. Forest Service to institute a nationwide policy of ecosystem management (Everett et al. 1994). In the Blue Mountains, as in many ecosystems, understanding current forest conditions and designing implementation plans for ecosystem management relies on quantitative estimates of the range of spatial as well as temporal variability of historical fire regimes (Everett et al. 1994, Swanson et al. 1994, Foster et al. 1996, Swetnam and Betancourt 1998). More

importantly, understanding the factors that controlled spatial variability in these fire regimes, such as the local- and regional-scale factors inferred here, will help land managers evaluate whether it will be feasible to maintain landscapes dramatically altered by twentieth-century human use within the range of historical disturbances.

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LITERATURE CITED

- Agee, J. K. 1993. Fire ecology of Pacific Northwest forests. Island Press, Washington, D.C., USA.
- Agee, J. K. 1996. Fire in the Blue Mountains: a history, ecology, and research agenda. Pages 119–145 in R. G. Jaundt and T. M. Quigley, editors. Search for a solution: sustaining the land, people, and economy of the Blue Mountains. American Forest, Washington, D.C., USA.
- Agee, J. K. 1998. The landscape ecology of western forest fire regimes. *Northwest Science* 72:24–34.
- Agee, J. K., M. Finney, and R. de Gouvenain. 1990. Forest fire history of Desolation Peak, Washington. *Canadian Journal of Forest Research* 20:350–356.
- Agee, J. K., R. H. Wakimoto, and H. H. Biswell. 1978. Fire and fuel dynamics of Sierra Nevada conifers. *Forest Ecology and Management* 1:255–265.
- Albini, F. A. 1976. Estimating wildfire behavior and effects. U.S. Forest Service General Technical Report INT-30.
- Allen, T. F. H., and T. W. Hoekstra. 1991. Role of heterogeneity in scaling of ecological systems under analysis. Pages 47–68 in J. Kolasa and S. T. A. Pickett, editors. Ecological heterogeneity. Ecological studies 86. Springer-Verlag, New York, New York, USA.
- Applequist, M. B. 1958. A simple pith locator for use with off-center increment cores. *Journal of Forestry* 56:141.
- Arno, S. F., J. H. Scott, and M. G. Hartwell. 1995. Age-class structure of old growth ponderosa pine/Douglas-fir stands and its relationship to fire history. U.S. Forest Service Research Paper INT-RP-481.
- Arno, S. F., and K. M. Sneek. 1977. A method for determining fire history in coniferous forests of the mountain west. U.S. Forest Service General Technical Report GTR-INT-42.
- Avalos, C. D. 1998. Space-time analysis of forest fires. Dissertation. University of Washington, Seattle, Washington, USA.
- Beers, T. W., P. E. Dress, and L. C. Wensel. 1966. Aspect transformation in site productivity research. *Journal of Forestry* 64:691–692.

- Bergeron, Y. 1991. The influence of island and mainland lakeshore landscapes on boreal forest fire regimes. *Ecology* **72**:1980–1992.
- Blackmarr, W. H. 1972. Moisture content influences ignitability of slash pine litter. U.S. Forest Service Research Note **SE-173**.
- Box, G. E. P., and D. R. Cox. 1964. An analysis of transformations. *Journal of the Royal Statistical Society* **B 26**: 211–243.
- Brubaker, L. B. 1978. Effects of defoliation by Douglas-fir tussock moth on ring sequences of Douglas-fir and grand fir. *Tree-Ring Bulletin* **38**:49–60.
- Bryson, R. A., and F. K. Hare. 1974. The climates of North America. Pages 1–47 in H. E. Landsberg, editor. *World survey of climatology*. Volume 11. Elsevier, New York, New York, USA.
- Burgan, R. E., C. C. Hardy, D. O. Olhen, and G. Fosnight. 1997. Landcover ground sample data. U.S. Forest Service General Technical Report **INT-GTR-368CD**.
- Cooper, C. F. 1960. Changes in vegetation, structure, and growth of southwestern pine forests since white settlement. *Ecological Monographs* **30**:129–164.
- Countryman, C. M. 1978. Radiation: heat—its role in wildland fire, Part 4. U.S. Forest Service, Pacific Southwest Forest and Range Experiment Station, Berkeley, California, USA.
- Covington, W. W., and M. M. Moore. 1994. Southwestern ponderosa pine forest structure: changes since Euro-American settlement. *Journal of Forestry* **92**:39–47.
- Daly, C., N. P. Neilson, and D. L. Phillips. 1994. A statistical-topographic model for mapping climatological precipitation over mountainous terrain. *Journal of Applied Meteorology* **33**:140–158.
- Dieterich, J. H. 1980. The composite fire interval: a tool for more accurate interpretation of fire history. Pages 8–14 in M. A. Stokes and J. H. Dieterich, technical coordinators. *Proceedings of the Fire History Workshop*, 20–24 October 1980, Tucson. U.S. Forest Service General Technical Report **RM-81**.
- Duncan, R. P. 1989. An evaluation of errors in tree age estimates based on increment cores in kahikatea (*Dacrydium dacrydioides*). *New Zealand Natural Sciences* **16**:31–37.
- Duncan, R. P., and G. H. Stewart. 1991. The temporal and spatial analysis of tree age distributions. *Canadian Journal of Forest Research* **21**:1703–1710.
- EarthInfo. 1990. Climate data. Volume 3.3: summary of the data—west 2. Boulder, Colorado, USA.
- Englemark, O. 1987. Fire history correlations to forest type and topography in northern Sweden. *Annales Botanica Fennici* **24**:317–324.
- Evans, J. W. 1990. Powerful rocky: the Blue Mountains and the Oregon Trail, 1811–1883. Eastern Oregon State College, La Grande, Oregon, USA.
- Everett, R., P. Hessburg, M. Jensen, and B. Bormann. 1994. Volume I: executive summary. U.S. Forest Service General Technical Report **PNW-GTR-317**.
- Foster, D. R., D. A. Orwig, and J. S. McLachlan. 1996. Ecological and conservation insights from reconstructive studies of temperate old-growth forests. *Tree* **11**:419–424.
- Fritts, H. C. 1976. *Tree rings and climate*. Academic Press, New York, New York, USA.
- Gill, M. 1974. Toward an understanding of fire-scar formation: field observation and laboratory simulation. *Forest Science* **20**:198–205.
- Gordon, A. D. 1981. *Classification: methods for the exploratory analysis of multivariate data*. Chapman and Hall, New York, New York, USA.
- Graumlich, L. G. 1987. Precipitation variation in the Pacific Northwest (1675–1975) as reconstructed from tree rings. *Annals of the Association of American Geographers* **77**: 19–29.
- Grimm, E. 1984. Fire and other factors controlling the Big Woods vegetation of Minnesota in the mid-nineteenth century. *Ecological Monographs* **54**:291–311.
- Grissino-Mayer, H. D. 1995. *Tree-ring reconstructions of climate and fire history at El Malpais National Monument, New Mexico*. Dissertation. University of Arizona, Tucson, Arizona, USA.
- Hayes, G. L. 1941. Influence of altitude and aspect on daily variations in factors of forest-fire danger. Circular 591. U.S. Department of Agriculture, Washington, D.C., USA.
- Hayes, G. L. 1942. Differences in fire danger with altitude, aspect, and time of day. *Journal of Forestry* **40**:318–323.
- Heinselman, M. L. 1973. Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. *Quaternary Research* **3**:329–382.
- Hemstrom, M. A., and J. F. Franklin. 1982. Fire and other disturbances of the forests in Mount Rainier National Park. *Quaternary Research* **18**:32–51.
- Heyerdahl, E. K. 1997. *Spatial and temporal variation in historical fire regimes of the Blue Mountains, Oregon and Washington: the influence of climate*. Dissertation. University of Washington, Seattle, Washington, USA.
- Holland, P. G., and D. G. Steyn. 1975. Vegetational responses to latitudinal variation in slope angle and aspect. *Journal of Biogeography* **2**:179–183.
- Holmes, R. L. 1983. Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bulletin* **43**: 69–78.
- Irwin, L. L., J. G. Cook, R. A. Riggs, and J. M. Skovlin. 1994. Effects of long-term grazing by big game and livestock in the Blue Mountains forest ecosystems. U.S. Forest Service General Technical Report **PNW-GTR-325**.
- Johnson, C. G., Jr., and R. R. Clausnitzer. 1992. Plant associations of the Blue and Ochoco Mountains. R6-ERW-T-036-92. U.S. Forest Service, Pacific Northwest Region, Portland, Oregon, USA.
- Johnson, C. G., Jr., and S. A. Simon. 1987. Plant associations of the Willowa-Snake Province. Willowa-Whitman National Forest. R6-ECOL-TP-255A-86. U.S. Forest Service, Pacific Northwest Region, Willowa-Whitman National Forest, Portland, Oregon, USA.
- Landsberg, J. D., P. H. Cochran, M. M. Finck, and R. E. Martin. 1984. Foliar nitrogen content and tree growth after prescribed fire in ponderosa pine. U.S. Forest Service Research Note **PNW-412**.
- Langston, N. 1995. *Forest dreams, forest nightmares: the paradox of old growth in the inland west*. University of Washington, Seattle, Washington, USA.
- Legendre, P., and M.-J. Fortin. 1989. Spatial pattern and ecological analysis. *Vegetatio* **80**:107–138.
- Lertzman, K., and J. Fall. 1998. From forest stands to landscapes: spatial scales and the roles of disturbances. Pages 339–367 in D. L. Peterson and V. T. Parker, editors. *Ecological scale: theory and applications*. Columbia University Press, New York, New York, USA.
- Levin, S. A. 1992. The problem of pattern and scale in ecology. *Ecology* **73**:1943–1967.
- Loveland, T. R., J. W. Merchant, D. O. Ohlen, and J. F. Brown. 1991. Development of a land-cover characteristics database for the conterminous U.S. *Photogrammetric Engineering and Remote Sensing* **57**:1453–1463.
- Maruoka, K. R. 1994. *Fire history of Pseudotsuga menziesii and Abies grandis stands in the Blue Mountains of Oregon and Washington*. Thesis. University of Washington, Seattle, Washington, USA.
- McBride, J. M. 1983. Analysis of tree rings and fire scars to establish fire history. *Tree-Ring Bulletin* **43**:51–67.
- Mock, C. J. 1996. Climatic controls and spatial variations of

- precipitation in the western United States. *Journal of Climate* **9**:1111–1125.
- Morris, W. G. 1934. Lightning storms and fires on the national forests of Oregon and Washington. *Monthly Weather Review* **62**:370–375.
- Mutch, R. W., S. F. Arno, J. K. Brown, C. E. Carlson, R. D. Ottmar, and J. L. Peterson. 1993. Forest health in the Blue Mountains: a management strategy for fire-adapted ecosystems. U.S. Forest Service General Technical Report **PNW-GTR-310**.
- National Oceanic and Atmospheric Administration (NOAA). 1997. Oregon Climate Service, Oregon State University, Corvallis, Oregon, USA. Online: (http://www.ocs.orst.edu/pub ftp/climate_data/tcp/).
- Natural Resources Conservation Service (NRCS), National Water and Climate Center. 1997. Historical snow-cover data. Portland, Oregon, USA. Online: (<ftp://162.79.124.23/data/snow/snotel/snohist/>).
- Oden, N. L. 1984. Assessing the significance of a spatial correlogram. *Geographical Analysis* **16**:1–16.
- Ohmann, J. L., and T. A. Spies. 1998. Regional gradient analysis and spatial pattern of woody plant communities of Oregon forests. *Ecological Monographs* **68**:151–182.
- Oliver, C. D., and B. C. Larson. 1990. *Forest stand dynamics*. McGraw-Hill, New York, New York, USA.
- Parsons, D. J., and J. W. van Wagtenonk. 1996. Fire research and management in the Sierra Nevada national parks. Pages 25–48 in W. L. Halvorson and G. E. Davis, editors. *Science and ecosystem management in the national parks*. University of Arizona Press, Tucson, Arizona, USA.
- Payette, S., C. Morneau, L. Sirois, and M. Despons. 1989. Recent fire history of the Northern Quebec biomes. *Ecology* **70**:656–673.
- Pyne, S. J. 1982. *Fire in America—a cultural history of wildland and rural fire*. Princeton University Press, Princeton, New Jersey, USA.
- Ricklefs, R. E. 1987. Community diversity: relative roles of local and regional processes. *Science* **235**:167–171.
- Robbins, W. G., and D. W. Wolf. 1994. Landscape and the intermontane northwest: an environmental history. U.S. Forest Service General Technical Report **PNW-GTR-319**.
- Romme, W. 1980. Fire history terminology: report of the ad hoc committee. Pages 135–137 in M. A. Stokes and J. H. Dieterich, technical coordinators. *Proceedings of the Fire History Workshop, 20–24 October 1980, Tucson*. U.S. Forest Service General Technical Report **RM-81**.
- Rorig, M. L., and S. A. Ferguson. 1999. Characteristics of lightning and wildland fire ignition in the Pacific Northwest. *Journal of Applied Meteorology* **38**:1565–1575.
- Rothermel, R. C. 1983. How to predict the spread and intensity of forest and range fires. U.S. Forest Service General Technical Report **INT-143**.
- Schroeder, M., and C. C. Buck. 1970. *Fire weather*. U.S. Forest Service Handbook 360. Washington, D.C., USA.
- Schwantes, C. 1989. *The Pacific Northwest: an interpretive history*. University of Nebraska Press, Lincoln, Nebraska, USA.
- Sutherland, E. K., W. W. Covington, and S. Andariese. 1991. A model of ponderosa pine growth response to prescribed burning. *Forest Ecology and Management* **44**:161–173.
- Swanson, F. J., J. A. Jones, D. O. Wallin, and J. H. Cissel. 1994. Natural variability—implications for ecosystem management. Pages 80–94 in M. E. Jensen and P. S. Bourgeron, technical editors. Volume II: *Ecosystem management: principles and applications*. U.S. Forest Service General Technical Report **PNW-GTR-318**.
- Swanson, F. J., T. K. Kratz, N. Caine, and R. G. Woodmansee. 1988. Landform effects on ecosystem patterns and processes. *BioScience* **38**:92–98.
- Swetnam, T. W., and C. H. Baisan. 1996. Historical fire regime patterns in the southwestern United States since AD 1700. Pages 11–32 in C. D. Allen, technical editor. *Fire effects in southwestern forests, proceedings of the second La Mesa Fire Symposium, Los Alamos, New Mexico, 1994 March 29–31*. U.S. Forest Service General Technical Report **RM-GTR-286**.
- Swetnam, T. W., and J. L. Betancourt. 1998. Mesoscale disturbance and ecological response to decadal climatic variability in the American Southwest. *Journal of Climate* **11**:3128–3147.
- Swetnam, T. W., M. A. Thompson, and E. Kennedy-Sutherland. 1985. Using dendrochronology to measure radial growth of defoliated trees. U.S. Forest Service Handbook No. **639**.
- Swetnam, T. W., B. E. Wickman, H. G. Paul, and C. H. Baisan. 1995. Historical patterns of western spruce budworm and Douglas-fir tussock moth outbreaks in the northern Blue Mountains, Oregon, since A.D. 1700. U.S. Forest Service Research Paper **PNW-RP-484**. (Data archived at the World Data Center-A for Paleoclimatology, Boulder, Colorado, USA.) Online: (<http://www.ngdc.noaa.gov/paleo/treering.html>).
- Tande, G. F. 1979. Fire history and vegetation pattern of coniferous forests in Jasper National Park, Alberta. *Canadian Journal of Botany* **57**:1912–1931.
- Taylor, A. H., and C. N. Skinner. 1998. Fire history and landscape dynamics in a late-successional reserve, Klamath Mountains, California, USA. *Forest Ecology and Management* **111**:285–301.
- Urban, D. L., R. V. O'Neill, and H. H. Shugart, Jr. 1987. Landscape ecology. *BioScience* **37**:119–127.
- U.S. Forest Service. 1993. National forest fire report, 1938–1959 and 1977–1993 (was: Annual fire report for the national forests 1960–1968, National forests fire report 1969–1976). U.S. Forest Service, Washington, D.C., USA.
- Weaver, H. 1959. Ecological changes in the ponderosa pine forest of the Warm Springs Indian Reservation in Oregon. *Journal of Forestry* **57**:15–20.
- Weaver, H. 1961. Ecological changes in the ponderosa pine forest of Cedar Valley in southern Washington. *Ecology* **42**:416–420.
- Wiens, J. A. 1989. Spatial scaling in ecology. *Functional Ecology* **3**:385–397.
- Wright, C. S. 1996. *Fire history of the Teanaway River drainage, Washington*. Thesis. University of Washington, Seattle, Washington, USA.
- Zar, J. H. 1984. *Biostatistical analysis*. Second edition. Prentice Hall, Englewood Cliffs, New Jersey, USA.