

Local-scale controls of a low-severity fire regime (1750–1950), southern British Columbia, Canada¹

Emily K. HEYERDAHL², Ken LERTZMAN & Stephen KARPUK, School of Resource and Environmental Management, Simon Fraser University, Burnaby, British Columbia V5A 1S6, Canada.

Abstract: Historical low-severity fire regimes are well characterized in ponderosa pine and mixed-conifer forests at many sites in the western United States, but not in the southern interior of British Columbia, Canada. We reconstructed a history of low-severity fires (1750–1950) near the northern limit of ponderosa pine and demonstrated that local-scale spatial variation in fire frequency varied with topography and that the intra-ring position of fire scars (a proxy for fire seasonality) varied somewhat with topography but more strongly by tree species. Fires were significantly more frequent on the south than the north aspect (14 versus 24 y mean plot fire intervals, respectively), likely due to differences in fuel type and condition. Frequency did not vary with elevation, although our range of elevation is likely too narrow to detect such variation (227 m). Ring-boundary scars were 5.6 times more likely on Douglas-fir than ponderosa pine, 1.8 times more likely on north than south aspects, and 1.6 times more likely at low than high elevation. Our results confirm the importance of understanding the effect of interspecific variation and topography on cambial phenology and hence intra-ring position before inferring historical fire seasonality from fire scars.

Keywords: British Columbia, Canada, dendrochronology, Douglas-fir, fire frequency, fire scars, intra-ring position, low-severity fire history, ponderosa pine, season, topography, tree species.

Résumé : L'historique des régimes de feux de faible intensité est bien décrit pour le pin ponderosa et les forêts mixtes de conifères dans plusieurs sites de l'ouest américain mais pas pour l'intérieur sud de la Colombie-Britannique, Canada. Nous avons reconstitué l'historique des feux de faible intensité (1750-1950) près de la limite nord de répartition du pin ponderosa et démontré que la variabilité spatiale à l'échelle locale de la fréquence des feux variait avec la topographie et que la position des cicatrices de feu par rapport aux cernes (un indice de la saisonnalité des feux) variait peu en fonction de la topographie mais beaucoup selon l'espèce d'arbre. Les feux étaient significativement plus fréquents pour les orientations sud que nord (des intervalles moyens de feu par parcelle de 14 et 24 ans, respectivement) probablement dû à des différences dans le type et les conditions du combustible. La fréquence de feux ne variait pas avec l'élévation quoique notre étendue d'élévation était probablement trop faible pour détecter une telle variation (227 m). Les cicatrices à la limite des cernes étaient 5,6 fois plus probables chez le sapin Douglas que chez le pin ponderosa, 1,8 fois plus probables pour les orientations nord que sud et 1,6 fois plus probables à basse qu'à haute élévation. Nos résultats confirment l'importance de comprendre les effets de la variation interspécifique et de la topographie sur la phénologie du cambium et donc sur la position par rapport aux cernes avant d'inférer l'historique saisonnier des feux à partir de cicatrices de feu.

Mots-clés : Canada, cicatrices de feu, Colombie-Britannique, dendrochronologie, espèce d'arbre, fréquence de feux, historique de feux de faible intensité, pin ponderosa, position par rapport aux cernes, saison, sapin Douglas, topographie.

Nomenclature: Canadian Biodiversity Information Facility, 2005.

Introduction

Local- to regional-scale spatial variation in past low-severity fire regimes is well characterized at numerous sites in forests dominated or co-dominated by ponderosa pine at many sites in the western United States (*Pinus ponderosa* ssp. *scopulorum*; e.g., Heyerdahl, Brubaker & Agee, 2001; Taylor & Skinner, 2003; Falk, 2004; Hessel, McKenzie & Schellhaas, 2004; Wright & Agee, 2004). At these sites, spatial variation was historically controlled by temporally and spatially complex interactions of bottom-up controls (*i.e.*,

those that vary at local scales, such as fuels, topography, and forest type) and top-down controls (*i.e.*, those that vary at regional scales, such as climate; Lertzman, Fall & Dorner, 1998; Heyerdahl, Brubaker & Agee, 2001). However, in southern British Columbia, the northern limit of ponderosa pine, we lack information on low-severity fire regimes and the factors that control their spatial variation, despite abundant tree-ring evidence of such fires (Wong, Dorner & Sandmann, 2003).

The historical importance of topographic controls of local-scale variation has been demonstrated for some parameters of low-severity fire regimes but not for others. For example, topography, through its influence on microclimate and hence fuel amount and condition, has been shown to be an important driver of spatial variation

¹Rec. 2006-04-03; acc. 2006-08-21.

Associate Editor: Lee E. Frelich.

²Author for correspondence. Present address: US Department of Agriculture Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory, 5775 US West Highway 10, Missoula, Montana 59808, USA, e-mail: eheyerdahl@fs.fed.us

in fire frequency at some sites but not others. In northeastern Oregon, fires were more frequent on south aspects in steep topography, but aspect was not a significant driver of spatial variation in frequency in gentle topography, or where different aspects were not separated by fire barriers (Heyerdahl, Brubaker & Agee, 2001). Fire frequency also decreased with increasing elevation at some sites in the western United States (Caprio & Swetnam, 1995; Wolf & Mast, 1998; Taylor, 2000; Heyerdahl, Brubaker & Agee, 2001). In contrast, we know little about bottom-up controls of fire seasonality anywhere in western North America. This parameter, which can be inferred from the intra-ring position of fire scars (Dieterich & Swetnam, 1984), is determined by the seasonal timing of 2 processes acting simultaneously: fire occurrence and cambial growth. Topography influences both of these processes. For example, near our study area in southern British Columbia, modern fires at low elevations (≈ 500 m) can ignite several months earlier than those at high elevations ($\approx 1\ 000$ m; 1950–1994, BCFS, 1995a), and while low- and high-elevation (≈ 800 versus $\approx 1\ 000$ m) ponderosa pine trees in Idaho began radial growth simultaneously, the low-elevation trees ceased growth earlier (Daubenmire, 1946). The seasonal timing of cambial growth also varies by species, because species can respond differently to the environmental parameters that control their growth (Fritts, 1976; Schmidt & Lotan, 1980). However, the variation in intra-ring position due solely to variation among species is rarely examined when inferring fire seasonality from intra-ring position.

We used tree rings to reconstruct a history of low-severity fires and explored controls of local-scale variation in those fires. The mouth of the Stein River, a west-to-east tributary of the Fraser River in the southern interior of British Columbia (Figure 1), is well suited to examining the controls of such variation. The area lies at a latitude where aspect strongly drives spatial variation in solar insolation, and hence microclimate, on the steep north and south slopes of the Stein Valley. The forests are dominated by Rocky Mountain Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) and ponderosa pine, both of which retain scars from past low-severity fires. Our objectives were to characterize historical low-severity fire regimes at a site near the northern limit of ponderosa pine occurrence, and to determine if topography (aspect or elevation) and/or species were important drivers of spatial variation in the frequency and/or intra-ring position of these fires. This work was conducted as part of a broader study of the way natural disturbances shape long-term dynamics of forests across spatial scales from stands (< 10 ha) to landscapes (10^5 ha; Riccius, 1998; Wong, 1999; Dorner, Lertzman & Fall, 2002).

Methods

STUDY AREA

The study area lies at the mouth of the Stein River, in the Stein Valley Nlaka'pamux Heritage Provincial Park, in the Very Dry Hot Ponderosa Pine (PPxh2) and Very Dry Hot Interior Douglas-fir (IDFxh2) variants of the Ponderosa Pine and Interior Douglas-fir biogeoclimatic zones (Meidinger & Pojar, 1991). Throughout the study area, the overstory is co-dominated by these 2 species, with other tree species

occurring in riparian areas or on talus slopes, including black cottonwood (*Populus balsamifera* ssp. *trichocarpa*), quaking aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), and western redcedar (*Thuja plicata*). Common understory species include Saskatoon serviceberry (*Amelanchier alnifolia*), pinegrass (*Calamagrostis rubescens*), shrubby penstemon (*Penstemon fruticosus*), Lewis' mock orange (*Philadelphus lewisii*), Douglas maple (*Acer glabrum* var. *douglasii*), and kinnikinnick (*Arctostaphylos uva-ursi*). However, there are differences in both the over- and understory vegetation between the north and south slopes. Ponderosa pine is more abundant than Douglas-fir on the south aspect, whereas the opposite is true on the north aspect. The understory on the south aspect is generally sparse, and choke cherry (*Prunus virginiana* var. *melanocarpa*) and redstem ceanothus (*Ceanothus sanguineus*) are common. In contrast, the understory on the north aspect is relatively dense, and orange honeysuckle (*Lonicera ciliosa*), oceanspray (*Holodiscus discolor*), falsebox (*Gyminda latifolia*), birch-leaved spirea (*Spiraea betulifolia*), and tall Oregon grape (*Mahonia nervosa*) are common.

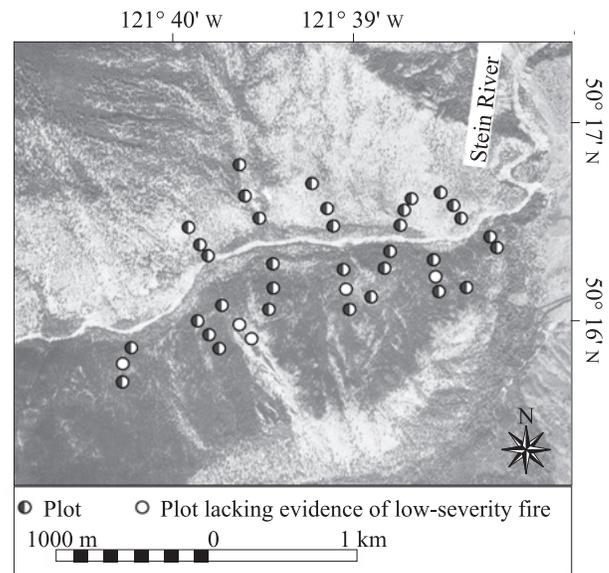


FIGURE 1. The lower Stein Valley, showing the location of the sampling plots (top). Location of the study area in southern British Columbia, west of the Fraser River (bottom). The orthophoto was taken in 1993.

Annual precipitation in the Stein Valley is low (423 mm at Lytton, ≈6 km southeast of the study area; 1970–1990, Environment Canada, 1993). Winters are cold and summers hot (daily January minimum is -6°C ; daily July maximum is 28°C), and most precipitation falls as snow in winter (77%). Recent lightning and lightning-ignited fires occur primarily in July and August (1950–1994, BCFS, 1995a,b).

The study area lies within the traditional territory of the Lytton Nlaka'pamux First Nation band. There is no evidence of permanent village sites within the study area, but it was and still is used for sustenance, cultural, and ceremonial activities (M'Gonigle & Wickwire, 1988). Although some European influence had arrived from the coast by 1808, the time of Simon Fraser's journey, the great influx of non-aboriginal people following the gold rush along the Fraser River in 1858 led to great changes in Nlaka'pamux culture (Laforet & York, 1998). Beginning in the early 1860s, the Fraser Canyon, perhaps including the mouth of the Stein River, was grazed by domestic livestock, primarily cattle, during the spring and summer (Weir, 1964).

SYSTEMATIC SAMPLING DESIGN

Over 262 ha, we identified topographic facets, contiguous areas of relatively homogeneous slope and aspect (Daly, Neilson & Phillips, 1994), and sampled one transect along the elevational gradient in each, for a total of 13 transects (5 north of the river and 8 south; Figure 1). The transects begin near the river and are separated horizontally by about 500 m. However, some adjacent transects diverge or converge because their facets have different orientations. On each transect, we identified 3 plots, with the low-elevation plot ≈10 m above the river terrace (282 m average elevation). The moderate- and high-elevation plots were ≈65 m apart in elevation (average elevations of 346 m and 410 m, respectively). However, we excluded 2 plots because they lacked trees old enough to retain a record of past fires and therefore sampled a total of 37 plots (15 north of the river and 22 south), approximately 1 plot per 7 ha (range: 3–23 ha). As an indication of the composition of the forest overstory, we identified the species of all trees greater than 5 cm basal diameter in one 10- × 10-m area at each plot and assessed whether species (ponderosa pine or Douglas-fir) was independent of aspect (north or south; SAS Proc Freq, SAS Institute, 2001).

HISTORICAL FIRE REGIME

To reconstruct the history of low-severity fires within each plot, we used a chain saw to remove fire-scarred partial cross sections from an average of 5 (range: 2–6) of those trees with the greatest number of visible, well-preserved fire scars. These trees were located between 0 and 70 m from the plot centre (average 33 m), corresponding to plots of 0 to 1.5 ha (average 0.3 ha). We sanded the sections until the cell structure was visible with a binocular microscope and assigned calendar years to tree rings using a combination of visual crossdating of ring widths and other ring features and cross-correlation of measured ring-width series (Holmes, 1983). We could not crossdate sections from 6% of the sampled trees and so excluded them from further analyses. In addition to fire scars, we obtained a small amount of supporting evidence of low-severity fires from visually identi-

fied abrupt changes in the width of annual rings. However, because factors other than low-severity fires can cause abrupt changes in cambial growth, we used such a change in a given sample as evidence of a low-severity fire only when it was synchronous with a fire scar in other samples.

To compute plot fire intervals, we composited the fire dates from all trees sampled in a plot (average 0.3 ha) into a single record of fire occurrence and computed the intervals between years in which a fire scarred at least one tree. Trees are not perfect recorders of fire, and fire records composited from multiple trees in a plot yield a less biased reconstruction of fire frequency than the record from a single tree (Fall, 1998). We analyzed fire intervals and fire season for the period after which at least 20% of the plots on each side of the river had recorded fire on at least one tree and before the recent abrupt change in low-severity fires in the study area (1750–1950).

To estimate the area burned by each fire within the study area, we used a geographic information system to construct a triangular irregular network (*i.e.*, Thiessen polygons) around the plots. We buffered the outer edge of the network by one-half the average distance between plots, and summed the area of all the polygons containing evidence of fire (*i.e.*, a fire scar or abrupt change in ring width) in a given year into a fire size for that year (Jordan, 2002).

We identified the calendar year in which each scar formed and the position of each scar within the ring (ring boundary, earlywood, latewood, or unknown; Dieterich & Swetnam, 1984; Baisan & Swetnam, 1990). In the study area, the season of cambial dormancy (*i.e.*, the period corresponding to the ring boundary) spans 2 calendar years: from the time the cambium stops growing in one year until it resumes the following year. We assigned ring-boundary scars to the preceding calendar year because lightning strikes and recent fires generally burn in mid to late summer in the study area (BCFS, 1995a,b), after the cambium has likely ceased growing. We were unable to determine the intra-ring position of some scars (38%) because they were obscured by rot or insect galleries or the rings were very narrow.

CONTROLS OF SPATIAL VARIATION

We assessed the influence of topography on fire frequency by testing for an effect of aspect (north or south) and/or elevation (low, moderate, or high) on mean fire intervals among plots, using analysis of variance (ANOVA, SAS Proc Mixed, SAS Institute, 2001). To meet the assumption of normal residuals, we log-transformed the fire intervals. We modeled temporal correlation among multiple intervals within each plot as a repeated measures component of the analysis of covariance structure because a likelihood ratio test (Littell *et al.*, 1996) indicated that significant temporal correlation was present ($P = 0.015$). However, a second likelihood ratio test indicated that significant spatial correlation among plots was not present ($P = 0.44$), so we did not include it in the model. To account for heterogeneity in the variance between the 2 sides of the river, we allowed the covariance structure to vary among effects classes. We excluded 3 of the 22 plots south of the river from this analysis because they recorded only a single fire, in 1936, precluding the calculation of fire intervals, and had few tree rings before this date that could have recorded fires (average 44 y).

We assessed the influence of topography and species on the intra-ring position of fire scars using multiple logistic regression (SAS Proc GLIMMIX, SAS Institute, 2005). We included a component for spatial correlation among plots because the estimated covariance parameters indicated spatial structure in the distribution of scars by intra-ring position. We assessed the significance of 3 effects (aspect, elevation, and species) and their two-way interactions in predicting the probability of growing-season scars. To estimate the relative effect of significant main effects, we estimated odds ratios and their 95% confidence intervals. To estimate the relative effect of significant interaction effects, we estimated odds ratios from separate models in which we held the levels of one of the interaction terms constant. For our model, these ratios indicate the odds that scars formed during the cambial growing season, given that the variable takes one of its values *versus* the other, *e.g.*, given that a tree is ponderosa pine *versus* Douglas-fir or that it occurs on the north aspect *versus* the south aspect (Hosmer & Lemeshow, 2000).

Results

FOREST COMPOSITION

Based on our sample of 411 Douglas-fir and ponderosa pine trees (average of 11 trees per plot), overstory composition was not independent of aspect ($P < 0.0001$). On the south aspect there are significantly more ponderosa pine than Douglas-fir trees (63% of 163 trees), whereas on the north aspect there are significantly more Douglas-fir (75% of 248 trees).

HISTORICAL FIRE REGIME

We crossdated fire-scarred sections from 162 trees whose species were sampled roughly in proportion to their occurrence in the overstory, *i.e.*, most of the trees from the south aspect were ponderosa pine (86%) while on the north aspect most were Douglas-fir (69%). We dated a total of 748 fire scars and 44 abrupt changes in ring width (1638–1996, Figure 2), but based our analyses on the 710 fire scars and 36 abrupt changes in ring width that occurred within the analysis period (1750–1950, Table I). The fire-scar dates and associated metadata are available through the International Multiproxy Paleofire Database (<http://www.ncdc.noaa.gov/paleo/impd/paleofire.html>).

Low-severity fires were frequent in the study area. Between 1750 and 1950, the intervals between low-severity fires in the plots, pooled across the study area varied from 2 to 83 y, with an average interval of 16 y (Figure 3).

During the analysis period, individual low-severity fires burned between 4 and 227 ha within the study area, with an average size of 40 ha (Figure 4). During most fire years (77%), the fire boundaries we reconstructed intersected the boundary of the study area, indicating that we likely did not reconstruct the full size of these fires. Most fires burned only a small portion of the study area; 78% of the fires burned less than 50 ha, which is 20% of the study area. As a consequence, more total area was burned by relatively small fires than by large ones. From 1750 to 1950, 85% of the total area estimated to have burned within the study area

(2 290 ha) was burned by fires that covered less than half the study area.

We were able to assign an intra-ring position to a majority (62%) of the 710 fire scars that occurred during the analysis period (Figure 5). About half of these were ring-boundary scars (55%) and half earlywood plus latewood scars (45% = 11% + 34%, respectively). We were able to assign an intra-ring position to a greater percentage of ponderosa pine than Douglas-fir scars overall (71% *versus* 42%).

CONTROLS OF SPATIAL VARIATION

Fire intervals varied with aspect but not with elevation (Figure 3). There were more fires in our sample on the south

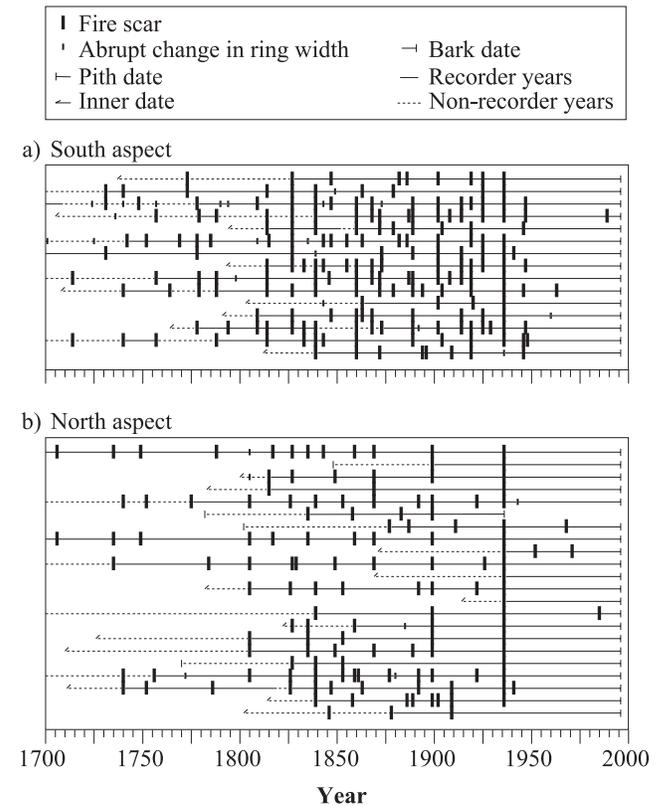


FIGURE 2. Composite fire charts. On each horizontal line the fires recorded at a plot (average 0.3 ha) are shown through time, arranged from high-elevation plots at the top to low-elevation plots at the bottom. Four trees, on average, were dated per plot (range = 1–6 trees), and a fire may have scarred more than one of these trees. Non-recorder years are those preceding formation of the first scar at a plot and periods during which any record of fire was consumed by subsequent fires or rot. Inner and outer dates are the dates of the earliest or latest rings sampled at plots where pith or bark was not sampled.

TABLE I. Amount of evidence used to reconstruct low-severity fires in the study area. Number of scars is for the analysis period (1750–1950). Most trees (95%) were living when sampled.

Aspect	Number of crossdated trees	Number of fire scars	Abrupt changes in ring width
South	74	414	22
North	88	296	14
Total	162	710	36

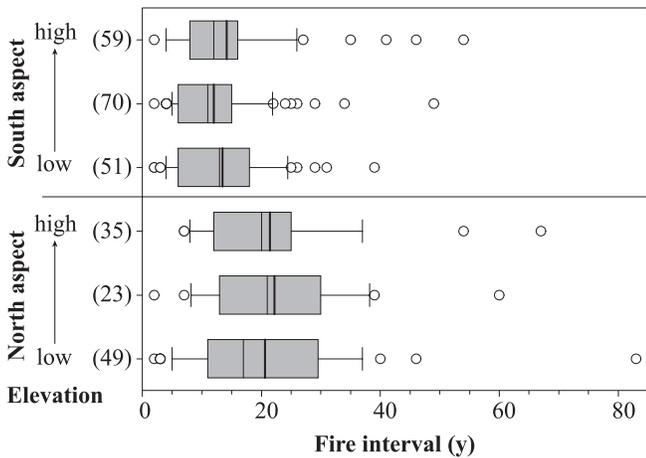


FIGURE 3. Composite fire intervals in the plots (average 0.3 ha), pooled by aspect and elevation for the period 1750–1950. The number of intervals is given in parentheses. The boxes enclose the 25th to 75th percentiles, the whiskers enclose the 10th to 90th percentiles of the distribution of frequencies among plots. The light vertical line across each box indicates the median, the heavy line indicates the mean, and all values falling outside the 10th to 90th percentiles are shown as circles.

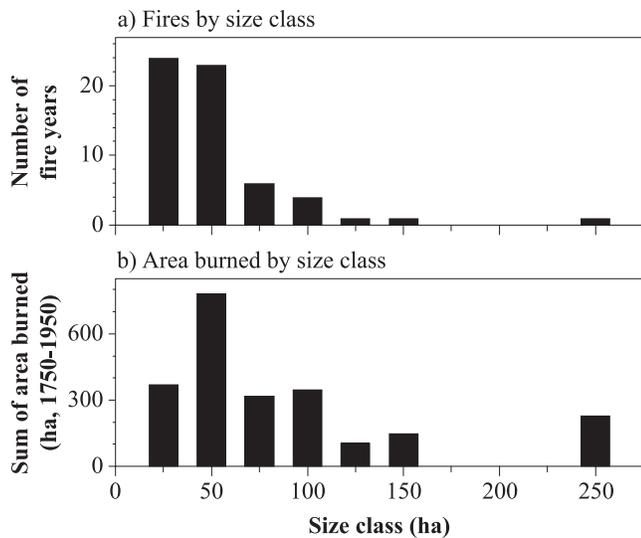


FIGURE 4. Reconstructed fire size (within the study area) for historical surface fires (1750–1950).

aspect, and the retransformed least-squares mean fire interval was significantly shorter for plots on the south aspect (24 ± 1.4 y) than on the north one (14 ± 1.3 y, $P = 0.0002$). However, fire intervals were not significantly different among our elevation classes, nor were they affected by interactions between aspect and elevation ($P = 0.73$ and 0.74 , respectively).

The intra-ring position of fire scars varied strongly with species and somewhat with elevation depending on aspect (Figure 5, Table II). Growing season scars were much more likely to occur on ponderosa pine than Douglas-fir trees (odds ratio 6.3 with 95% confidence intervals [CI] 3.0–13.2). From models of the effect of species and elevation on intra-ring position in which only north aspects were included, growing season scars

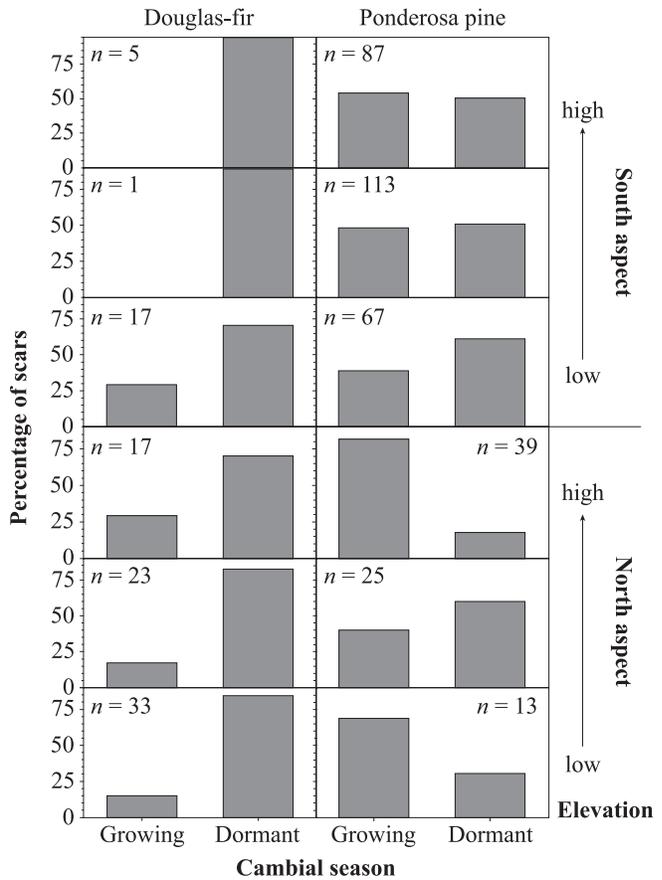


FIGURE 5. Intra-ring position of fire scars (1750–1950), as a percentage of scars for which position could be determined (62% of 706 total scars), pooled by aspect, elevation, and species. Earlywood and latewood scars are formed by fires burning during the cambial growing season, whereas ring-boundary scars are formed by fires that burn when the cambium is dormant.

TABLE II. Effect of topography (low, moderate, or high elevation and north or south aspect) and species (Douglas-fir or ponderosa pine) on the intra-ring position of fire scars (growing or dormant season), from multiple logistic regression that accounted for spatial correlation among plots (SAS Proc GLIMMIX, SAS Institute, 2005).

Effect	<i>P</i> -value
species	< 0.0001
aspect	0.3088
elevation	0.8908
aspect × elevation	0.0424
species × aspect	0.8431
species × elevation	0.1198
Model fit statistics	
log-likelihood (–2 residual log pseudo-likelihood)	1 910.03
generalized chi-square	445.31
generalized chi-square/DF	1.04

were equally likely to occur at high than low elevations (1.0 CI: 0.4–2.3 and 1.0 CI: 0.5–2.1, for low *versus* high and moderate *versus* high plots, respectively). In contrast, on the south aspect, growing season scars were less likely to occur at low than high elevation (0.5 CI: 0.1–1.8 and 0.3 CI: 0.1–1.1, for low *versus* high and moderate *versus* high plots, respectively). The odds of growing season scars

forming on ponderosa pine rather than Douglas-fir trees were similar in these models to the odds in the full model (5.3 CI: 1.5–18.8 and 7.3 CI: 3.1–17.1, respectively).

Discussion

FREQUENCY VARIED WITH ASPECT

Historically, fires were more frequent on the south than the north aspect of our study area, probably because fuel type and condition differ between these aspects and they are separated by a significant barrier to fire spread, the Stein River (Figure 1). Forest composition varies between these aspects, with ponderosa pine trees more common on the south aspect and Douglas-fir more common on the north one. Consequently, fine fuels on the south aspect likely had a high proportion of long-needled ponderosa pine litter with low bulk density that facilitated the spread of low-severity fires (Agee, Wakimoto & Biswell, 1978). In contrast, the north aspect likely had a fuel bed dominated by short Douglas-fir needle litter with high bulk density that may have inhibited the spread of surface fires relative to the south aspect (Agee, Wakimoto & Biswell, 1978; Stephens, Finney & Schantz, 2004). 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. As a consequence, they 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, thereby lowering fuel moisture (Hayes, 1941; 1942; Countryman, 1978). This local-scale variation in fire frequency with aspect in the study area is consistent with aspect-driven variation in fire frequency elsewhere in North America (Taylor, 2000; Heyerdahl, Brubaker & Agee, 2001; Taylor & Skinner, 2003).

Elevation was not an important driver of fire frequency within the study area, probably because the difference in microclimate across the range of elevation that we sampled (227 m) was not great enough to create a significant gradient in fuel condition or type. Furthermore, there were no significant barriers to fire spread on either the north or the south aspect. Historical surface fire intervals in ponderosa pine and mixed-conifer forests did vary with elevation elsewhere in western North America (Caprio & Swetnam, 1995; Wolf & Mast, 1998; Taylor, 2000; Heyerdahl, Brubaker & Agee, 2001). However, the elevation ranges of these studies were more than 3 times the range in ours (600–800 m *versus* 227 m).

INTRA-RING POSITION VARIED WITH SPECIES, ASPECT, AND ELEVATION

Intra-ring position is a function of the seasonal timing of both fire and cambial growth of trees. In our study area, we suggest that interspecific differences in the timing of cambial growth had a greater effect on intra-ring position than did topographic control of either cambial growth or the seasonal timing of fire. The difference in intra-ring position we found between Douglas-fir and ponderosa pine was likely not due to seasonal differences in the timing of fire for 2 reasons. First, many fires scarred both species intermingled on the same aspect, and second, the seasonal timing of mod-

ern fires in and around the study area is similar on north and south slopes (Figure 6, BCFS, 1995a). In light of this, and given that Douglas-fir was significantly more likely to have ring-boundary scars than ponderosa pine (Figure 5), we conclude that Douglas-fir likely ceases radial growth earlier in the season than does ponderosa pine. There is little data on the phenology of cambial growth anywhere in North America, but the cambium of 26 Douglas-fir trees (8 to 35 cm diameter) near Merritt, 70 km southeast of the study area, began growing in mid-May and ceased between mid-June and mid-August, depending on the year (2000–2002, D. Simpson, pers. comm.). If this is representative of the phenology of Douglas-fir in the study area, then fires that generally ignited in July or August, the recent lightning season in our study area, and sometimes continued burning into September, after cambial growth had ceased, would create a preponderance of ring-boundary scars on Douglas-fir trees, as we found.

Although we have no comparable data on the cambial phenology of ponderosa pine in British Columbia, it appears that it differs from that of Douglas-fir in the study area, as it does in the American Southwest (Fritts, 1976). One of the largest fires we reconstructed in the study area started on July 16, 1936 and burned on both aspects (J. Parminter, pers. comm.). The intra-ring positions of the fire scars we dated from this fire are consistent with our inference that the overall differences we found in intra-ring position are due to differences in cambial phenology. Of the 54 scars from this fire, half (27 scars) were found on each aspect. On the south aspect, all the scars were on ponderosa pine trees and most were growing season scars (74%), consistent with the overall distribution for ponderosa pine scars. Similarly, on the north aspect, the 14 scars on ponderosa pine trees were mostly growing season scars (79%), whereas all 13 scars found on Douglas-fir trees were dormant season scars. Cambial phenology varies among species elsewhere (Fritts, 1976), suggesting that the effect of interspecific variation on

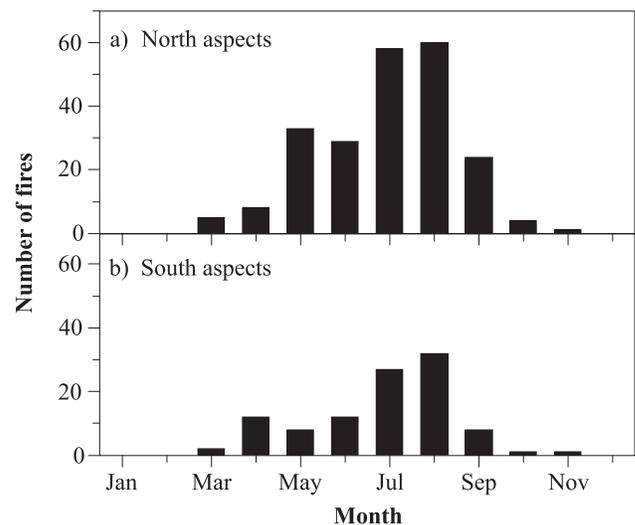


FIGURE 6. Seasonal distribution of modern fires around the study area (lightning- plus human-ignited fires occurring 1950–1994 at elevations less than 500 m; BCFS, 1995a).

cambial phenology should be assessed before inferring fire seasonality from the intra-ring position of fire scars.

Topography also affected intra-ring position in our study area, although not as strongly as with species, likely due to its effects on cambial phenology. Trees in the relatively mesic topographic positions (north aspect and high elevation) were somewhat more likely to have ring-boundary scars than were trees in the relatively dry topographic positions. Assuming that fires burned about the same time in all topographic positions across our study area (Figure 6), we suggest that, as with the difference between species, this variation in intra-ring position may be due to differences in cambial phenology, with cambial growth ceasing earlier in the mesic topographic positions. However, the effect of topography on cambial phenology should be assessed before inferring fire seasonality from the intra-ring position of fire scars across landscapes.

Our assessment of the effects of topography and inter-specific variation on intra-ring position might be biased for 2 reasons. First, we were able to identify the intra-ring position of only 62% of the fire scars we dated. However, these scars were evenly distributed among our aspect and elevation categories and through time. Second, fires ignited by humans before the mid-summer lightning season might have created ring-boundary scars if they burned before initiation of cambial growth. However, if such fires were common, we would expect to find earlywood scars when in fact we found few (only 11% of scars with an intra-ring position), and very few of these were in the early-earlywood (only 1% of scars with an intra-ring position).

GENERAL FEATURES OF THE HISTORICAL FIRE REGIME

Although we only reconstructed low-severity fires, moderate- and high-severity fires and other disturbances probably also occurred in the study area. Such disturbances occurred on the terraces of the Stein River that lie between our north and south aspects (Wong, 1999), and our 5 plots with only young trees may have established after such fires. However, it would be difficult to reconstruct the history of moderate- and high-severity fires in the open forests on these slopes because Rocky Mountain Douglas-fir can establish in the understory as well as after a high-severity fire or other disturbance, and therefore we would not expect to find even-aged cohorts of this species.

Low-severity fires were historically frequent in the study area even though it lies near the northern range limit of ponderosa pine (overall mean interval of 16 y, Figure 3). This frequency is comparable to that of past low-severity fires at sites farther south in the range of ponderosa pine (Heyerdahl, Brubaker & Agee, 2001; Wright & Agee, 2004), suggesting there is not a simple gradient of decreasing frequency with increasing latitude in ponderosa pine-dominated forests in North America, in spite of evidence for such gradients at sub-regional scales elsewhere (Brown & Shepperd, 2001). Rather, the historical frequency of low-severity fires at a site was likely determined by a complex mix of bottom-up controls, such as topography, that we explored at a local scale in the Stein Valley, and top-down controls that operate at broader spatial scales.

Acknowledgements

For help in the field, we thank K. Beavis, B. Brett, J. Brown, B. Dorner, J. Dymont, M. Eng, J. Fall, D. Irving, K. Karpuk, A. MacKinnon, J. Mulowany, J. Parminter, E. Riccius, H. Sandmann, J. Stamp, and C. Wong. We thank H. Sandman, G. Jordan, and R. Parsons for GIS analysis and mapping; R. King for guidance on statistical analyses; the Stein Valley Nlaka'pamux Heritage Provincial Park Co-management Board for permission to sample in the valley and for logistical support; and G. Dean, B. Keane, J. P. Riser II, M. Weber, C. Wong, and two anonymous reviewers for comments on the manuscript. Funding was provided by Forest Renewal-BC, Simon Fraser University, and the USDA Forest Service, Rocky Mountain Research Station.

Literature cited

- Agee, J. K., R. H. Wakimoto & H. H. Biswell, 1978. Fire and fuel dynamics of Sierra Nevada conifers. *Forest Ecology and Management*, 1: 255–265.
- Baisan, C. H. & T. W. Swetnam, 1990. Fire history on a desert mountain range: Rincon Mountain Wilderness, Arizona, USA. *Canadian Journal of Forest Research*, 20: 1559–1569.
- British Columbia Forest Service (BCFS), 1995a. Historical Fire Database. Protection Branch, Victoria, British Columbia.
- British Columbia Forest Service (BCFS), 1995b. Historical Lightning Database. Protection Branch, Victoria, British Columbia.
- Brown, P. M. & W. D. Shepperd. 2001. Fire history and fire climatology along a 5° gradient in latitude in Colorado and Wyoming, USA. *Palaeobotanist*, 50: 133–140.
- Canadian Biodiversity Information Facility, 2005. Integrated Taxonomic Information System. [Online] URL: http://www.cbif.gc.ca/pls/itisc/taxaget?p_ifx = cbif [accessed June 15, 2005].
- Caprio, A. C. & T. W. Swetnam, 1995. Historic fire regimes along an elevational gradient on the west slope of the Sierra Nevada, California. Pages 173–179 in *Proceedings: Symposium on Fire in Wilderness and Park Management*. US Department of Agriculture Forest Service, General Technical Report INT-GTR-320, Ogden, Utah.
- Countryman, C. M., 1978. Radiation: Heat—Its Role in Wildland Fire, Part 4. US Department of Agriculture Forest Service, Pacific Southwest Forest and Range Experiment Station, Berkeley, California.
- Daly, C., N. P. Neilson & D. L. Phillips, 1994. A statistical-topographic model for mapping climatological precipitation over mountainous terrain. *Journal of Applied Meteorology*, 33: 140–158.
- Daubenmire, R. F., 1946. Radial growth of trees at different altitudes. *Botanical Gazette*, 107: 462–467.
- Dieterich, J. H. & T. W. Swetnam, 1984. Dendrochronology of a fire-scarred ponderosa pine. *Forest Science*, 30: 238–247.
- Dorner, B., K. Lertzman & J. Fall, 2002. Landscape pattern in topographically complex landscapes: Issues and techniques for analysis. *Landscape Ecology*, 17: 729–743.
- Environment Canada, 1993. Canadian Climate Normals 1961–1990. [Online] URL: http://www.climate.weatheroffice.ec.gc.ca/climate_normals [accessed February 11, 2002].
- Falk, D. A., 2004. Scaling Rules for Fire Regimes. Ph.D. thesis, University of Arizona, Tucson, Arizona.
- Fall, J. G., 1998. Reconstructing the historical frequency of fire: A modeling approach to developing and testing methods. Master of Natural Resource Management thesis, Simon Fraser University, Burnaby, British Columbia.

- Fritts, H. C., 1976. *Tree Rings and Climate*. Academic Press, New York, New York.
- Hayes, G. L., 1941. Influence of altitude and aspect on daily variations in factors of forest-fire danger. Circular 591. US Department of Agriculture, Washington, DC.
- Hayes, G. L., 1942. Differences in fire danger with altitude, aspect, and time of day. *Journal of Forestry*, 40: 318–323.
- Hessl, A. E., D. McKenzie & R. Schellhaas, 2004. Drought and Pacific Decadal Oscillation linked to fire occurrence in the inland Pacific Northwest. *Ecological Applications*, 14: 425–442.
- Heyerdahl, E. K., L. B. Brubaker & J. K. Agee, 2001. Spatial controls of historical fire regimes: A multiscale example from the Interior West, USA. *Ecology*, 82: 660–678.
- Holmes, R., 1983. Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bulletin*, 44: 69–75.
- Hosmer, D. W. & S. Lemeshow, 2000. *Applied Logistic Regression*. Second Edition. John Wiley & Sons, New York, New York.
- Jordan, G. J., 2002. *Space, Time, and Uncertainty: Detecting and Characterizing Boundaries in Forest Fire Disturbances*. Ph.D. thesis, Simon Fraser University, Burnaby, British Columbia.
- Laforet, A. & A. York, 1998. *Spuzzum: Fraser Canyon Histories, 1808–1939*. UBC Press, Vancouver, British Columbia.
- Lertzman, K., J. Fall & B. Dorner, 1998. Three kinds of heterogeneity in fire regimes: At the crossroads of fire history and landscape ecology. *Northwest Science*, 72: 4–23.
- Littell, R. C., G. A. Milliken, W. W. Stroup & R. D. Wolfinger, 1996. *SAS System for Mixed Models*. SAS Institute, Cary, North Carolina.
- M'Gonigle, M. & W. Wickwire, 1988. *Stein. The Way of the River*. Talonbooks, Vancouver, British Columbia.
- Meidinger, D. & J. Pojar, 1991. *Ecosystems of British Columbia*. British Columbia Ministry of Forests Special Report Series Number 6, Victoria, British Columbia.
- Riccius, E., 1998. *Scale Issues in the Fire History of a Fine Grained Landscape*. Master of Natural Resource Management thesis, Simon Fraser University, Burnaby, British Columbia.
- SAS Institute, 2001. *SAS Release 8.01*. Cary, North Carolina.
- SAS Institute, 2005. *The GLIMMIX procedure*. Cary, North Carolina. [Online] URL: <http://support.sas.com/rnd/app/da/glimmix.html> [accessed July 11, 2006].
- Schmidt, W. C. & J. E. Lotan, 1980. *Phenology of Common Forest Flora of the Northern Rockies: 1928 to 1937*. US Department of Agriculture Forest Service Research Paper INT-259, Intermountain Forest and Range Experiment Station, Ogden, Utah.
- Stephens, S. L., M. A. Finney & H. Schantz, 2004. Bulk density and fuel loads of ponderosa pine and white fire forest floors: Impacts of leaf morphology. *Northwest Science*, 78: 93–100.
- Taylor, A. H., 2000. Fire regimes and forest changes in mid and upper montane forests of the southern Cascades, Lassen Volcanic National Park, California, USA. *Journal of Biogeography*, 27: 87–104.
- Taylor, A. H. & C. N. Skinner, 2003. Spatial patterns and controls on historical fire regimes and forest structure in the Klamath Mountains. *Ecological Applications*, 13: 704–719.
- Weir, T. R., 1964. *Ranching in the Southern Interior Plateau of British Columbia*. Memoir 4. Revised Edition. Geographical Branch, Mines and Technical Surveys, Ottawa, Ontario.
- Wolf, J. J. & J. N. Mast, 1998. Fire history of mixed-conifer forests on the North Rim, Grand Canyon National Park, Arizona. *Physical Geography*, 19: 1–14.
- Wong, C. M., 1999. *Memories of natural disturbance in ponderosa pine–Douglas-fir age structure, southwestern British Columbia*. Master of Natural Resource Management thesis, Simon Fraser University, Burnaby, British Columbia.
- Wong, C. M., B. Dorner & H. Sandmann, 2003. *Estimating Historical Variability of Natural Disturbances in British Columbia*. British Columbia Ministries of Forests and Sustainable Resource Management, Victoria, British Columbia.
- Wright, C. S. & J. K. Agee, 2004. Fire and vegetation history in the eastern Cascade Mountains, Washington. *Ecological Applications*, 14: 443–459.