Spatial and Temporal Variation of Fire Regimes in a Mixed Conifer Forest Landscape, Southern Cascades, California, USA
Author(s): R. Matthew Beaty and Alan H. Taylor
Source: *Journal of Biogeography*, Vol. 28, No. 8 (Aug., 2001), pp. 955-966
Published by: Blackwell Publishing
Stable URL: http://www.jstor.org/stable/827489
Accessed: 28/06/2011 13:02

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at http://www.jstor.org/page/info/about/policies/terms.jsp. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at http://www.jstor.org/action/showPublisher?publisherCode=black.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Blackwell Publishing is collaborating with JSTOR to digitize, preserve and extend access to *Journal of Biogeography*.

http://www.jstor.org

Journal of Biogeography, **28**, 955–966

Spatial and temporal variation of fire regimes in a mixed conifer forest landscape, Southern Cascades, California, USA

R. Matthew Beaty and Alan H. Taylor* *Department of Geography, The Pennsylvania State University, University Park, PA, USA*

Abstract

Aim In this study, we evaluated the fire-forest mosaic of a mixed conifer forest landscape by testing the hypothesis that pre-fire suppression fire regime parameters vary with species composition (tree species), and environment (i.e. slope aspect, slope position, elevation).

Location Our study was conducted in the 1587 ha Cub Creek Research Natural Area (CCRNA), Lassen National Forest, CA, USA.

Methods We quantified the return interval, seasonal occurrence, size, rotation period, and severity of fires using dendroecology.

Results Slope aspect, potential soil moisture, forest composition, and fire regime parameters in our study area co-vary. Median composite and point fire return intervals (FRI) were longest on higher, cooler, more mesic, north-facing (NF) slopes covered with white fir (*Abies concolor*), Douglas fir (*Pseudotsuga menziesii*)–white fir, and red fir (*A. magnifica*)–white fir forests, shortest on the dry, south-facing (SF) slopes covered with ponderosa pine (*Pinus ponderosa*)–white fir forests and intermediate on west-facing slopes dominated by white fir–sugar pine (*P. lambertiana*)–incense cedar (*Libocedrus decurrens*) forests. The spatial pattern for length of fire rotation (FR) was the same as that for FRI. Fires in CCRNA mixed conifer forests occurred mainly (90%) in the dormant season. Size of burns in CCRNA mixed conifer forests were generally small (mean = 106 ha), however, during certain drought years widespread fires burned across fuel breaks and spread throughout the watershed. Fire severity was mainly high on upper slopes, low on lower slopes and moderate and low severity on middle slopes. Patterns of fire severity also varied with slope aspect. Fire frequency decreased dramatically in CCRNA after 1905.

Conclusions In CCRNA, fire regime parameters [e.g. FRI, fire extent, FR, fire severity] varied widely with species composition, slope aspect and slope position. There was also temporal variation in fire extent with the most widespread fires occurring during drought years. The important contributions of topography and climate to variation in the fire regime indicates that exogenous factors play a key role in shaping the fire-forest structure mosaic and that the fire-forest structure mosaic is more variable, less predictable and less stable than previously thought. Finally, some characteristics of the fire regime (i.e. fire severity, season of burn) in CCRNA are different than those described for other mixed conifer forests and this suggests that there are geographical differences in mixed conifer fire regimes along the Pacific slope.

Keywords
Fire regimes, mixed conifer forest, dendroecology, disturbance, California.

*Correspondence: Department of Geography, The Pennsylvania State University, 302 Walker Building, University Park, PA 16802, USA.
E-mail: mbeaty@psu.edu, aht1@psu.edu

© 2001 Blackwell Science Ltd

INTRODUCTION

Species distribution and abundance patterns in forested landscapes are strongly influenced by both site conditions (e.g. soils, temperature, moisture) (e.g. Whittaker, 1956) and the type severity, and extent of natural disturbances (e.g. White, 1979). Disturbances such as fire (e.g. Romme & Knight, 1981), windstorms (e.g. Foster, 1988; Foster & Boose, 1992), and debris flows (e.g. Parker, 1993) are all known to affect vegetation patterns at landscape scales. Moreover, disturbance and disturbance effects on community dynamics are strongly influenced by current vegetation patterns which are, in part, an artefact of the history of disturbance. Feedbacks between vegetation structure and composition and the frequency, spread, and severity of disturbance have been documented (e.g. Harmon *et al.*, 1983; Foster & Boose, 1992; Miller & Urban, 2000a; Taylor, 2000) and appear to play a key role in shaping community structure in some forests such as the fire-prone mixed conifer forests of California (e.g. Bonnicksen & Stone, 1981, 1982). In these forests, frequent (e.g. median fire interval = 3–20 years) low intensity surface fires create fine-grained multi-aged stands (e.g. Kilgore & Taylor, 1979; Caprio & Swetnam, 1995; Skinner & Chang, 1996). Burns influence the spatial patterns of future fires by temporarily reducing fuels in the burn patch (e.g. van Wagtendonk, 1995; Miller & Urban, 2000b; Minnich *et al.*, 2000) and the forest pattern resulting from this process has been described as a shifting mosaic steady-state (e.g. Bormann & Likens, 1979) at the landscape scale with patch sizes of < 0.2 ha (e.g. Bonnicksen & Stone, 1981, 1982). The fire-forest structure mosaic is potentially self-organizing (e.g. Holling *et al.*, 1996) and time-dependent because of the period needed for sufficient fuel to accumulate to carry the next fire. Recent research, however, suggests that fire regimes (i.e. frequency, extent, and severity) in mixed conifer forests are also strongly influenced by exogenous factors such as variation in weather (e.g. Miller & Urban, 2000b; Bekker & Taylor, in press), climate (e.g. Swetnam, 1993), or topography (e.g. Taylor & Skinner, 1998; Taylor, 2000). Consequently, the fire-forest mosaic may be more variable, less predictable, and less stable than previously thought, and a non-equilibrium view (e.g. Botkin, 1990; Sprugel, 1991) of mixed conifer forest dynamics may be more appropriate.

Mixed conifer forests cover 1,642,500 ha (Franklin & Fites-Kaufman, 1996) of the mid-montane zone (900–2200 m) in the Sierra Nevada and Cascade Ranges of California (Barbour, 1988). Any of the six conifer species (ponderosa pine (*Pinus ponderosa* Dougl.), Douglas fir [*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco], incense cedar (*Calocedrus decurrens* Torr. Florin), sugar pine (*P. lambertiana* Dougl.), Jeffrey pine (*P. jeffreyi* Grev. & Balf. in A. Murr), and white fir (*Abies concolor* Gord. and Glend.) may co-occur and share dominance in a stand depending on site conditions, latitude, and stand history (Parker, 1995; Barbour, 1988). Mixed white fir and red fir (*A. magnifica* A. Murr) forests occur above the mixed conifer zone (Parker, 1995). Tree cover in the mixed conifer zone is often interrupted by patches of montane chaparral. Chaparral shrubs are usually less than 2 m tall and the most common shrubs are green-leaf manzanita (*Arctostaphylos patula* Greene), California lilac (*Ceanothus* spp.) and dwarf oak (*Quercus* spp.). Montane chaparral species are fire adapted (i.e. post-fire regeneration from fire-scarified seed, or from sprouts) (Kauffman, 1990) and chaparral appears to occupy sites that have experienced severe fire or are too poor to support trees (Wilken, 1967; Rundel *et al.*, 1977; Weatherspoon, 1988; Bolsinger, 1989).

Although fire is considered a key disturbance process that regulates mixed conifer forest dynamics there has been little research that quantifies spatial and temporal variability in pre-fire suppression fire regimes (e.g. seasonal timing, return interval, rotation period, extent, severity) in the Sierra Nevada or Cascade Ranges, especially at landscape scales (Skinner & Chang, 1996). Determining how fire regime characteristics vary is essential for identifying the role of fire in the long-term dynamics of mixed conifer forest ecosystems. Limited tree-ring evidence of fire mainly from the southern and central Sierra Nevada suggest that fire return intervals (FRI) may be longer on north vs. south slopes, at high vs. low elevations, on fir vs. pine dominated sites, on shallow vs. deep soils, and in the fire suppression vs. pre-fire suppression period (e.g. Kilgore & Taylor, 1979; Caprio & Swetnam, 1995; Fites-Kaufman, 1997; Bekker & Taylor, in press). There are no data on mixed conifer fire regimes for the southern Cascades (Skinner & Chang, 1996) and only the fire return interval and season of burn have been quantified elsewhere in the mixed conifer zone. Regional differences in precipitation and species dominance between the central Sierra Nevada and the southern Cascades (e.g. Parker, 1995; Skinner & Chang, 1996) may be sufficient to lead to geographical differences in fire regimes within the mixed conifer forest type. Geographical variation in disturbance regimes have been identified in several widespread forest types and this variation contributes to regionally distinct vegetation patterns at landscape scales (e.g. Spies & Franklin, 1989; Shinneman & Baker, 1997; Taylor & Skinner, 1998).

In this study, we evaluate the efficacy of the mixed conifer fire-forest mosaic model by testing the hypothesis that pre-fire suppression fire regime parameters vary with species composition (tree species), and environment (i.e. slope aspect, slope position, elevation) in a mixed conifer forest landscape. Our premise is that a spatially variable fire regime leads to a more variable, less predictable, and less stable fire-forest mosaic and therefore to a non-equilibrium explanation for mixed conifer forest dynamics. For this study, we quantified the return interval, seasonal occurrence, size, rotation period and severity of fires using dendroecology.

STUDY AREA

Our study was conducted in the 1587 ha Cub Creek Research Natural Area (CCRNA), Lassen National Forest, CA, USA (Fig. 1). Elevations range from 1136 to 2044 m. The climate

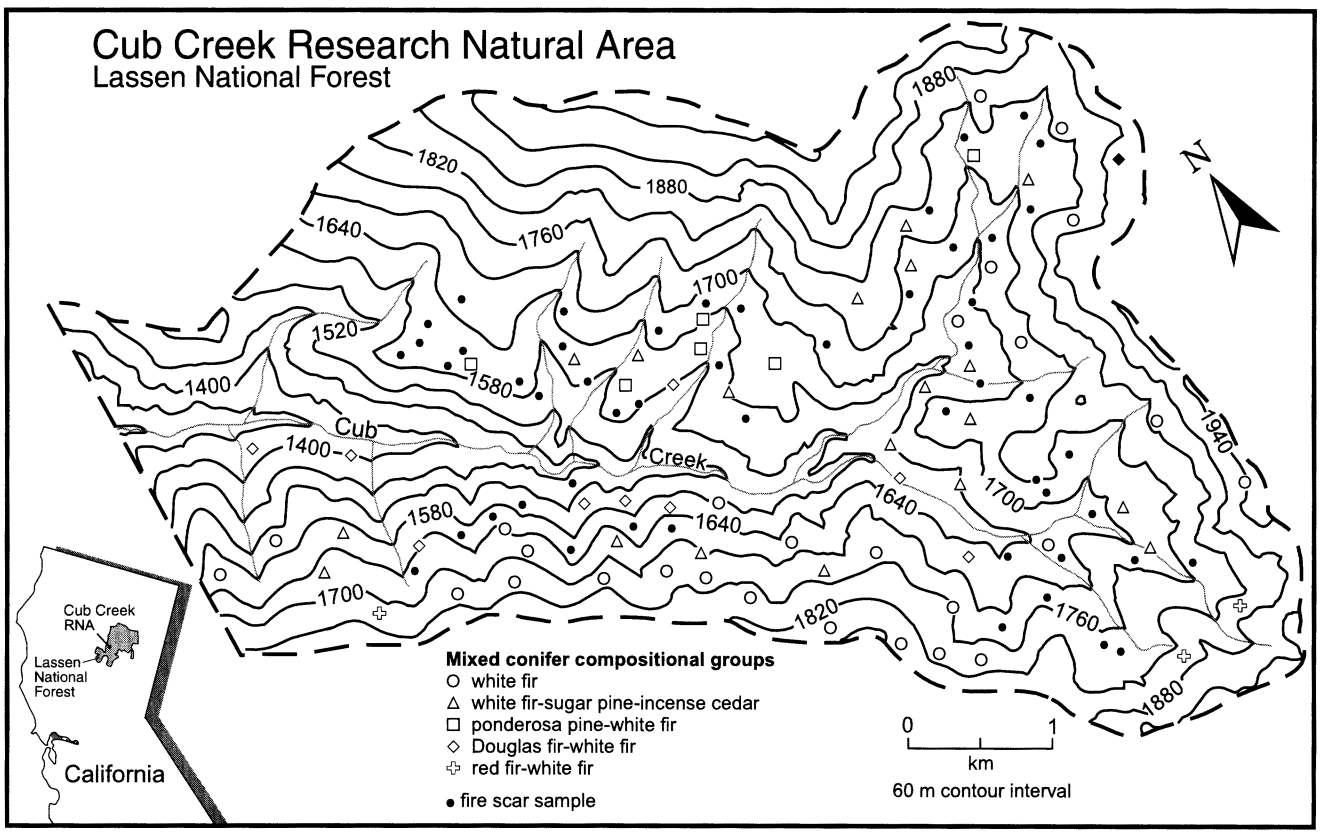

Figure 1 Location of study area, forest sample plots, and fire scar samples in the Cub Creek Research Natural Area (CCRNA), Lassen National Forest, CA, USA. The different symbols represent ponderosa pine–white fir (PP–WF), Douglas fir–white fir (DF–WF), white fir–sugar pine–incense cedar (WF–SP–IC), red fir–white fir (RF–WF), and white fir (WF) forests (see Table 1).

is characterized by warm, dry summers and cold, wet winters. Mean monthly temperature at Mineral, California (1478 m), 20 km north of CCRNA, ranges from –0.8 °C in January to 17.2 °C in July, and annual precipitation averages 134 cm with most (81%) falling as snow between November and April. Forests grow on soils derived from Tertiary (Pliocene) aged volcanic rocks and the landscape has been deeply incised by fluvial erosion. Slopes are steep (25–30°) except for a flat bench adjacent to the north side of Cub Creek that occurs in the lower third of the drainage. Cub Creek runs southeast to northwest so the dominant slope aspects in the study area are northeast and southwest. Cliffs and rock outcrops occur throughout the watershed separating areas of continuous vegetation. These barren areas may serve as fuel breaks that retard the spread of fire.

People have influenced fire regimes in CCRNA in known and unknown ways. Fire is known to have been used by the native Yana tribe to drive game and encourage certain plants used for food and fibre (Schulz, 1954), but there is no direct evidence that they set fires in the watershed (Taylor & Randall, 1979). Euro-americans entered the Lassen region in 1849 with the opening of the Noble and Lassen trails north of the study area (Amesbury, 1967; Strong, 1973; Calhoon & Eaton, 1987). Livestock grazing and forest burning by herders affected fire regimes in nearby areas (McKelvey & Johnston, 1992), but we do not know if these activities occurred in the CCRNA. In 1905, the Lassen National Forest Reserve was established and a policy of fire suppression was implemented (Strong, 1973).

METHODS

Forest composition

Variation in forest composition by slope aspect and slope position in CCRNA was determined by first stratifying the study area by forest cover type (forest cover type map), elevation, and aspect (topographic map), and then sampling forests using 400 m^2 plots ($n = 66$). Plots were placed in strata that were homogenous in species composition, structure, and environment and the location of each plot was determined with a global positioning system (GPS) and then placed on a 1 : 24,000 topographic map. In each plot, all stems > 5.0 cm diameter at breast height (d.b.h.) were measured and the elevation, slope aspect, slope configuration, and topographic position of each plot was recorded. The last four variables were used to calculate each plot's Topographic Relative Moisture Index (TRMI), a measure of potential soil moisture based on topography that ranges from 0 (xeric) to mesic (60) (Parker, 1982).

We identified forest compositional groups using cluster analysis. First, we calculated species importance values (IV) as the sum of relative basal area (BA) and relative density (range 0–200). Secondly, we clustered species IV using relative Euclidean distance and Ward's method. Ward's clustering method minimizes within group variance relative to between group variance (Gauch, 1982; van Tongeren, 1995). We then identified variation in species composition (IV) and environment (TRMI, elevation) among compositional groups by comparing values for each group using a distribution free Kruskal–Wallis *H*-test (Sokal & Rohlf, 1995).

Fire regimes

Fire regime parameters (i.e. return interval, season, extent, rotation, severity) were quantified using four types of data: (1) written fire records (1905–97); (2) fire scars in partial wood cross-sections removed from fire scarred trees; (3) radial growth changes in trees; and (4) age-class distribution of trees in plots (e.g. Arno & Sneck, 1977; Barrett & Arno, 1988). One hundred and fifteen fire scarred trees were located within CCRNA but only fifty-six were collected. The following criteria were used in choosing samples: (1) location in the watershed (i.e. forest cover type, aspect and elevation strata), (2) number of external fire scars and (3) sample integrity (i.e. decay). Many fire scarred trees were too decayed to sample. Samples were removed by cutting a partial cross-section from each tree with a chain saw (e.g. Arno & Sneck, 1977) and the location of each sample was then determined with a GPS and recorded on the topographic map. Fire dates in each cross-section were identified by first sanding wood samples to a high polish and then cross-dating (e.g. Stokes & Smiley, 1968) the annual growth rings with a nearby tree-ring chronology (Holmes *et al.*, 1986). The calendar year of the tree-ring with a fire scar was then recorded as the fire date. Fire history data were analysed using FHX2 software (Grissino-Mayer, 1996).

The season in which a fire occurred was identified by recording the position of each fire scar within an annual growth ring. Scar positions were assigned to one of five categories (cf. Baisan & Swetnam, 1990): (1) early (first one-third of earlywood), (2) middle (second one-third), (3) late (last one-third), (4) latewood (in latewood) or (5) dormant (at ring boundary). In northern California, dormant season fires represent fires that burn in late summer or fall after trees stop growing for the year (e.g. Caprio & Swetnam, 1995).

Fires can initiate distinct age-classes in forest stands, so we aged a sub-sample of trees in each plot to identify fire related cohorts (Arno & Sneck, 1977). We cored an average of fifteen trees (range, six to twenty-one) at 30 cm above the ground in each plot; trees > 1.0 m d.b.h. were cored at 1.0 m. Tree ages were then determined by sanding each core to a high polish, cross-dating the annual growth rings, and then determining the year of the innermost ring. Distinct pulses of recruitment lasting at least 10–30 years were deemed fire related if the onset of recruitment corresponded to the date of a fire in a nearby fire scar sample.

Fires that injure but do not scar trees can cause sudden changes in the radial growth of trees (Arno & Sneck, 1977; Barrett & Arno, 1988; Means, 1989; Brown & Swetnam, 1994). Consequently, we used variation in radial growth suppressions or releases (200% change in radial growth for 5 years compared with the previous 5 years) to identify fire occurrence in cross-sections and cores that did not have a fire scar in them. Dates of radial growth changes were determined to be fire-related if a nearby fire scar sample recorded a fire in the same year.

Spatial variation in FRI in CCRNA was determined by comparing both point and composite FRI for different slope aspect and forest composition groups. Composite FRI include all recorded fires in a slope aspect or forest compositional group, including small spot fires, and they tend to shorten as sample areas increase (e.g. Arno & Petersen, 1983). Point FRI, or the record of successive fires in single samples, in contrast, are longer and reflect the time dependence of fire occurrence associated with fuel accumulation at a single point (Dieterich, 1980; Kitzberger & Veblen, 1997). Group composite and group point FRI were compared using a distribution free Kruskal–Wallis *H*-test (Sokal & Rohlf, 1995). Composite FRI of more widespread fires were also compared by slope aspect group by calculating FRI for fires that scarred 25% or more of the samples in each group (Grissino-Mayer, 1996).

We identified variation in fire occurrence that may be related to land use change by comparing composite FRI for the pre-settlement (1700–1849), settlement (1850–1904), and fire suppression (1905–97) periods using a *t*-test. The composite FRI for the entire watershed was used for the temporal comparisons because composite FRIs are more sensitive to change in fire occurrence related to land use change than are point FRI (Dieterich, 1980).

Fire extent was estimated using fire boundary maps (cf. Taylor, 2000). Maps were produced by drawing boundaries on the topographic map around groups of three or more sites (i.e. fire scars, radial growth changes) that recorded a fire in a given year. Boundaries were drawn equidistant between points with and without evidence of a fire, except when breaks in the continuity of fuels (e.g. cliffs, rock outcrops, perennial streams) occurred between points. When fuel breaks were present, boundaries were placed along the fuel break. Fuel breaks were identified using aerial photographs (1941, 1993). The extent of each fire was then estimated using a dot-grid overlay. Some fires extended beyond the study area boundaries but these areas were not measured as part of a fire.

The fire rotation (FR; Heinselman, 1973), or the time (years) needed for an area equal in size to the study area to burn given the extent of burning over a specified period, was calculated by each aspect and forest composition group and for the entire study area using the burn area maps. FRS were calculated separately for the pre-settlement (1700–1849), settlement (1850–1904), and fire suppression (1905–97) periods because of potential differences in burning rates during these periods.

Spatial variation in fire severity in CCRNA was determined by identifying the cumulative area burned at high, moderate, or low severity using tree age data from plots and forest patch characteristics evident on 1941 and 1993 aerial photographs. Our analysis only characterizes the cumulative pattern of fire severity for fires between 1883 and 1926 because evidence of fire severity for earlier burns is erased by more recent events (Taylor & Skinner, 1998). Stands were grouped into three fire severity classes based on the density of different tree height classes evident on the aerial photographs: (1) high severity < 10 emergent stems ha^{-1}, (2) moderate severity = 10–20 emergent stems ha^{-1} and (3) low severity > 20 emergent stems ha^{-1} (cf. Taylor & Skinner, 1998). This approach assumes that stands with mainly older and taller trees experienced only low or moderate severity fires while stands with young short stems that are similar in height experienced high severity fire. Stands of montane chaparral present on both the 1941 and 1993 aerial photographs were excluded from the fire severity analysis because they may not have originated after severe fire (Rundel *et al.*, 1977; Weatherspoon, 1987; Bolsinger, 1989). Tree age and size data from the plots were also used to confirm fire severity class membership. Spatial patterns of fire severity were then identified by calculating the percentage of area burned by high, moderate, and low severity burns by slope position (low, middle, high) and slope aspect.

RESULTS

Forest composition

Five forest compositional groups were identified based on cluster analysis of species IV and they are segregated by slope aspect, elevation and potential soil moisture (Kruskal–Wallis *H*-test, $P < 0.05$) (Table 1). The white fir (WF) group ($n = 28$) is strongly dominated by white fir and is concentrated on mesic, northeast- and northwest-facing slopes; Douglas fir and sugar pine are important associates in sheltered coves. The white fir–sugar pine–incense cedar (WF–SP–IC) group ($n = 19$) is compositionally variable and occupies drier west-facing slopes. The Ponderosa pine–white fir (PP–WF) group ($n = 6$) occupies dry mid-elevation (1600–1770 m) sites on southwest-facing slopes and it is strongly dominated by ponderosa pine; incense cedar and Douglas fir are common associates. The Douglas fir–white fir (DF–WF) ($n = 8$) and red fir–white fir (RF–WF) groups ($n = 5$) occupy low (1370–1635 m) and high (>1850 m) elevation sites on northeast-facing slopes, respectively (Table 1).

Fire regimes

Slope aspect, potential soil moisture, and forest composition in our study area co-vary (Table 1). Consequently, we compared fire regime characteristics for the following slope aspect groups: (1) south-facing (SF), (2) northern headwaters (NHW), (3) southern headwaters (SHW), and (4) north-facing (NF).

Table 1 Mean importance value (IV, maximum 200), basal area (BA) (m^2 ha^{-1}) and density (ha^{-1}) of trees (>5.0 cm d.b.h.) and environmental characteristics of forest types identified by cluster analysis of species importance values (IV) in Cub Creek Research Natural Area (CCRNA). Forest types are ponderosa pine–white fir (PP–WF), Douglas fir–white fir (DF–WF), white fir–sugar pine–incense cedar (WF–SP–IC), red fir–white fir (RF–WF), and white fir (WF). n = Number of samples in each forest type. TRMI varies between 0 (xeric) and 60 (mesic)

	PP–WF ($n = 6$)			DF–WF ($n = 8$)			WF–SP–IC ($n = 19$)			RF–WF ($n = 5$)			WF ($n = 28$)		
Species	IV	BA	Density	IV	BA	Density	IV	BA	Density	IV	BA	Density	IV	BA	Density
White fir*	85.1	14.1	620.8	99.4	38	753.1	117.3	58	694.7	120.4	60.6	605	189.4	92.9	1278.7
Red fir*							1.9	1.2	6.6	76.6	36.3	580	0.3	0.3	1.9
Bigleaf maple*				4.2	1.3	43.8				2.5	0.1	30	0.1	0	0.9
Incense cedar*	16.3	13.5	70.8	13.9	2.4	153.1	30.7	18.9	213.2				1	0.4	5.6
Pacific dogwood*				6.9	0.4	90.6	1.7	0.1	18.4						
Jeffrey pine							3.7	2.6	3.9				0.4	0.1	1.9
Sugar pine*	1.7	0.1	16.7	18.6	18.8	62.5	39.8	35.5	52.6				6.4	4.2	22.2
Western white pine*										0.5	0.1	10			
Ponderosa pine*	93.1	86.9	112.5	3.5	2.6	9.4	3.8	3.1	3.9				0.1	0.1	0.9
Douglas fir*	3.8	0.2	37.5	52.8	49.2	65.6	0.1	0	1.3				2.2	0.8	13
Canyon live oak				0.2	0	3.1	0.2	0	2.6				0.1	0	0.9
	Mean	SD		Mean	SD		Mean	SD		Mean	SD		Mean	SD	
Elevation (m)*	1657	61.8		1548	112		1661	57		1856	89		1731	81	
Aspect*	SW	–		NE	–		W	–		NE	–		N	–	
TRMI*	27.2	3.8		36.3	7.4		33	6.3		35	4.7		36	5.7	

Values for variables with an asterisk were significantly different among forest types ($P < 0.05$, Kruskal–Wallis *H*-test).

Table 2 Characteristics of the fire record and sample areas in CCRNA. Time period spans between the earliest fire and data collection. Slope aspect groups are NF = north face, SHW = southern headwaters, NHW = northern headwaters, and SF = south face. See Table 1 for description of forest types

Slope aspect group	Area (ha)	Dominant aspect	Dominant forest type	Number of samples	Time period	Number of fire scars	Number of years with fire scars
NF	105.4	NE	WF/DF–WF	8	1616–1997	17	6
SHW	87	W	WF–SP–IC	14	1642–1997	29	8
NHW	101.5	W	WF–SP–IC/WF	15	1795–1997	50	17
SF	133.5	SW	PP–WF	19	1714–1997	160	28
All	427.4	–	–	56	1616–1997	256	59

Fire record

A total of fifty-nine fires were recorded in the fifty-six samples between 1616 and 1926, but the number of samples, the length of the fire record and the number of fires in each slope aspect group varies (Table 2, Fig. 2). SF had the most fires (twenty-eight) and the longest fire record (1616–1997) while seventeen fires were recorded in NHW between 1642 and 1997. There were fewer fires and shorter fire records for SHW and NF. Between 1795 and 1997 SHW had eight fires while NF had six fires between the years 1714 and 1997.

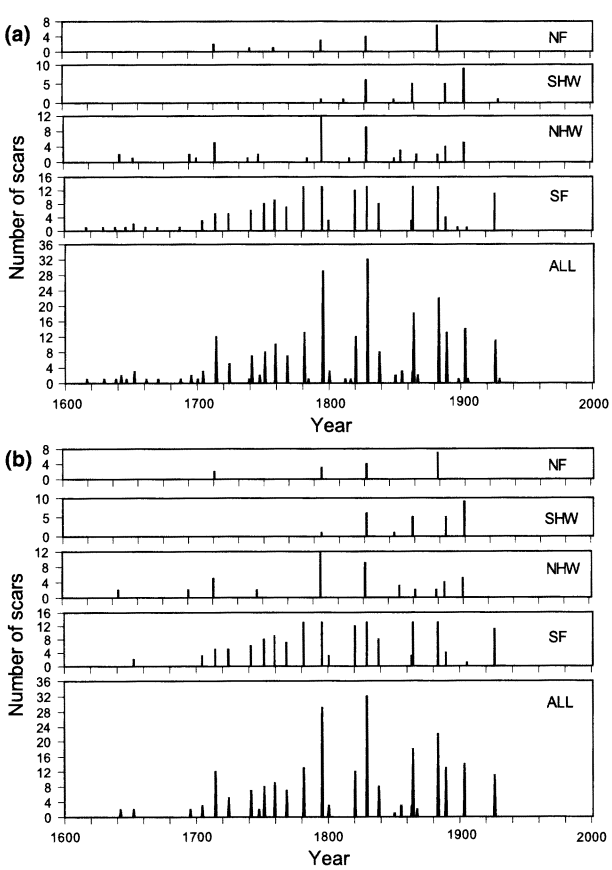

Figure 2 Composite fire chronology for (a) all scarred and (b) >25% scarred samples by slope aspect group for Cub Creek Research Natural Area (CCRNA).

Season of fire occurrence

Fire scar positions within annual growth rings indicate that fires mainly (90.3%) burned in the dormant season after trees stopped growth for the year. However, there was some spatial variation in burn season by slope aspect (Table 3). NF experienced only dormant season fires, while SF experienced some (13%) growing season burns. Percentage of growing season burns was intermediate for SHW (7.1%) and NHW (3.7%).

Fire return intervals

The median and mean composite FRI for all fires in the study area were 7 and 7.6 years (range, 1–21), respectively (Table 4). The median for the composite FRI for more widespread events (i.e. 25% scarred) was longer at 14.2 years.

Spatial patterns

The composite FRI for all fires and widespread fires (>25% scarred) and point FRI varied by slope aspect group ($P < 0.05$, Kruskal–Wallis H-test) (Table 4). Median composite FRI were shortest on SF (9 years) and NHW (13.5 years) and longer on SHW (17 years) and NF (34 years). Overall, median point FRI were longer than composite FRI but the pattern of spatial variation was the same. Point FRI were shortest on SF (19 years) and NHW (34 years) and longer on SHW (37 years) and NF (54 years). Composite FRI for widespread fires (>25% scarred) were shortest on SF (10 years) and SHW (17 years) and longer on NHW (29.5 years) and NF (34 years). The composite FRI for widespread fires on NF may be underestimated because of the relatively small number of samples ($n = 8$) in this group.

Temporal patterns

Composite FRI varied by time period (Table 5). The mean composite FRI was similar ($P > 0.05$, t-test) in the settlement (6.6 years) and pre-settlement (7.7 years) period, but longer ($P < 0.05$, t-test) in the fire suppression period (after 1905). Only two fires occurred in the study area between 1905 and 1997.

Fire extent

Fire extent varied by year and by slope aspect (Fig. 3). The average extent of a fire between 1704 and 1926 ($n = 23$) was 106 ha (range, 7–379 ha) and most fires burned only one or

Table 3 Position of fire scars within annual growth rings by slope aspect group in CCRNA

Slope aspect group	*n*	Undetermined	Scar position		
			Middle (%)	Latewood (%)	Dormant (%)
NF	18	5	–	–	100
SHW	29	15	–	7.1	92.9
NHW	54	27	–	3.7	96.3
SF	160	60	6	7	87
All	261	107	5.8	5.8	90.3

two slopes. Large (>150 ha) fires did burn throughout the study area. Six large burns that burned three or more slopes occurred in 1714, 1795, 1829, 1883, and 1889. Average fire sizes were largest on NF (80 ha, range, 37–120 ha) and SF (75 ha, range 21–105 ha) and smaller on NHW (40 ha, range 7–48 ha) and SHW (73 ha, range 36–106 ha).

Fire rotations

Fire rotations also varied by slope aspect (Table 6). Pre-fire suppression FR was longest (42.5 years) for NF, shortest (17.4 years) for SF, and intermediate for NHW (27.2 years) and SHW (37.2 years). The overall pre-1905 FR was 28.2 years. In contrast, the suppression period FR for the whole study area was 406 years.

Fire severity

The cumulative area (%) burned at low, moderate, and high severity varied by topographic position and slope aspect (Table 7). Fire severity was mainly high (85.7%) on upper slopes, low (60%) on lower slopes and moderate and low severity (46.8% and 29.9%) on middle slopes. SF and NF had similar fire severity patterns with mainly (>60%) low and moderate severity burns while NHW and SHW experienced mainly (>60%) high severity burns (Table 8).

Table 4 Fire return intervals (FRI) (years) by slope aspect groups in CCRNA

Slope aspect group	Mean	Median	Range	SD	Skewness	Number of intervals
Composite fire return intervals, all scarred						
NF	33.8	34	18–54	13.3	0.42	5
SHW	19.1	17	14–26	4.95	0.33	7
NHW	16.3	13.5	5–43	11	1.12	16
SF	11.5	9	1–25	5.58	0.63	27
All	7.6	7	1–21	4.7	0.83	30
Point FRI, all scarred						
NF	54.3	54	34–88	19.4	0.59	9
SHW	39.4	37	14–74	20.6	0.74	14
NHW	37.8	34	8–108	24.9	1.06	35
SF	21.6	19	5–61	12.1	0.78	139
All	27.2	25	5–108	18.1	1.51	185
Composite FRI, 25% or more scarred						
NF	33.8	34	18–54	13.3	0.42	5
SHW	21.6	17	14–35	8.5	0.73	5
NHW	26.1	29.5	5–48	14.7	–0.02	10
SF	13.5	10	6–37	7.5	1.16	23
All	14.2	11.5	6–35	7.8	1.46	14

DISCUSSION

Mixed conifer forests in CCRNA varied widely in composition. Species distribution and abundance patterns were controlled by slope aspect, topographically influenced patterns of soil moisture and elevation. Elevation, slope aspect and soil moisture, are all recognized as important determinants of regional species abundance patterns in the southern Cascades (e.g. Taylor, 1990; Parker, 1991, 1992, 1995; Bekker & Taylor, in press) and the central and southern Sierra Nevada (Parker, 1989). In CCRNA, these same variables strongly influence species distribution patterns at more local and landscape scales.

Fire regime parameters also varied with forest composition and environmental setting (i.e. slope aspect, slope position, elevation). Median composite and point FRI were longest on higher, cooler, more mesic, NF slopes covered with WF, DF–WF, and RF–WF forests, shortest on the dry, SF slopes covered with PP–WF forests and intermediate on west-facing slopes dominated by WF–SP–IC forests. The spatial pattern for length of FR was the same as that for FRI. Actual FRI may be shorter than our tree ring derived FRI estimates. Low intensity fires may not scar trees because of thick bark (Agee, 1993; Taylor, 1993; Taylor & Skinner, 1998). Variation in FRI with slope aspect, slope position, elevation, and species dominance has also been identified in several fire history studies in mixed conifer forests in the Sierra Nevada (e.g. Kilgore & Taylor, 1979; Caprio & Swetnam, 1995; Fites-Kaufman, 1997) and the spatial

Table 5 Composite fire return intervals (FRI) (years) for the pre-settlement (1700–1849), settlement (1850–1904), and fire suppression (1905–97) periods in CCRNA. There was no difference in the mean fire return interval between pre-settlement and settlement period, but it was longer ($P < 0.05$, *t*-test) during the suppression period

	Time period	Mean	Median	Range
Pre-settlement	1700–1849	7.7	8.5	2–15
Settlement	1850–1904	6.6	5.5	1–16
Suppression	1905–97	30.7	21	3–68

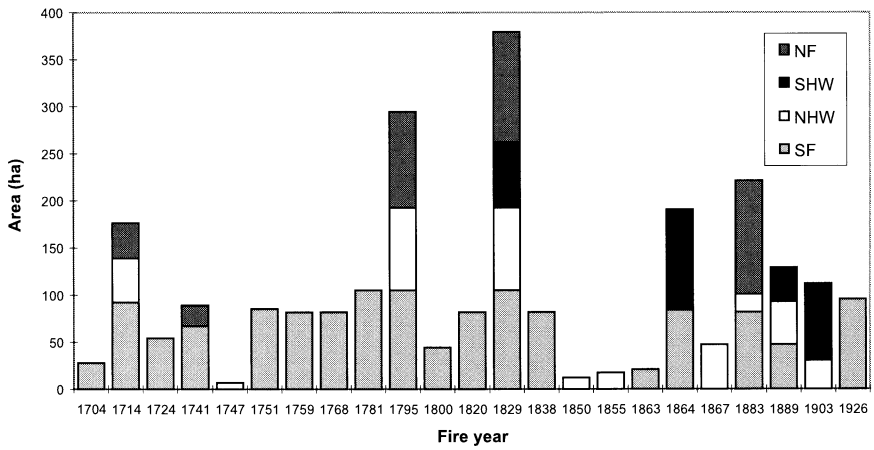

Figure 3 Fire extent by slope aspect in Cub Creek Research Natural Area (CCRNA). NF = north face, SHW = southern headwaters, NWH = northern headwaters, and SF = south face. The fire record for SHW does not extend before 1795.

patterns of FRI, we identified in CCRNA are similar. Moreover, our point and composite estimates for pre-fire suppression FRI are in the range of values for mixed conifer forests in the southern Cascades (Bekker & Taylor, in press; Norman & Taylor, in press), the Klamath Mountains (Taylor & Skinner, 1998), the Sierra Nevada (Kilgore & Taylor, 1979; Caprio & Swetnam, 1995; Fites-Kaufman, 1997), the San Bernardino range (McBride & Lavin, 1976) and the San Pedro Mártir in Baja California (Burk unpublished in Savage, 1997). All of these studies underscore the importance of frequent fire in mixed conifer forest development.

Spatial variation in pre-fire suppression FRI is probably the result of several factors related to species composition and slope aspect that affect flammability of fuels. First, forest litter from species with long needles (i.e. ponderosa pine, sugar pine) is less dense than from species with short needles (i.e. Douglas fir, white fir, red fir) (e.g. Albini, 1976; van Wagtendonk, 1998) and fire intensity and spread are greater in lower density fuel beds (Albini, 1976; Rothermel, 1983; Fonda *et al.*, 1998). Secondly, fuels are dry enough to burn for a longer period each year on SF slopes compared with NF ones and this increases the probability of an ignition turning into a fire (Agee, 1993). Finally, fine fuel production is greater in pine vs. fir dominated mixed conifer forests (e.g. Agee *et al.*, 1978; Stohlgren, 1988; J. van Wagtendonk pers. comm.) so fires can burn again sooner in WF–PP than in WF forests.

FRI increased dramatically in CCRNA after 1905 because of a federal management policy of suppressing fires and similar declines in fire occurrence are characteristic of mixed conifer forests in the Cascade, Klamath and Sierra Nevada Mountains (Vankat, 1977; Vankat & Major, 1978; Kilgore & Taylor, 1979; Taylor, 2000; Bekker & Taylor, in press; Norman & Taylor, in press). The increase in length of FR from 28 to 407 years underscores the decline in the importance of fire in CCRNA. In some California mixed conifer forests an

Table 6 Fire rotation (FR) by slope aspect group for the pre-suppression (1795–1904) and suppression (1905–97) periods in CCRNA

	Fire rotation (years)	
Slope aspect group	Pre-suppression (1795–1904)	Suppression (1905–97)
NF	42.5	–
SHW	37.2	37,352
NHW	27.2	–
SF	17.4	100.9
All	28.2	406

Table 7 Percentage of area burned between 1883 and 1926 at low, moderate and high severity by topographic position in CCRNA

	NF	SHW	NHW	SF	All
Lower slopes					
Low	67.6	39.7	73.5	52.9	59.6
Moderate	31.8	36.2	11.8	46.1	34.6
High	0.6	24.1	14.7	1	5.8
Middle slopes					
Low	22.4	40.7	0	47.5	29.9
Moderate	48.5	37.3	45.6	47.5	46.8
High	29.1	22	54.4	5.2	23.4
Upper slopes					
Low	0.7	0	0	1.5	0.5
Moderate	28.4	2	0	29.4	13.8
High	70.9	98	100	69.1	85.7

Table 8 Percentage of area burned between 1883 and 1926 at low, moderate and high severity by slope aspect group in CCRNA

	NF	SHW	NHW	SF
Low	33.3	17.7	13.7	38.1
Moderate	35.8	17.4	16.4	43.9
High	30.9	64.9	69.9	18

earlier settlement period fire decline has been observed and attributed to reduction of grassy fuels by intensive livestock grazing in the mid to late nineteenth century (e.g. Caprio & Swetnam, 1995). There was no settlement period reduction in fire occurrence in CCRNA, or in other nearby mixed conifer (e.g. Norman & Taylor, in press) or mid- and upper-montane forests (Taylor, 2000; Bekker & Taylor, in press) suggesting there was little influence of grazing on pre-settlement period fire regimes at least in this part of the southern Cascades. Consequently, forests in CCRNA experienced a pre-settlement period fire regime until 1905 when fire suppression was implemented.

Season of burn has a strong influence on species response to fire (e.g. Kauffman & Martin, 1989; Kauffman, 1990) and burns in CCRNA mixed conifer forests occurred mainly (90%) in the dormant season. Fires in nearby (< 25 km) mixed conifer forests also mainly (80%) burned in the dormant season (Norman & Taylor, in press). Lighting activity peaks in July and August in the Lassen National Forest and ignitions are highest during this period (Hood, 1995). The positions of scars within growth rings in CCRNA are different than those reported for central Sierra Nevada mixed conifer forests. In the central Sierra Nevada, most (50%) scars occurred in latewood near the end of the growing season while only 30% occurred in the dormant season (Caprio & Swetnam, 1995). Geographical differences in season of burn are probably related to the south (early) to north (late) gradient for the onset of summer drought along the Sierra Nevada–Cascade axis (e.g. Major, 1977; Parker, 1994) which would influence how long fuels are dry enough each year to burn. These data suggest there is considerable variability in season of burn within mixed conifer forests and this variability may lead to regionally distinct vegetation responses to fire.

Sizes of burns in CCRNA mixed conifer forests were generally small (mean = 106 ha) and the average fire burned on only one or two slope aspects. Tree ring evidence of burns suggest that fire boundaries in most fire years were associated with breaks in the continuity of fuels such as along rock outcrops and stream courses. However, during certain years widespread fires burned across fuel breaks and spread throughout the watershed. Large fires occurred in 1795, 1829, 1883, 1889 and tree ring re-constructions of drought (e.g. GP-5, Palmer Drought Severity Index) show these as being dry or very dry years (Cook *et al.*, 1996). Widespread fires also occurred in dry or very dry years in 1829, 1841, 1846, 1864, 1883 and 1889 in nearby (< 50 km) mixed conifer and upper montane forests (e.g. Bekker & Taylor, in press; Norman & Taylor, in press). This suggests that regional scale climate variation, specifically drought, strongly influences the characteristics of mixed conifer forest fire regimes.

Fires in mixed conifer forests are described as being primarily low and moderate in severity (e.g. Kilgore & Taylor, 1979; Bonnicksen & Stone, 1982; Skinner & Chang, 1996) but in CCRNA high severity burns are an intrinsic part of the fire regime and burn severity varied with slope aspect and topographic position. The influence of topography on patterns of fire severity is poorly known but the fire severity/slope position gradient identified for mixed conifer forests in CCRNA is also present in Douglas fir forests growing on steep terrain in the Klamath Mountains (e.g. Taylor & Skinner, 1998). Higher fire induced tree mortality at mid and upper slope positions would occur because of higher fire line intensities at mid- and upper-slope positions caused by pre-heating of fuels (e.g. Rothermel, 1983). The fire severity/slope position association suggests that the interplay of topography and fire behaviour can lead to highly variable dynamics and structures in mixed conifer forests at both stand and landscape scales.

CONCLUSIONS

Fires in mixed conifer forests have been previously described as being frequent and low to moderate in severity (e.g. Kilgore, 1973; Kilgore & Taylor, 1979; Agee, 1993). Low and moderate severity fires consume patches of fuel and kill mostly seedlings and saplings in the understory and occasionally small groups of main canopy trees (e.g. Kilgore & Taylor, 1979; Parsons & DeBenedetti, 1979; Skinner & Chang, 1996). This fire regime is purported to create a fine grained (< 0.2 ha) multi-aged forest with open and closed canopy conditions and heterogeneous fuels which impedes development of high severity fire and leads to a shifting mosaic steady-state forest at the landscape scale (e.g. Bonnicksen & Stone, 1982). The mixed conifer forest fire regime we quantified in CCRNA does not fit the fire-forest structure mosaic model developed mainly from mixed conifer forests in the central and southern Sierra Nevada. In CCRNA, fire regime parameters (e.g. FRI, fire extent, FR, fire severity) varied widely with species composition, slope aspect and slope position. Fine grained multi-aged forests were present in CCRNA, mainly at lower slope positions, but stands of even-aged forest that established after high severity fire were more widespread. There was also considerable temporal variation in fire extent with the most widespread fires occurring during drought years. The important contributions of topography and climate to variation in the fire regime indicates that exogenous factors play a key role in shaping the fire-forest structure mosaic and that the fire-forest structure mosaic is more variable, less predictable and less stable than previously thought. Finally, some characteristics of the fire regime (i.e. fire severity, season of burn) in CCRNA are different than those described for mixed conifer forests in the Sierra Nevada (Kilgore & Taylor, 1979; Caprio & Swetnam, 1995; Fites-Kaufman, 1997), the San Bernardino range (McBride & Lavin, 1976) and the San Pedro Mártir in Baja California (Savage, 1997; Minnich *et al.*, 2000), and this suggests that there are geographical differences in mixed conifer fire regimes along the Pacific slope. Geographical differences in disturbance regimes and species response to disturbance are known to contribute to structural and compositional diversity within widespread forest types (e.g. Spies & Franklin, 1989). Consequently, fire-forest structure mosaic models developed for one area should be extrapolated cautiously to other locations.

ACKNOWLEDGMENTS

We would like to thank the Research Natural Areas Committee for permission to work in CCRNA, and Robert Olson, Judy Forbes, and Marva Wiley of the Lassen National Forest for logistical support. We also thank P. Warker, K. Grambley, and Z. Knupp for field and laboratory assistance; P. Warker for cartographic work; and J. K. Agee, S. P. Norman, and C. N. Skinner for comments on an earlier draft of this paper. This research was funded by a co-operative agreement between the Lassen National Forest and The Pennsylvania State University.

REFERENCES

Agee, J.K. (1993) *Fire Ecology of Pacific Northwest Forests*. Island Press, Washington, D.C.

Agee, J.K., Wakimoto, R.H. & Biswell, H.H. (1978) Fire and fuel dynamics of Sierra Nevada Conifers. *Forest Ecology and Management*, **1**, 255–265.

Albini, R. (1976) Estimating wildfire behavior and effects. USDA Forest Service General Technical Report INT-GTR-156.

Amesbury, R. (1967) *Noble's Emigrant Trail*. Published privately.

Arno, S.F. & Petersen, T.D. (1983) Variation in estimates of fire intervals: a closer look at fire history on the Bitterroot National Forest. USDA Forest Service Research Paper INT-30.

Arno, S.F. & Sneck, K.M. (1977) A method for determining fire history in coniferous forest of the mountain west. USDA Forest General Technical Report INT-GTR-42.

Baisan, C.H. & Swetnam, T.W. (1990) Fire history on a desert mountain range: Rincon Mountain Wilderness, Arizona, U.S.A. *Canadian Journal of Forest Research*, **20**, 1559–1569.

Barbour, M. (1988) California upland forests and woodlands. *North American Terrestrial Vegetation* (eds M.G. Barbour and W.D. Billings), pp. 131–164. Cambridge University Press, Cambridge, MA.

Barrett, S.W. & Arno, S.F. (1988) Increment-borer methods for determining fire history in coniferous forests. USDA Forest Service General Technical Report INT-GTR-244.

Bekker, M.F. & Taylor, A.H. (in press) Gradient analysis of fire regimes in montane forests of the southern Cascade Range, Thousand Lakes Wilderness, California, USA. *Plant Ecology*.

Bolsinger, C. (1989) Shrubs of California's chaparral, timberland, and woodland: area ownership and stand characteristics. USDA Forest Service Resource Bulletin PNW-RB-160.

Bonnicksen, T.M. & Stone, E.C. (1981) The Giant Sequoia-Mixed Conifer forest community characterized through pattern analysis as a mosaic of aggregations. *Forest Ecology and Management*, **3**, 307–328.

Bonnicksen, T.M. & Stone, E.C. (1982) Reconstruction of a presettlement Giant Sequoia-Mixed Conifer forest community using the aggregation approach. *Ecology*, **63**, 1134–1148.

Bormann, F.H. & Likens. G.E. (1979) *Pattern and Process in a Forested Ecosystem*. Springer Verlag, New York.

Botkin, D. (1990) *Discordant Harmonies: A New Ecology for the Twenty-First Century*. Oxford University, New York.

Brown, P.M. & Swetnam, T.W. (1994) A cross-dated fire history from coast redwood near Redwood National Park, California. *Canadian Journal of Forest Research*, **24**, 21–31.

Calhoon, F.D. & Eaton, J. (1987) *The Lassen Trail*. Cal-Con Press, Sacramento, CA.

Caprio, A.C. & Swetnam, T.W. (1995) Historic fire regimes along an elevational gradient on the west slope of the Sierra Nevada, California. *Symposium on fire in wilderness and park management: Proceedings* (Technical Co-ordinators J.K. Brown, R.W. Mutch, C.W. Spoon, and R.H. Wakimoto), pp. 173–179. USDA Forest Service General Technical Report INT-GTR-320.

Cook, E.R., Meko, D.M., Stahle, D.W. & Cleaveland, M.K. (1996) Tree-ring reconstructions of past drought across the coterminous United States: tests of a regression method and calibration/verification results. *Tree Rings, Environment, and Humanity* (eds J.S. Dean, D.M. Meko and T.W. Swetnam), pp. 155–169. Radiocarbon, Tucson, AZ.

Dieterich, J.H. (1980) The composite fire interval – a tool for more accurate interpretation of fire history. *Proceedings of the Fire History Workshop* (eds M. Stokes and J.H. Dieterich), pp. 8–14. USDA Forest Service General Technical Report RM-GTR-81.

Fites-Kaufman, J. (1997) *Historic landscape pattern and process: fire, vegetation, and environment interactions in the northern Sierra Nevada*. PhD Thesis. University of Washington, Seattle, WA.

Fonda, R., Belanger, L. & Burley, L. (1998) Burning characteristics of western conifer needles. *Northwest Science*, **72**, 1–9.

Foster, D.R. (1988) Species and stand response to catastrophic wind in central New England, USA. *Journal of Ecology*, **76**, 135–151.

Foster, D. & Boose, E. (1992) Patterns of forest damage resulting from catastrophic wind in central New England, USA. *Journal of Ecology*, **80**, 79–98.

Franklin, J. & Fites-Kaufmann, J. (1996) *Assessment of late-successional forests of the Sierra Nevada. Sierra Nevada ecosystem project: final report to Congress, II, assessments and scientific basis for management options*, pp. 627–662. University of California Davis, Center for Wildland Resources, Davis, CA.

Gauch, H.G. (1982) *Multivariate analysis in community ecology*. Cambridge University Press, New York.

Grissino-Mayer, H.D. (1995) *Tree-ring reconstructions of climate and fire history at El Malpais National Monument, New Mexico*. PhD Dissertation, The University of Arizona, Tucson, AZ.

Grissino-Mayer, H.D. (1996) *FHX2 User's Manual: Software for the Analysis of Fire History from Tree Rings*.

Harmon, M.E., Bratton, S.P. & White, P.S. (1983) Disturbance and vegetation response in relation to environmental gradients in the Great Smoky Mountains. *Vegetatio*, **55**, 129–139.

Heinselman, M.L. (1973) Fire in the Boundary Waters Canoe Area, Minnesota. *Quaternary Research*, **3**, 329–382.

Holling, C.S., Peterson, G., Marples, P., Sendzimir, J., Redford, K., Gunderson, L. & Lambert, D. (1996) Self-organization in ecosystems: lumpy geometrics, periodicities and morphologies. *Global Change and Terrestrial Ecosystems* (eds B. Walker and W. Steffen), pp. 346–384. Cambridge University Press, Cambridge.

Holmes, R.L., Adams, R.K. & Fritts, H.C. (1986) *Tree-Ring Chronologies of Western North America: California, Eastern Oregon, and Northern Great Basin*. Laboratory of Tree-Ring Research. University of Arizona, Tucson, AZ.

Hood, L. (1995) Prescribed natural fire risk assessment for the Thousand Lakes Wilderness Area, Hat Creek Ranger District, Lassen National Forest, Susanville, CA.

Kauffman, J.B. (1990) Ecological relationships of vegetation and fire in Pacific Northwest Forests. *Natural and Prescribed Fire in Pacific Northwest Forests* (eds J.D. Walstad, S.R. Radosevich and D.V. Sandberg), pp. 39–52. Oregon State University Press, Corvallis, OR.

Kauffman, J.B. & Martin, R.E. (1989) Fire behavior, fuel consumption, and forest-floor changes following prescribed understory fires in Sierra Nevada mixed conifer forests. *Canadian Journal of Forest Research*, **19**, 455–462.

Kilgore, B.M. (1973) The ecological role of fire in sierran conifer forests. *Quaternary Research*, **3**, 496–513.

Kilgore, B.M. & Taylor, D. (1979) Fire history of a Sequoia-mixed conifer forest. *Ecology*, **60**, 129–142.

Kitzberger, T. & Veblen, T.T. (1997) Influences of humans and ENSO on fire history of *Austrocedrus chilensis* woodlands in northern Patagonia, Argentina. *Ecoscience*, **4**, 508–520.

Major, J. (1977) California climate in relation to vegetation. *Terrestrial Vegetation of California* (eds M. Barbour and J. Major), pp. 11–74. John Wiley & Sons, New York.

McBride, J.R. & Lavin, R.D. (1976) Scars as an indicator of fire frequency in the San Bernardino Mountains, California. *Journal of Forestry*, 74, 439–442.

McKelvey, K.S. & Johnston, J.D. (1992) Historical perspectives on forests of the Sierra Nevada and the Transverse Ranges of southern California: forest conditions at the turn of the century. USDA Forest Service General Technical Report PSW-GTR-133.

Means, J. (1989) Estimating the date of a single bole scar by counting tree rings in increment cores. *Canadian Journal of Forest Research*, **19**, 1491–1496.

Miller, C. & Urban, D. (2000a) Connectivity of forest fuels and surface fire regimes. *Landscape Ecology*, **15**, 145–154.

Miller, C. & Urban, D. (2000b) Interactions between forest heterogeneity and surface fire regimes in the southern Sierra Nevada. *Canadian Journal of Forest Research*, **29**, 202–212.

Minnich, R., Barbour, M., Burk, J. & Sosa-Ramirez, J. (2000) Californian mixed-conifer forests under unmanaged fire regimes in the Sierra San Pedro Mártir, Baja California, Mexico. *Journal of Biogeography*, **27**, 105–129.

Norman, S.P. & Taylor, A.H. (in press) Variation in fire return intervals across a mixed conifer forest landscape. *Proceedings of Fire in California Ecosystems: Integrating Ecology, Prevention, and Management*. Center for Wildland Resources. University of California, Davis, CA.

Parker, A.J. (1982) The topographic relative moisture index: an approach to soil-moisture assessment in mountain terrain. *Physical Geographyraphy*, **3**, 160–168.

Parker, A.J. (1989) Forest/environment relationships in Yosemite National Park, California, USA. *Vegetatio*, **82**, 41–54.

Parker, A.J. (1991) Forest/environment relationships in Lassen Volcanic National Park, California, USA. *Journal of Biogeography*, **18**, 543–552.

Parker, A.J. (1992) Spatial variation in diameter structures in forests of Lassen Volcanic National Park, California. *Professional Geographer*, **44**, 147–160.

Parker, A.J. (1993) Structural variation and dynamics of lodgepole pine forests in Lassen Volcanic National Park, California. *Annals of the Association of American Geographers*, **83**, 613–629.

Parker, A.J. (1994) Latitudinal gradients of coniferous tree species, vegetation, and climate in the Sierra-Cascade axis of northern California. *Vegetatio*, **115**, 145–155.

Parker, A.J. (1995) Comparative gradient structure and forest cover types in Lassen Volcanic and Yosemite National Parks, California. *Bulletin of the Torrey Botanical Club*, **122**, 58–68.

Parsons, D.J. & DeBenedetti, S.H. (1979) Impact of fire suppression on a mixed-conifer forest. *Forest Ecology and Management*, **2**, 21–33.

Romme, W.H. & Knight, D.H. (1981) Fire frequency and subalpine forest succession along a topographic gradient in Wyoming. *Ecology*, **62**, 319–326.

Rothermel, R. (1983) How to predict the spread and intensity of wildfires. USDA Forest Service General Technical Report INT-GTR-143.

Rowe, J.S. (1983) Concepts of fire effects on plant individuals and species. *The Role of Fire in Northern Circumpolar Ecosystems I* (eds R.W. Wein and D.A. MacLean), pp. 135–154. John Wiley and Sons, New York.

Rundel, P., Parsons, D. & Gordon, D. (1977) Montane and subalpine vegetation of the Sierra Nevada and Cascade ranges. *Terrestrial Vegetation of California* (eds M. Barbour and J. Major), pp. 559–599. John Wiley & Sons, New York.

Savage, M. (1997) The role of anthropogenic influences in a mixed-conifer forest mortality episode. *Journal of Vegetation Science*, **8**, 95–104.

Schulz, P. (1954) *Indians of Lassen Volcanic National Park*. Loomis Museum Associates, Red Bluff, CA.

Shinneman, D.J. & Baker, W.L. (1997) Nonequilibrium dynamics between catastrophic disturbances and old-growth forests in ponderosa pine landscapes of the black hills. *Conservation Biology*, **11**, 1276–1288.

Skinner, C.N. & Chang, C. (1996) *Fire regimes, past and present. Sierra Nevada ecosystem project: final report to Congress, II, Assessments and scientific basis for management options*, pp. 1041–1069. University of California Davis, Center for Wildland Resources, Davis, CA.

Sokal, R. & Rohlf, F. (1995) *Biometry: The Principles and Practice of Statistics in Biology Research*. W.H. Freeman, New York.

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

Sprugel, D.G. (1991) Disturbance, equilibrium, and environmental variability: what is 'natural' vegetation in a changing environment? *Biological Conservation*, **58**, 1–18.

Stohlgren, T.J. (1988) Litter dynamics in two Sierran mixed conifer forests, I. Litter fall and decomposition rates. *Canadian Journal of Forest Research*, **18**, 1127–1135.

Stokes, M.A. & Smiley, T.L. (1968) *An Introduction to Tree-Ring Dating*. University of Chicago Press, Chicago, IL.

Strong, D.H. (1973) *These happy grounds: a history of the Lassen region*. Loomis Museum Association, Red Bluff, CA.

Swetnam, T.W. (1993) Fire History and climate change in giant seqvoia groves. *Science*, **262**, 885–889.

Taylor, A.H. (1990) Habitat segregation and regeneration patterns of red fir and mountain hemlock in ecotonal forests, Lassen Volcanic National Park, California. *Physical Geography*, **11**, 36–48.

Taylor, A.H. (1993) Fire history and structure of red fir (*Abies magnifica*) forests, Swain Mountain Experimental Forest, northeastern California. *Canadian Journal of Forest Research*, **23**, 1672–1678.

Taylor, A.H. (2000) Fire regimes and forest changes in the mid and upper montane forests of the southern Cascades, Lassen National Park, California, USA. *Journal of Biogeography*, **27**, 87–104.

Taylor, D.W. & Randall, D.C. (1979) Ecological survey of the vegetation of the Cub Creek watershed, Almanor Ranger District, Lassen National Forest, California.

Taylor, A.H. & Skinner, C.N. (1998) Fire history and landscape dynamics in a late-successional reserve, Klamath Mountains, California, USA. *Forest Ecology and Management*, **44**, 1–17.

van Tongeren, O.F.R. (1995) Cluster analysis. *Data Analysis in Community and Landscape Ecology* (eds R.H.G. Jongman, C.J.F. ter Braak and O.F.R. van Tongeren), pp. 174–212. Cambridge University Press, Cambridge, MA.

Vankat, J.L. (1977) Fire and man in Sequoia National Park. *Annals of the Association of American Geographers*, **67**, 17–27.

Vankat, J.L. & Major, J. (1978) Vegetation changes in Sequoia National Park, California. *Journal of Biogeography*, **5**, 377–402.

Veblen, T., Kitzberger, T. & Lara, A. (1992) Disturbance and forest dynamics along a transect from Andean rain-forest to Patagonian shrubland. *Journal of Vegetation Science*, **3**, 507–520.

van Wagtendonk, J. (1995) Large fires in wilderness areas. *Symposium on Fire in Wilderness and Park Management, Proceedings* (eds J. Brown, R. Mutch, C. Spoon and R. Wakimoto), pp. 113–116. USDA Forest Service General Technical Report INT-GTR-320.

van Wagtendonk, J. (1998) Fuel bed characteristics of Sierra Nevada Conifers. *Western Journal of Applied Forestry*, **13**, 73–84.

Weatherspoon, C.P. (1988) Preharvest prescribed burning for vegetation management: effects on *Ceanothus veluntinus* seed in duff and soil. *Ninth Annual Forest Vegetation Conference*, (eds J. H. Tomascheski, D. Combes, F. Burch, R. Stewart, D. Thomas and B. Heeld), pp. 125–141. Forest Vegetation Management Conference, Redding, CA.

White, P.S. (1979) Pattern, process, and natural disturbance in vegetation. *Botanical Review*, **45**, 229–299.

Whittaker, R.H. (1956) Vegetation of the Great Smokey Mountains. *Ecological Monographs*, **26**, 1–80.

Wilken, G. (1967) History and fire record of a timberland brushfield in the Sierra Nevada of California. *Ecology*, **48**, 302–304.

BIOSKETCHES

R. Matthew Beaty is a PhD candidate in Geography at the Pennsylvania State University with interests in vegetation dynamics, palaeoecology and landscape ecology. His current research is focused on reconstructing disturbance regimes and vegetation dynamics of mixed conifer forests in the central Sierra Nevada by integrating repeat historic aerial photography, dendroecology, and fossil pollen and charcoal analysis.

Alan H. Taylor is Professor of Geography at the Pennsylvania State University and he is interested in plant ecology, biogeography and conservation. His current research is focused on the role of natural and human disturbance, and climate on vegetation dynamics at time scales of weeks to centuries and at plot to landscape scales. He has worked extensively in the montane conifer forests of western North America and south-western China. He serves on the editorial board of *Physical Geography*.