Springer

Gradient Analysis of Fire Regimes in Montane Forests of the Southern Cascade Range, Thousand Lakes Wilderness, California, USA

Author(s): Matthew F. Bekker and Alan H. Taylor

Source: *Plant Ecology*, Vol. 155, No. 1 (Jul., 2001), pp. 15-28
Published by: Springer
Stable URL: http://www.jstor.org/stable/20051104
Accessed: 25-05-2016 00:10 UTC

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at http://about.jstor.org/terms

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.

Springer is collaborating with JSTOR to digitize, preserve and extend access to *Plant Ecology*

This content downloaded from 128.114.34.22 on Wed, 25 May 2016 00:10:06 UTC
All use subject to http://about.jstor.org/terms

Plant Ecology **155:** 15–28, 2001.
© 2001 *Kluwer Academic Publishers. Printed in the Netherlands.*

Gradient Analysis of Fire Regimes in Montane Forests of the Southern Cascade Range, Thousand Lakes Wilderness, California, USA

Matthew F. Bekker* & Alan H. Taylor**
*Department of Geography, The Pennsylvania State University, 302 Walker Building, University Park, PA 16802, * Present address: Department of Geography, The University of Iowa, Iowa City, IA 52242, USA; **Author for correspondence (Tel: 814 865-3433; Fax: 814 863-7943; E-mail: aht1@psu.edu.);*

Received 11 October 1999; accepted in revised form 17 May 2000

Key words: Dendroecology, Disturbance, Fire regimes, Landscape ecology, Vegetation dynamics

Abstract

Species distribution and abundance patterns in the southern Cascades are influenced by both environmental gradients and fire regimes. Little is known about fire regimes and variation in fire regimes may not be independent of environmental gradients or vegetation patterns. In this study, we analyze variation in fire regime parameters (i.e., return interval, season, size, severity, and rotation period) with respect to forest composition, elevation, and potential soil moisture in a 2042 ha area of montane forest in the southern Cascades in the Thousand Lakes Wilderness (TLW). Fire regime parameters varied with forest composition, elevation, and potential soil moisture. Median composite and point fire return intervals were shorter (4–9 yr, 14–24 yr) in low elevation and more xeric white fir (*Abies concolor*)-sugar pine (*Pinus lambertiana*) and white fir-Jeffrey pine (*P. jeffreyi*) and longest (20–37 yr, 20–47 yr) in mesic high elevation lodgepole pine (*Pinus contorta*) and red fir (*Abies magnifica*)-mountain hemlock (*Tsuga mertensiana*) forests. Values for mid-elevation red fir-white fir forests were intermediate. The pattern for fire rotation lengths across gradients was the same as for fire return intervals. The percentage of fires that occurred during the growing season was inversely related to elevation and potential soil moisture. Mean fire sizes were larger in lodgepole pine forests (405 ha) than in other forest groups (103-151 ha). In contrast to other parameters, fire severity did not vary across environmental and compositional gradients and >50% of all forests burned at high severity with most of the remainder burning at moderate severity. Since 1905, fire regimes have become similar at all gradient positions because of a policy of suppressing fire and fire regime modification will lead to shifts in landscape scale vegetation patterns.

Introduction

The role of temperature and soil moisture in controlling landscape-scale species distribution and abundance patterns is widely recognized (e.g., Merriam 1898; Whittaker 1956; Peet 1978; Gosz 1992). Landscape-scale vegetation patterns, however, are also influenced by the spatial and temporal patterns of natural or human caused disturbance. In forested landscapes, disturbances such as fire (e.g,. Romme & Knight 1981; Romme 1982; Taylor & Skinner 1998), windstorms (e.g., Foster 1988; Foster & Boose 1992), and insect attacks (e.g., Veblen et al. 1991) have all been documented to affect vegetation patterns. Therefore, landscape-scale vegetation patterns are a composite of the superimposed patterns of species response to environment and disturbance (e.g., Romme 1982; Harmon et al. 1983; Veblen et al. 1992). Moreover, spatial and temporal patterns of disturbance may not be independent of environmental or forest compositional gradients making it difficult to distinguish the contributions of disturbance or environment to species distribution and abundance patterns (e.g., Harmon et al. 1983; Barton 1993). Identifying how disturbances and disturbance regimes (i.e., type, severity, seasonality, return interval, size, rotation period) vary across environmental gradients is therefore essential for understanding how natural disturbance

This content downloaded from 128.114.34.22 on Wed, 25 May 2016 00:10:06 UTC
All use subject to http://about.jstor.org/terms

influences landscape-scale vegetation patterns (e.g., Harmon et al. 1983; Veblen et al. 1992).

In the southern Cascades, tree species distribution is controlled primarily by temperature (elevation) and secondarily by topographically controlled patterns of soil moisture (Franklin & Dyrness 1973; Rundell et al. 1977; Barbour 1988; Parker 1991, 1995). Low elevation (<1700 m) well drained uplands are dominated by Jeffrey pine (*Pinus Jeffreyi* Grev. & Balf.) and/or ponderosa pine (*P. ponderosa* Laws). White fir (*Abies concolor* (Gord. & Glend.) Lindl.) is locally abundant on mesic sites at low elevation and it increases in abundance with elevation where it forms mixed stands with ponderosa pine, Jeffrey pine, sugar pine (*P. lambertiana* Dougl.) and incense cedar (*Calocedrus decurrens* (Torr.) Florin) between 1700 and 2000 m. Between 2000 and 2400 m, the zonal dominant is red fir (*A. magnifica* A. Murr.) and white fir and western white pine (*P. monticola* Dougl.) are common red fir associates at lower and upper elevations, respectively. Subalpine forests, above 2400 m, are dominated by mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.). Mesic flats that have a high water table, receive cold air drainage, have poor soils, or have experienced high severity fire are usually occupied by lodgepole pine (*P. contorta* Dougl. ex Loud. var. murrayana (Grev. & Balf.) Engelm.).

Fire was the most frequent and widespread disturbance affecting montane forests in the Pacific Northwest prior to Euro-American settlement. Fire occurrence changed with Euro-American settlement and declined after 1905 due to a Federal policy of suppressing fires (Strong 1973). Limited evidence of pre-fire suppression fire occurrence in the Cascade and Sierra Nevada Ranges derived from fire scarred trees suggests that there is some variation in fire regime parameters along gradients of elevation and potential soil moisture. Median fire return intervals are shorter (5–14 years) in warmer low elevation pine dominated forests and longer in cool upper montane red fir (20–65 years) forests (McNeil & Zobel 1980; Pitcher 1987; Taylor 1993; Caprio & Swetnam 1995; Chappell & Agee 1996). The few data for lodgepole pine forests suggest that fire return intervals are similar (39–60 years) to upper montane red fir forests (Solem 1995; Agee 1981). Patterns of fire severity also appear to parallel temperature and moisture gradients in the montane zone. Fires in warmer low elevation pine and mixed conifer forests are characterized as being low in severity with most burns killing understory seedlings and saplings (Kilgore 1973; Kilgore & Taylor 1979; Bonnicksen & Stone 1982; Agee 1993). In cooler, more mesic upper montane red fir and lodgepole pine forests, fire severity patterns appear to be more variable. High, moderate, and low severity patches occur within the perimeter of most burns. Moderate and high severity fires kill parts or all of an existing stand (e.g., Kilgore 1973; Agee 1993; Taylor 1993; Chappell and Agee 1996). Other fire regime parameters have not been quantified in the montane zone and no one has quantified variation along continuous environmental and compositional gradients in the southern Cascades. Characterizations of fire regime parameters from scattered data over a wide area may mask important geographic differences in fire regimes and species response to disturbance (e.g., Veblen 1989; Spies & Franklin 1989; Agee 1991; Taylor & Skinner 1998).

To determine how fire regimes may influence landscape-scale vegetation patterns we use dendroecology and gradient analysis to test the hypothesis that pre-fire suppression fire regime parameters vary across compositional (tree species) and environmental (elevation, topographic moisture index) gradients in the southern Cascade Range. Fire regime parameters we analyzed in this study include the return interval, seasonal occurrence, size, rotation period, and severity of fires.

Study area

Our study was conducted in a 2042 ha area of the 6618 ha Thousand Lakes Wilderness (TLW) at the southern tip of the Cascade Range, in northern California (Figure 1). Elevations in TLW range from 1700 to 2646 m and the climate is characterized by cold wet winters and warm dry summers (Major, 1977). Mean monthly temperatures at Manzanita Lake (1750 m), 13 km south of TLW, range from −1°C in January to 17°C in July and annual precipitation averages 105 cm, with most (84%) of it falling as snow between November and April. Depth of the April snowpack commonly exceeds 5 m in the upper montane (>2400 m) zone (Taylor 1990a, 1995). Forests in TLW grow on soils underlain by Tertiary and Quaternary aged volcanic rocks that have been extensively modified by Pleistocene glaciation (Kane 1980; Norris & Webb, 1990). Soil depth is highly variable but most are well drained except those in the Thousand Lakes Valley. The southern and western portions of TLW are mountainous and dominated by Crater (2646 m) and Magee (2606 m) Peaks, while the eastern portion is

This content downloaded from 128.114.34.22 on Wed, 25 May 2016 00:10:06 UTC
All use subject to http://about.jstor.org/terms

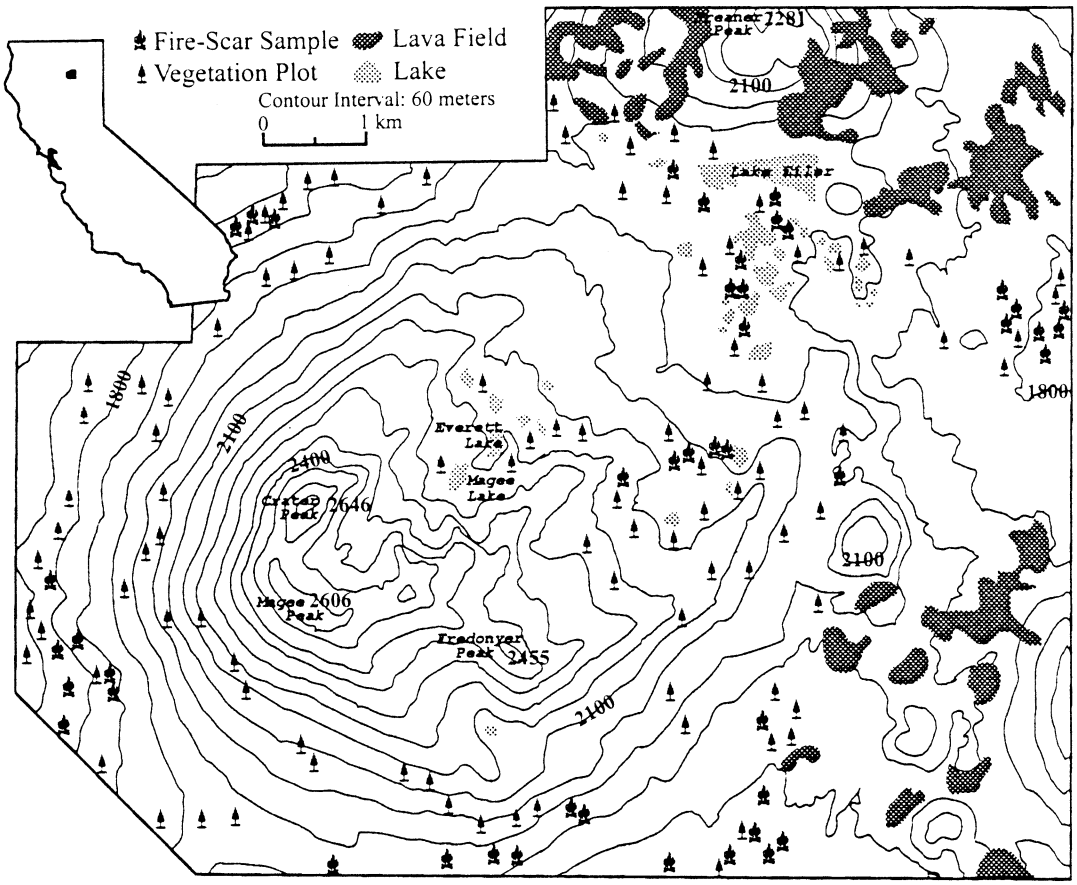

Figure 1. Location of study area, vegetation plots, and fire scar samples in the Thousand Lakes Wilderness, southern Cascades, California.

part of a gently sloping volcanic tableland punctuated with tephra cones.

People have influenced fire regimes in TLW in known and unknown ways. Native Americans used TLW seasonally and are known to have used fire to drive game and to manage plant populations for food and fibre (Schultz 1954). However, we have no direct evidence that they set fires in TLW. The first Euro-American settlements in the vicinity were established in 1850. Large numbers of sheep and cattle grazed surrounding meadows and forest between 1860 and 1904 (e.g., Durbin 1930; Hatcher 1940; Strong 1973; Taylor 1990b), and grazing may influence fire regimes by reducing grassy fuels (e.g., Savage & Swetnam 1990). Stock numbers were reduced when a grazing permit system was introduced in 1905 when the area became part of the Lassen National Forest Reserve. TLW became part of the Lassen National Forest in 1907. Grazing of 20–40 cattle continued in an allotment that included the southeast corner of TLW until 1956 (USDA 1995). TLW became part of the national wilderness system in 1965. A policy of suppressing fire was implemented in 1905 with the establishment of the forest reserve system (Strong 1973).

Methods

Forest composition

We characterized forest composition in TLW by first stratifying forest type by elevation and slope aspect using a forest cover type map, and then sampling 100 400-m^2 plots in strata in stands that were homogenous in structure, composition and environment (Figure 1). The geographic location of each plot was then determined (GPS) and plot locations were placed on the topographic/forest cover type map. In each plot, the diameter of all stems $\geq$4.0 cm dbh was measured and the elevation, slope aspect, slope pitch, slope configuration, and topographic position of each

This content downloaded from 128.114.34.22 on Wed, 25 May 2016 00:10:06 UTC
All use subject to http://about.jstor.org/terms

plot were recorded. The last four values were used to identify each plot's Topographic Relative Moisture Index (TRMI), a measure of potential soil moisture that ranges from 0 (xeric) to 60 (mesic) (Parker 1982).

Compositional groups were identified using two-way indicator species analysis (TWINSPAN; Hill, 1979). TWINSPAN is a polythetic, divisive, hierarchical clustering technique that produces successive binary splits of a reciprocal averaging ordination (Gauch 1982). Plots were grouped by species importance values (IV) which were calculated as the sum of relative basal area, relative density, and relative frequency (range 0–300) of each species in each plot (e.g., Cottam & Curtis 1956). A minimum group size of 10 was used for the forest plot classification.

We used the forest compositional groups to establish sample units for fire regime sampling by drawing boundaries equidistant between adjacent plots in different groups. Because some stands did not contain external tree ring evidence of fire, only a restricted set of plots (n=66) is included in the fire regime sample units. Therefore, the fire regime data come only from part of the environmental gradient in the TLW. The area of each sample unit was then determined from the topographic/forest cover type map using a planimeter.

Fire regimes

Fire regime parameters (i.e., return interval, season, extent, rotation, severity) in forest compositional units were quantified using three types of dendroecological evidence: (1) fire scars in partial wood cross sections removed from fire scarred trees; (2) radial growth changes in trees; and (3) the age-class distribution of trees in plots (e.g., Arno & Sneck 1977; Barrett & Arno 1988). We identified 145 fire-scarred trees in all compositional groups in TLW, but only 50 were collected because most of the scarred trees were too decayed to sample. Fire scar samples were collected by cutting partial cross sections from live and dead trees using a chainsaw (Arno & Sneck 1977) and the location of each sample was determined (GPS) and placed on the topographic/forest cover-type map. Fire dates in each cross section were identified by sanding each sample to a high polish, cross dating its annual rings with a nearby tree ring chronology (Drew 1972; Holmes et al. 1986), and recording the year of each tree ring that contained a fire scar.

The season each fire occurred in was estimated 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, early earlywood (first one-third of earlywood); (2) middle, middle earlywood (second one-third): (3) late, late earlywood (last one-third; (4) latewood, latewood; or (5) dormant, dormant (between growth rings). In these high elevation forests, dormant season scars represent fires that occurred after trees stop growth for the year in late summer or fall (Caprio & Swetnam 1995).

Variation in fire return intervals (FRI) by compositional group was identified by calculating both composite and point median FRI for all fires in samples from each group. Composite FRI include all recorded fires in an area, including small spot fires and therefore they tend to shorten as the area considered increases. In contrast, point FRI reflect the time dependence of fire occurrence related to fuel accumulation at a single point and thus give a conservative estimate of fire occurrence (Kilgore & Taylor 1979; Arno & Petersen 1983).

In order to identify temporal variation in FRI that may be related to land use changes we calculated FRI for the presettlement (1652–1849), settlement (1850–1904), and fire suppression periods (1905–present). Composite FRI were used for temporal comparisons because they are more sensitive to changes in fire occurrence related to land use changes than are point intervals (Dieterich 1980).

Fire can generate distinct age-classes in forest stands so we aged a subsample of trees in each plot to identify fire-related cohorts of trees (e.g., Arno & Sneck 1977). An average of 19 trees (range, 11–27), in the range of size-classes present in each plot, were cored 30 cm above the ground. Trees >100 cm dbh were cored at 1 m. Tree ages were then determined by sanding cores to a high polish and counting the tree rings beneath a binocular microscope. Distinct pulses of recruitment lasting for 10–30 years were deemed fire related if the onset of high tree recruitment corresponded to a fire date 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; Rowe et al. 1974; Barrett & Arno 1988; Means 1989; Brown & Swetnam 1994). Consequently, we used radial growth suppressions and releases (200% change in radial growth for five years compared to the previous five years) to identify fire dates in cross sections and cores with no associated scar in the sample. Tree rings in cores or cross sections with radial growth suppressions or releases were cross dated and the dates of radial growth changes were

This content downloaded from 128.114.34.22 on Wed, 25 May 2016 00:10:06 UTC
All use subject to http://about.jstor.org/terms

identified and deemed fire related if a nearby fire scar sample recorded the fire in the same year.

Fire extent was estimated from the mapped locations of fire occurrence in cross sections and plots. Boundaries were drawn equidistant between points (minimum of 3) with and without fire evidence in a given year, and boundaries were extended upslope until a potential barrier to fire spread (i.e., lava flows of rock outcrops, compact short-needle fuel beds) was encountered (Agee et al. 1990; Agee 1993). The area of each fire was then determined with a planimeter.

The fire rotation (FR) (Heinselman 1973) was estimated for each compositional group using the fire extent data. FR is the number of years needed for an area equal to the size of the study unit to burn, given the extent of burning in that period. For any given period, some parts of a study unit may burn more than once and others not at all (Heinselman 1973).

Fires burn with variable severity across a landscape, killing many trees in some stands and few in others and variation in fire severity is reflected in the age-structure of forest stands. For example, stands that have experienced severe fires are usually even-aged (unimodal age-class distribution), while multi-aged stands (multi-modal distributions) reflect moderate severity fires that killed only portions of the stand. Low severity fires, in contrast, may not produce any discrete age classes (Heinselman 1973; Johnson 1979; Agee et al. 1990).

Spatial variation in fire severity was determined using tree age data in plots and forest patches evident on 1939–1941 and 1993 aerial photographs to map the cumulative proportion of the study area that burned at high, moderate, and low severity between 1864 and 1939. Stand boundaries were too diffuse to map earlier evidence of fire severity in the study area. Patches of forest that burned at different severity were identified on the aerial photographs using the relative density of short even-aged stems and taller, emergent trees that survived successive fires. High severity patches had <10 emergent stems ha^{-1}, moderate severity patches had 10–20 emergent stems ha^{-1}, and low severity patches had >20 emergent stems ha^{-1}. Brushfields were assumed to be caused by past high severity fire. Brushfields in the 1939–1941 photographs were mostly forest in the 1993 aerial photographs.

We also mapped landscape-scale patterns of severity for parts of three individual fires (1883, 1889, 1918). The area for each fire represents only the area where there was no overlap between fires.

Results

Forest composition and environmental gradients

Five forest compositional groups were identified by TWINSPAN based on species importance values, and they were segregated by elevation and potential soil moisture ($P<0.001$ ANOVA) (Table 1, Figure 2a). White fir-sugar pine (WF-SP) stands ($n=14$) occur at low elevations (1750–1965 m) on west facing slopes, and they contain a mixture of white fir, sugar pine, Jeffrey pine, and ponderosa pine. White fir-Jeffrey pine (WF-JP) forests ($n=34$) occur between 1750 and 2070 m on south, north, and east aspects; stands are strongly dominated by white fir, and Jeffrey pine is a common associate. Red fir-white fir (RF-WF) stands ($n=24$) occur between 1900 and 2170 m on all slope aspects; red fir is the dominant and white fir and western white pine are common associates. Lodgepole pine (LP) stands ($n=13$) occur on mesic flats between 1950 and 2110 m. They are strongly dominated by lodgepole pine, and red and white fir are important associates. Red fir-mountain hemlock (RF-MH) stands ($n=15$) occupy north-facing slopes at high elevations (1945–2210 m). They are co-dominated by red fir and mountain hemlock, and western white pine is a common associate.

Fire regimes and compositional/environmental gradients

Fire record

Sixty-five fire dates between 1652 and 1942 were identified from 310 fire scars in 50 samples. The length of the fire record varied by forest compositional group and was longest in WF-SP (1658–1904, $n=9$) and WF-JP (1652–1918, $n=18$) forests, and shorter in RF-WF (1694–1899, $n=7$), LP (1755–1883, $n=10$), and RF-MH (1717–1942, $n=6$) forests (Figure 3).

Composite fire return intervals were calculated for different periods for each compositional group, starting with the year fires were recorded by at least two samples. The period was 1658–1995 for WF-SP, 1710–1995 for WF-JP, 1749–1995 for RF-WF, 1755–1995 for LP, and 1783–1995 for RF-MH forests. For point fire return intervals, all recorded fires in multiple scarred samples ($n=43$) were included, so the length of the fire record varied with each sample.

Season of fire occurrence

The position of fire scars within annual rings varied across compositional (Table 2) and environmental

This content downloaded from 128.114.34.22 on Wed, 25 May 2016 00:10:06 UTC
All use subject to http://about.jstor.org/terms

Table 1. Mean importance value (maximum 300), basal area (m2ha-1) and density (ha-1) of trees (>4.0 cm dbh) in forest compositional groups identified by TWINSPAN in the Thousand Lakes Wilderness, southern Cascades, California. Compositional groups are white fir-sugar pine (WF-SP), white fir-Jeffrey pine (WF-JP), red fir-white fir (RF-WF), lodgepole pine (LP), and red fir-mountain hemlock (RF-MH). n is the number of samples in each group. Elevation and relative soil moisture (TRMI) varied among forest groups (P<0.001 ANOVA). TRMI varies between 0 (xeric) and 60 (mesic).

	Compositional group														
	WF-SP (n=14)			WF-JP (n=34)			RF-WF (n=24)			LP (n=13)			RF-MH (n=15)		
Species	IV	BA	Density	IV	BA	Density	IV	BA	Density	IV	BA	Density	IV	BA	Density
White fir	155.1	44.2	1730.4	200.3	53.5	1387.5	81.5	15.1	358.3	53.5	5.4	355.8	3.4	<0.1	5.0
Red fir	13.5	1.5	39.3	22.0	5.7	65.4	137.6	38.1	739.6	65.4	12.1	351.9	121.7	24.9	613.3
Lodgepole pine	0.0	0.0	0.0	4.9	0.7	12.5	13.1	2.3	42.7	152.0	34.7	1353.8	11.2	0.6	21.7
Jeffrey pine	47.2	12.0	176.8	58.7	16.3	73.5	24.2	4.5	53.1	7.7	3.0	5.8	0.0	0.0	0.0
W. white pine	0.0	0.0	0.0	3.0	0.6	5.9	31.6	6.5	71.9	19.4	3.4	40.4	63.5	14.7	118.3
Mt. Hemlock	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0	<0.1	1.9	100.2	22.0	431.7
Sugar pine	57.4	24.2	132.1	6.5	0.8	5.1	8.4	1.7	14.6	0.0	0.0	0.0	0.0	0.0	0.0
Ponderosa pine	18.1	5.6	28.6	4.6	1.5	5.9	2.2	0.5	3.1	0.0	0.0	0.0	0.0	0.0	0.0
Incense-cedar	8.8	3.7	7.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Whitebark pine	0.0	0.0	0.0	0.0	0.0	0.0	1.3	0.1	1.0	0.0	0.0	0.0	0.0	0.0	0.0
	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.
Elevation (m)	1830	1750	1965	1900	1750	2070	2050	1900	2170	1995	1950	2110	2150	1945	2210
TRMI	33	18	44	36	22	56	29	18	47	45	35	53	30	19	38

This content downloaded from 128.114.34.22 on Wed, 25 May 2016 00:10:06 UTC
All use subject to http://about.jstor.org/terms

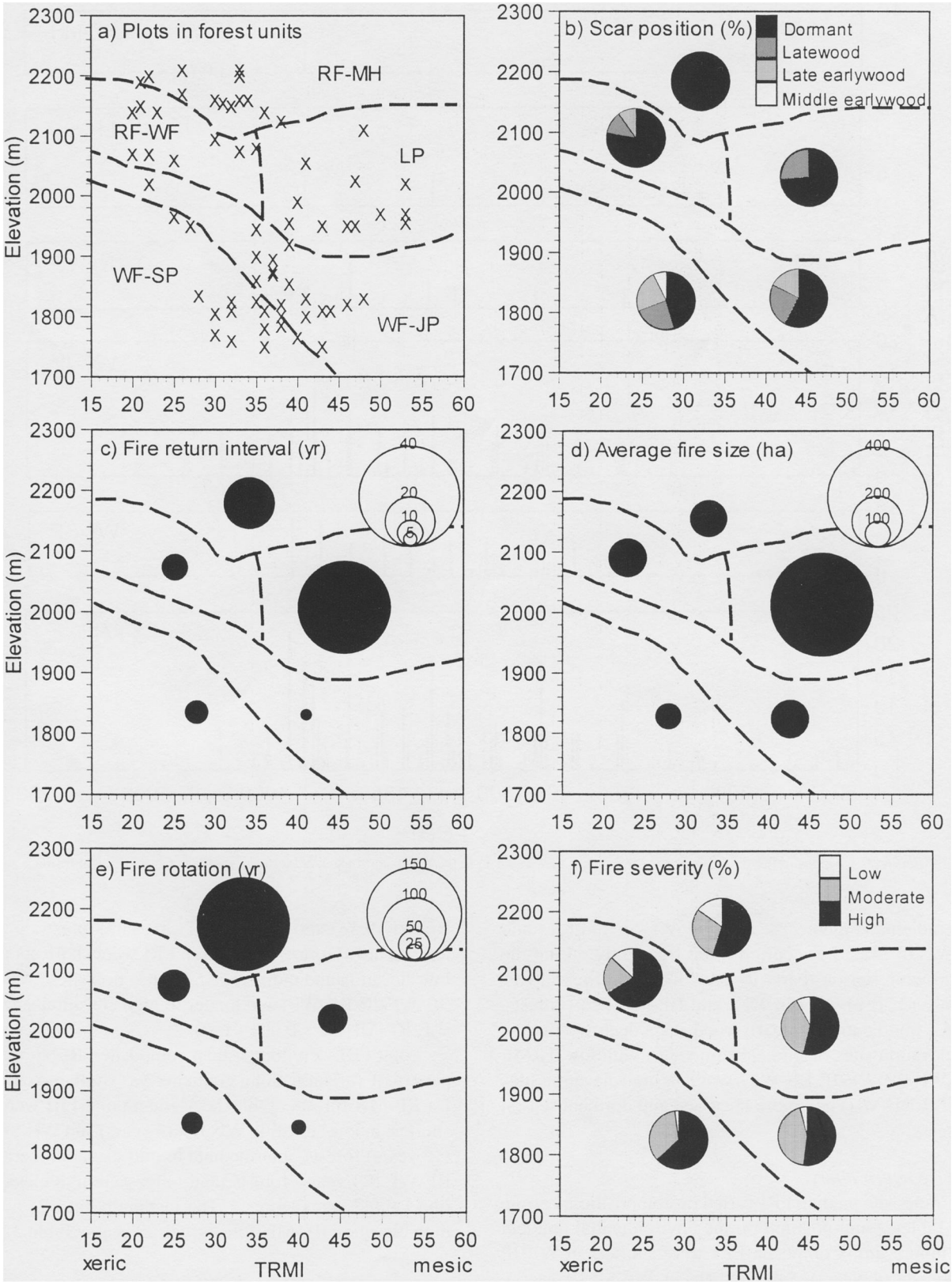

Figure 2. Diagram of (a) forest compositional group (see Table 1); (b) season of fire occurrence; (c) composite median fire return interval; (d) mean fire size; (e) fire rotation (pre-1905); and (f) cumulative fire severity since 1864 relative to elevation and relative soil moisture (Topographic Relative Moisture Index) (Parker 1982) in the Thousand Lakes Wilderness, southern Cascades, California.

This content downloaded from 128.114.34.22 on Wed, 25 May 2016 00:10:06 UTC
All use subject to http://about.jstor.org/terms

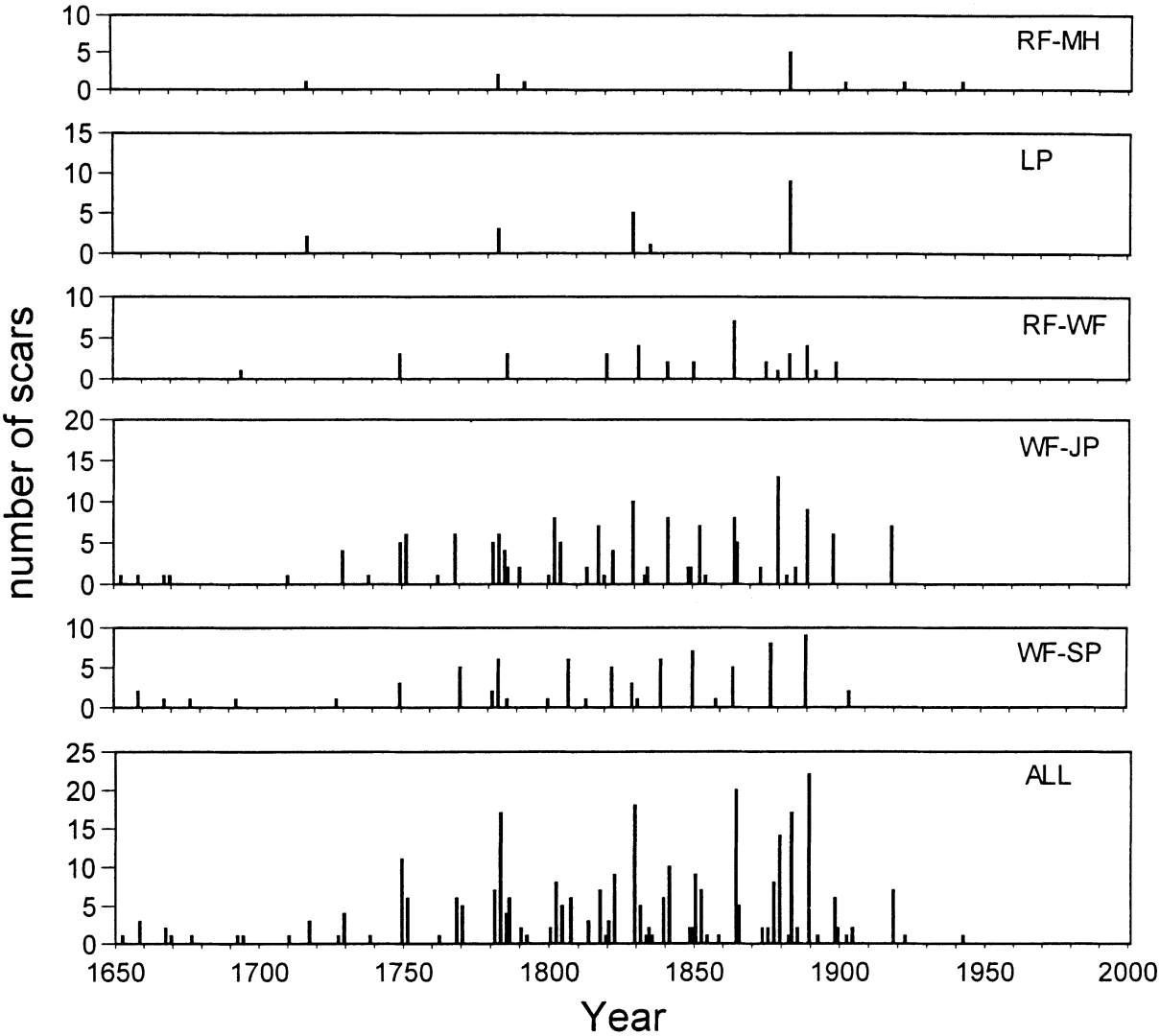

Figure 3. Composite fire chronology for forest types (see Table 1) in the Thousand Lakes Wilderness, southern Cascades, California.

gradients (Figure 2b). Fires in WF-SP (54.8%) and WF-JP (42.5%) occurred more frequently during the growing season (early to latewood) than fires in RF-WF (22.6%), LP (26.7%), and RF-MH (0%) forests. All middle and late earlywood scars occurred on low elevation sites or mid elevation sites with low TRMI, (WF-SP, WF-JP, RF-WF), whereas high elevation sites (LP, RF-MH) had more latewood and dormant season scars.

Fire return interval

Composite median FRI varied by compositional group (Table 2) and position on the environmental gradient (Figure 2c). Composite FRI were shortest in WF-JP forests (4 years), intermediate in WF-SP (9 years), RF-WF (9.5 years) and RF-MH (20 years) forests, and longest in LP forests (37 years). FRI were shortest on low elevation and more xeric mid elevation sites (WF-SP, WF-JP, RF-WF) and longer in high elevation sites (LP, RF-MH) ($P<0.001$ t-test).

Point FRI were longer than composite FRI but the pattern of variation along gradients was similar except for RF-MH forests (Table 2). Median point FRI were shortest in low elevation WF-JP (14 years) and WF-SP (15 years) forests, intermediate in mid-elevation xeric RF-WF (24 years) forests, and longest in high elevation LP (47 years) forests. The median point FRI for high elevation RF-MH forests was 20 years (Table 2).

This content downloaded from 128.114.34.22 on Wed, 25 May 2016 00:10:06 UTC
All use subject to http://about.jstor.org/terms

Table 2. Fire regime parameters for forest compositional groups (see Table 1) in the Thousand Lakes Wilderness, Southern Cascades, California.

Parameter	Compositional group				
	WF-SP	WF-JP	RF-WF	LP	RF-MH
Number of sample plots	13	20	9	18	6
Number of fire scar samples	9	18	10	7	6
Season of fire (%)					
Dormant	45.2	57.5	77.4	73.3	100
Latewood	23.8	25.0	12.9	26.6	0.0
Late	23.8	17.5	9.7	0	0
Middle	7.1	0	0	0	0
Early	0	0	0	0	0
Unknown	46.8	25.5	18.4	25.0	58.3
number of scars	79	161	38	20	12
Fire return interval (yr)					
Composite median (range)	9 (2–35)	4 (1–20)	9.5 (3–37)	37 (6–48)	20 (9–91)
Point median (range)	15 (7–43)	14 (7–25)	24 (4–55)	47 (28–54)	20 (9–91)
Sample area (ha)	335	537	30372	460	338
Fire size (ha)					
Mean (range)	103(12–335)	145.7 (34–388	151(34–372)	405(295–460)	140 (124–155)
Fire rotation (yr)	34	22	50	46	147
Fire severity (%)					
Low	2	4	13	8	15
Moderate	35	44	21	38	30
High	63	52	66	54	55

FRI also varied temporally (Table 3). Few or no fires burned after 1905 in any compositional group (Table 3; Figure 3). But fires burned frequently during the presettlement and settlement periods and there was no difference ($P>0.01$, t-test) in presettlement and settlement FRI for any compositional group or the study area as a whole.

Fire extent

Fire extent varied by year, by forest compositional group and on sites with different potential soil moisture (Table 2; Figure 2d). The average size of a fire (n=33) between 1729 and 1918 was 298 ha (range 34–1684 ha) and fires >600 ha occurred in 1783, 1864, 1883, 1885, and 1889. Average fire sizes were similar and smaller in WF-SP (103 ha, range 12–335 ha), RF-MH (140 ha, range 124–155 ha), WF-JP (146 ha, range 34–388 ha), and RF-WF forests (151 ha, range 34–372) than in LP forests (405 ha, range 295–460 ha). Average fire size also varied with potential soil moisture. Fires were smaller on low elevation xeric sites and largest on mesic mid elevation sites.

Fire rotations

FR for the pre-1905 period varied by compositional group (Table 2) and across environmental gradients (Figure 2e). FRs were shortest for WF-JP forests (21.5 years), followed by WF-SP (33.7 years), LP (45.8 years) and RF-WF (50.4 years) forests. The FR in RF-MH forests was longer (146.6 years) than in other compositional groups. Variation in FRs was also strongly associated with elevation.

Fire severity

The cumulative percentage of area burned at low, moderate, and high severity since 1864 was similar across environmental and compositional gradients (Table 2, Figure 2f). More area burned at high or moderate severity than low severity on all slope aspects, slope positions and in all compositional groups.

Fire severity patterns were strongly influenced by the severity of fires in 1883, 1889, and 1918. The 1883 fire burned most of the LP forest in the Thousand Lakes Valley and RF-MH forests on the north slope of Fredonyer Peak. Most of it burned at high severity. The 1889 fire burned low elevation WF-SP and WF-JP

This content downloaded from 128.114.34.22 on Wed, 25 May 2016 00:10:06 UTC
All use subject to http://about.jstor.org/terms

Table 3. Mean composite fire return interval (yr) for the presettlement, settlement, and fire suppression period by forest type (see Table 1) in the Thousand Lakes, Wilderness, southern Cascades, California. There was no difference ($P>0.01$, t-test) in the mean fire return interval for the presettlement and settlement period. Few fires burned during the suppression period. n is the number of intervals.

Forest type	Presettlement time period	mean	n	Settlement time period	Mean	n	Fire suppression time period	Mean	n
WF-SP	1658-1849	11.3	16	1850-1904	10.8	5	1905-1995	*	*
WF-JP	1710-1849	5.8	4	1850-1904	5.1	9	1905-1995	*	*
RF-WF	1749-1849	23.0	4	1850-1904	7.0	7	1905-1995	*	*
LP**	1755-1849	23.5	3	1850-1904	*	*	1905-1995	*	*
RF-MH**	1783-1849	33.5	2	1850-1904	27.0	2	1905-1995	45.0	2
All	1652-1849	5.2	37	1850-1904	3.6	15	1905-1995	12.0	2

**Too few intervals for comparison.

forests, and RF-WF forests, on the southern, western, and northern slopes of Crater and Magee Peaks, and it was mostly a high severity burn. Low elevation WF-JP forests southeast of Fredonyer Peak also burned at high severity in 1918.

Discussion

Species distribution and abundance patterns varied across environmental gradients in TLW. Tree species were segregated primarily by elevation and secondarily by topographically controlled patterns of potential soil moisture. Similar species distribution patterns have been identified elsewhere in the southern Cascades (e.g., Barbour 1988; Franklin & Dryness, 1973; Taylor 1990a; Parker 1991, 1995) and they are regionally typical.

Variation in some fire regime parameters in TLW paralleled environmental and compositional gradients. Both composite and point FRI were shortest in low elevation mixed conifer forests and longest in mid elevation mesic LP forests; xeric RF-WF and high elevation RF-MH forests were intermediate. Our FRI are probably conservative estimates of fire occurrence for compositional groups because low intensity fires may not scar trees and trees scarred by fires may heal over completely leaving no exteral evidence of fire (Agee 1993; Taylor 1993; Taylor & Skinner 1998). Our estimates, however, fall within the range for forests with similar composition elsewhere in the Sierra Nevada and Cascade ranges (e.g., Kilgore & Taylor 1973; McNeil & Zobel 1980; Taylor 1993, 2000; Caprio & Swetnam 1995; Solem 1995).

The increase in length of FRI with elevation is probably caused by factors that influence the production and flammability of fuels. Fine fuel production rates are higher in low elevation mixed conifer forests than in upper montane fir dominated forests or mixed species subalpine forests (Agee et al. 1978; Stohlgren 1988; van Wagtendonk, pers. commun.). Consequently, fires can can reburn in a low elevation mixed conifer site sooner. Fuel beds of long pine needles (i.e., Jeffrey pine, ponderosa pine, sugar pine) are also less dense than those composed of short needled species (i.e., white fir, red fir, lodgepole pine) (Agee 1993; van Wagtendonk 1998) and fire spread and intensity are greater in low density fuel beds (Albini 1976; Rothermel 1983; Fonda et al. 1998). Finally, the period fuels are dry enough to burn each year is longer on warmer low elevation sites than on cooler more mesic high elevation sites.

FRI declined dramatically in TLW after 1905 with the onset of a federal fire suppression policy. Fire suppression has reduced the frequency and extent of fires throughout the Sierra Nevada and Cascade ranges compared to the pre-suppression period (e.g., Kilgore & Taylor 1979; McNeil & Zobel 1980; Taylor 1993, 2000; Skinner & Change 1996). In some ponderosa pine dominated forests in the Sierra Nevada (e.g., Caprio & Swetnam 1995), and in Arizona (e.g., Savage & Swetnam 1990), an earlier settlement period reduction in fire occurrence has been identified and attributed to livestock grazing. There was no evidence of a settlement period decline in fire frequency in TLW that could be attributed to 19th century grazing. A presettlement fire regime persisted in TLW until fire suppression was implemented in 1905.

The season fires burn strongly affects species' response to fire (e.g., Kauffman 1990; Agee 1993), and the season fires burned varied along environmental and

This content downloaded from 128.114.34.22 on Wed, 25 May 2016 00:10:06 UTC
All use subject to http://about.jstor.org/terms

compositional gradients. Growing season fires were more frequent in drier, low elevation forests than in more mesic or high elevation forests. This pattern is probably due to earlier drying of fuels at low elevation. Fires may not start or spread into higher elevation forests until late summer when fuels are dry enough to carry fire.

Variation in fire size was inversely related to the soil moisture gradient and the average period between fires. The average fire was three-fold larger in mesic mid-elevation LP forests with long FRI than in other forests at either high or low elevation. This pattern is probably related to relatively long periods of fuel accumulations between unusually dry years that are needed to dry fuels to the point that they carry fire. Large fires in LP forests occurred in 1783, 1829, and 1883, which regional tree ring reconstructions of drought (Palmer Drought Severity Index) show as being dry or very dry years (Cooke et al. 1996). Relatively long periods of fuel accumulation between drought years would provide sufficient fuels for fires to burn over large areas.

Fire rotation lengths in TLW are strongly associated with elevation. Rotation periods are much shorter in low elevation mixed conifer forests than in high elevation RF-MH forests because similar sized fires burn more often. LP forests have intermediate rotation lengths, despite long FRI, because fires are more extensive.

Fire severity patterns in TLW, in contrast, did not vary much across compositional and environmental gradients. High severity fires comprised >50% of the cumulative area burned between 1864 and 1939 in all forest groups and most of the remaining area burned at moderate severity. The large proportion of high and moderate severity burns strongly reflects the severity patterns of three recent fires (1883, 1889, 1918). Each of these fires burned at high severity through two or more forest groups and they burned a combined area >2200 ha. Fire severity patterns for burns earlier in the 19th century could not be reconstructed because the recent severe burns consumed tree-ring evidence of them. It is therefore uncertain if the similarity in fire severity we identified across both environmental and compositional gradients is due to chance behavior of fires during recent burns or a persistent pattern for forests in TLW.

The patterns of fire severity we identified for TLW mixed conifer forests are inconsistent with general models of pre-Euro-American fire regimes in the Sierra Nevada (e.g., Kilgore 1973) and Cascade Range forests (e.g., Agee 1993). Fires in mixed conifer forests have been previously described as being frequent and low to moderate in severity (e.g., Kilgore 1973; Agee 1993). These frequent, low severity fires kill mostly seedlings and saplings, and occasionally parts of stands, creating fine-grained structures of open and closed canopy conditions and fuels, which impede development of high severity fires (e.g., Bonnicksen & Stone 1982; Kilgore 1973; Kilgore & Taylor 1979; Parsons & DeBenedetti 1979; Skinner & Chang 1996). In TLW, fires in mixed conifer forests (WF-SP, WF-JP) burned primarily at high and moderate severity and generated coarse-grained structures of even or multi-aged forests at landscape scales.

The large area of high and moderate severity patterns we identified in TLW mixed conifer forests is not the result of unusually high fuel accumulations from 20th century fire suppression, which have recently caused severe fires in mixed conifer forests in the Cascade and Sierra Nevada Ranges (Agee 1993; Weatherspoon et al. 1992; Husari & McKelvey 1996; Skinner & Chang 1996). Severe fires in the TLW pre-date the fire suppression period. Moreover, high severity fires also occurred in the 19th century in other southern Cascade mixed conifer forests (Beaty 1998; Taylor unpublished data). The predominantly high and moderate severity fires in mixed conifer forests in TLW indicate general models of mixed conifer should be modified to include greater variation in fire severity and it suggests that there may be geographic variation in mixed conifer forest fire regimes. Geographic location is known to contribute strongly to variation in disturbance regime parameters and to species response to disturbance in other forested landscapes (e.g., Spies & Franklin 1989; Veblen et al. 1992; Shinneman & Baker 1996; Taylor & Skinner 1998).

Conclusions

Species distribution and abundance patterns in the southern Cascades change markedly along temperature and moisture gradients. Along these same gradients there is also variation in fire regime parameters that can affect vegetation patterns. Changes in the return interval, rotation period, and season of fires are not independent of environmental or species distribution patterns because species composition, temperature, and moisture all influence the distribution, production, abundance, and flammability of fuels. Patterns of fire severity, in contrast, were independent of

This content downloaded from 128.114.34.22 on Wed, 25 May 2016 00:10:06 UTC
All use subject to http://about.jstor.org/terms

compositional and environmental gradients, and variation in fire severity is a potentially important source of diversity that affects vegetation patterns at landscape scales (Christensen 1993; Chappell & Agee 1996; Taylor & Skinner 1998). The pattern of mostly high and moderate severity fires at all positions on compositional and environmental gradients probably reflects chance events (i.e., extreme fire weather) that diminish the importance of variation in fuels in fire behavior (e.g., Bessie & Johnson 1995). These fire severity patterns underscore the influence of non-equilibrium processes on vegetation patterns in TLW. Managers have also modified fire regimes in TLW for nearly a century by suppressing fire at all gradient positions. This modification will undoubtedly cause some shifts in species composition, and change landscape scale vegetation patterns.

Acknowledgements

This research could not have been completed without the help of many individuals. R. Olson and L. Hood (Lassen National Forest) provided important logistic and administrative support for the duration of the project. P. Clement, B. Fletcher, J. Ritchie, G, Welc, J. Wood and S. Yapa, assisted in the field and P. Clement, B. Fletcher, T. Fearer, and J. Maylie helped in the lab. We thank P. Bogush for cartographic work. This research was funded by a cost share agreement between The Pennsylvania State University and the Lassen National Forest.

References

Agee, J. K. 1981. Fire effects on Pacific Northwest forests: flora, fuels, and fauna. Pp. 54–66. Proceedings of the Northwest fire council, Portland, Oregon. USA.

Agee, J. K. 1991. Fire history of Douglas-fir forests in the Pacific Northwest. Pp. 25–33. In: Ruggiero, L. F., Audry, K. B., Carey, A. B. & Huff, M. H. (eds), Wildlife and vegetation of unmanaged Douglas fir forests: USDA Forest Service General Technical Report PNW-285. Agee, J. K. 1993. Fire ecology of Pacific Northwest forests. Island Press, Covelo.

Agee, J. K., Finney, M. & DeGouvenain, R. 1990. Forest fire history of Desolation Peak, Washington. Can. J. For. Res. 20: 350–356.

Agee, J. K., Wakimoto, R. H. & Biswell, H.H. 1978. Fire and fuel dynamics of Sierra Nevada conifers. For. Ecol. Manag. 1: 255–265.

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

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-RS-301.

Arno, S. F. & Sneck, K. M. 1977. A method for determining fire history in coniferous forests of the mountain west. USDA Forest Service 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. Can. J. For. Res. 20: 1559–1569.

Barbour, M. G. 1988. California upland forests and woodlands. Pp. 131–164. In: Barbour, M. G. & Billings W. D. (eds.). North American Terrestrial Vegetation: Cambridge University Press, New York.

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.

Barton, A. M. 1993. Factors controlling plant distributions: drought, competition, and fire in montane pines in Arizona. Ecol. Monog. 63: 367–397.

Beaty. R. M. 1998. Spatial and temporal variation in fire regimes and forest dynamics along a montane forest gradient in the southern Cascades, California. Master's Thesis, The Pennsylvania State University.

Bessie, W. C. & Johnson, E. A. 1995. The relative importance of fuels and weather on fire behavior in subalpine forests. Ecology 76: 747–762.

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.

Brown, P. M. & Swetnam, T. W. 1994. A cross-dated fire history from coast redwood near Redwood National Park, California. Can. J. For. Res. 24: 21–31.

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

Chappell, C. B. & Agee, J. K. 1996. Fire severity and tree seedling establishment in Abies magnifica forests, southern Cascades, Oregon. Ecol. App. 6: 628–640.

Christensen, N. L. 1993. Fire regimes and ecosystem dynamics. Pp. 233–244. In: Crutzen, P. J., Goldhammer, J. G. (eds), Fire in the environment: the ecological, atmospherical, and climatic importance of vegetation fires. Wiley, New York,

Cooke, E. R., Meko, D. M., Stahle, D. W. & Cleavland, M. K. 1996. Tree ring reconstructions of past drought across the conterminous United States: tests of a regression method and calibration/verification results. Pp. 155–170. In: Dean, J. S., Meko, D. M. & Swetnam T. W. (eds), Tree rings, environment, and humanity. University of Arizona, Tucson, Arizona.

Cottam, G. & Curtis, J. T. 1956. The use of distance measures in phytosociological sampling. Ecology 37: 451–460.

Dieterich, J. 19080. The composite fire interval-a tool for more accurate interpretation of fire history. Pp. 8–14. In: Stokes, M. & Dieterich, J. (eds), Proceedings of the fire history workshop. USDA Forest Service General Technical Report RM-GTR-81.

Drew, L. G. 1972. Tree ring chronologies of western North America, Vol. 3, California and Nevada. Laboratory of Tree-Ring Research, University of Arizona, Tucson.

Durbin, W. G. 1930. Report on Thousand Lake Valley Primitive Area, Lassen National Forest. Unpublished report, on file at Lassen National Forest Headquarters, Susanville, CA.

Fonda, R. W., Belanger, L. A. & Burley, L. L. 1998. Burning characteristics of western conifer needles. Northwest Sci. 72: 1–9.

This content downloaded from 128.114.34.22 on Wed, 25 May 2016 00:10:06 UTC
All use subject to http://about.jstor.org/terms

Foster, D. R. 1988. Species and stand response to catastrophic wind in central New England, USA. J. Ecol. 76: 133–151.

Foster, D. R. and Boose, E. 1992. Patterns of forest damage resulting from catastrophic wind in central New England, USA. J. Ecol. 80: 753–772.

Franklin, J. F. & Dyrness, C. T. 1973. Natural vegetation of Oregon and Washington. USDA Forest Service General Technical Report PNW-GTR-8.

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

Gosz, J. R. 1992. Gradient analysis of ecological change in time and space: implications for forest management. Ecol. Appl. 2: 248–261.

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.

Hatcher, J. B. 1941. Unapproved report, Burney Project. Unpublished report, on file at Lassen National Forest Headquarters, Susanville, CA.

Heinselman, M. L. 1973. Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. Quat. Res. 3: 329–382.

Hill, M. O. 1979. TWINSPAN: A FORTRAN program for arranging multivariate data in an ordered two-way table by classification of individuals and attributes. Section on Ecology and Systematics, Cornell University, Ithaca, New York.

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.

Husari. S. & McKelvey, K. S. 1996. Fire management policies and programs. Pp. 1041–1069. Sierra Nevada ecosystem project: final report to congress, Vol. II, Assessments and scientific basis for management options. University of California Davis, Center for Water and Wildland Resources, Davis, California.

Johnson, E. A. 1979. Fire recurrence in the subarctic and its implications for vegetation composition. Can. J. Bot. 57: 1374–1379.

Kane, P. S. 1980. Through Vulcan's eye. The geology and geomorphology of Lassen Volcanic National Park. Loomis Museum Associates, Red Bluff, CA.

Kauffman, J. B. 1990. Ecological relationships of vegetation and fire in Pacific Northwest Forests. Pp. 39–52. In: Walstad, J. D., Radosevich, S. R. & Sandberg, D. V. (eds), Natural and prescribed fire in Pacific Northwest forests. Oregon State University Press, Corvallis, OR.

Kilgore, B. M. 1973. The ecological role of fire in Sierran conifer forests: its application to national park management. Quat. Res. 3: 496–513.

Kilgore, B. M. & Taylor, D. 1979. Fire history of a mixed-conifer forest. Ecology 55: 772–783.

Major, J. 1977. California climate in relation to vegetation. Pp. 11–74. In: Barbour, M. G. &. Major, J. (eds). Terrestrial vegetation of California. John Wiley & Sons, New York.

McNeil, R. C. & Zobel, D. B. 1980. Vegetation and fire history of a ponderosa pine - white fir forest in Crater Lake National Park. Northwest Sci. 54: 30–46.

Means, J. E. 1989. Estimating the date of a single bole scar by counting tree rings in increment cores. Can. J. For. Res. 19: 1491–1496.

Merriam, C. H. 1898. Life zones and crop zones of the United States. Bulletin of the US Biological Survey 10: 1–79.

Norris, R. M. & Webb, R. W. 1990. Geology of California. John Wiley & Sons, New York.

Parker, A. J. 1982. The topographic relative moisture index: an approach to soil moisture assessment in mountain terrain. Phys. Geogr. 3: 160–168.

Parker, A. J. 1991. Forest/environment relationships in Lassen Volcanic National Park, California, U.S.A. J. Biogeogr. 18: 534–552.

Parsons, D. J. & DeBenedetti, S. H. 1979. Impact of fire suppression on a mixed-conifer forest. For. Ecol. Manag. 2: 21–33.

Peet, R. K. 1978. Latitudinal variation in southern Rocky Mountain forests. J. Biogeogr. 5: 275–289.

Pitcher, D. C. 1987. Fire history and age structure of red fir forests in Sequoia National Park, California. Can. J. For. Res. 1: 582–587.

Romme, W. H. 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. Ecol. Monogr. 52: 199–221.

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. C. 1983. How to predict the spread and intensity of wildfires. USDA Forest Service General Technical Report INT-GTR-143.

Rowe, J. S., Bergsteinsson, J. L., Podbury, G. A. & Hermesh, R. 1974. Fire studies in the MacKenzie Valley. Canadian Department of Indian Affairs and Northern Development, Ottawa, Ontario. INA Publication QA-1567-000-EE-A1.

Rundel, P. W., Parsons, D. J. & Gordon, D. T. 1977. Montane and subalpine vegetation of the Sierra Nevada and Cascade Ranges. Pp. 559–599. In: Barbour, M. G. & Major J. (eds), Terrestrial vegetation of California: John Wiley & Sons, New York.

Savage, M. L & Swetnam, T. W. 1990. Early 19th-century fire decline following sheep pasturing in Navajo ponderosa pine forest. Ecology 71: 2374–2378.

Schulz, P. E. 1954. Indians of Lassen Volcanic National Park and vicinity. Loomis Museum Associates, Red Bluff, CA.

Shinneman, D. J. & Baker, W. L. 1996. Nonequilibrium dynamics between catastrophic disturbances and old-growth forests in ponderosa pine landscapes of the Black Hills. Cons. Biol. 11: 1276–1288.

Skinner, C. N. & Chang, C. R. 1996. Fire regimes, past and present. Pp. 1041–1069. Sierra Nevada ecosystem project: final report to congress, Vol. II, Assessments and scientific basis for management options, University of California Davis, Center for Water and Wildland Resources, Davis, California.

Solem, M. N. 1995. Fire history of the Caribou Wilderness, Lassen National Forest, California, USA. M.S. thesis, The Pennsylvania State University, University Park.

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

Stohlgren, T. J. 1988. Litter dynamics in two Sierran mixed conifer forests, I. Litter fall and decomposition rates. Can. J. For. Res. 18: 1127–1135.

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

Taylor, A. H. 1990a. Habitat segregation and regeneration of red fir and mountain hemlock in ecotonal forests of Lassen Volcanic National Park, California. Phys. Geogr. 11: 36–48.

Taylor, A. H. 1990b. Tree invasion of meadows in Lassen Volcanic National Park, California. Prof. Geogr. 42: 457–470.

Taylor, A. H. 1993. Fire history and structure of red fir (*Abies magnifica*) forests, Swain Mountain Experimental Forest, Cascade Range, northeastern California. Can. J. For. Res. 23: 1672–1678.

This content downloaded from 128.114.34.22 on Wed, 25 May 2016 00:10:06 UTC
All use subject to http://about.jstor.org/terms

Taylor, A. H. 1995. Forest expansion and climate change in the mountain hemlock (*Tsuga mertensiana*) zone, Lassen Volcanic National Park, California, U.S.A. Arc. & Alp. Res. 27: 207–216.

Taylor, A. H. 2000. Fire regimes and forest changes in mid and upper montane forests in the southern Cascades, Lassen Volcanic National Park, California, USA. J. Biogeogr. 27: 87–104.

Taylor, A. H. & Skinner, C. N. 1998. Fire history and landscape dynamics in a late successional reserve, Klamath Mountains, California, USA. For. Ecol. Manag. 111: 285–301.

USDA 1995. Range management plan Magee Peak Allotment. USDA Forest Service, Lassen National Forest, Supervisors Office, Susanville, California.

Veblen, T. T. 1989. Tree regeneration responses to gaps along a transandean gradient. Ecology 70: 541–543.

van Wagtendonk, J. W. 1998. Fuel bed characteristics of Sierra Nevada conifers. Western J. Appl. For. 13: 73–84.

Veblen, T. T., Hadley, K. S., Reid, M. S. & Rebertus, A. J. 1991. The response of subalpine forests to spruce beetle outbreak in Colorado. Ecology 72: 213–231.

Veblen, T. T., Kitzberger, T. & Lara, A., 1992. Disturbance and forest dynamics along a transect from Andean rain forest to Patagonian shrubland. J. Veg. Sci. 3: 507–520.

Weatherspoon, C. P., Husari, S. & van Wagtendonk, J. W. 1992. Fire and fuels management in relation to owl habitat in forests of the Sierra Nevada and southern California. Pp. 247–260. In: Verner, J., Mckelvey, K. S., Noon, B. R., Gutierrez, R. J. & Gould, G. I. Jr. (Tech. Coor.), California spotted owl: a technical assessment of its current status: USDA Forest Service General Technical Report PSW-GTR-133.

Whittaker, R. H. 1956. Vegetation of the Great Smoky Mountains. Ecol. Monogr. 26: 1–80.

Whittaker, R. H. 1967. Gradient analysis of vegetation. Biol. Rev. 42: 207–264.

This content downloaded from 128.114.34.22 on Wed, 25 May 2016 00:10:06 UTC
All use subject to http://about.jstor.org/terms