

RESEARCH ARTICLE

## VEGETATION RESPONSES TO CHANGING FIRE REGIMES IN A ROCKY MOUNTAIN FOREST

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### ABSTRACT

In western North America, subalpine forests experience fires that vary greatly in terms of severity and extent. However, beyond observational and dendroecological records, little is known about past fire severity and magnitude. This is because metrics used to identify fire and ecological impacts in the deep past (i.e., sedimentary charcoal and pollen data) are coarse tools for examining fine-scale environmental responses. Yet large fires should result in changes in pollen abundance and composition, which in turn can be used to identify event types, or severity of past events. We compare pollen spectra changes from a subalpine forest following identified fire events, to pollen spectra from periods between fires. From the pollen data, two types of fire events may be inferred. Fire events that affect understory plant composition (low to mid-severity) result in increases in canopy pollen. Fire events that consume both understory and canopy plants (high severity) result in decreases in canopy pollen relative to understory pollen and likely reflect differences in the recovery rates of trees compared to shrubs, grasses, and forbs. Inferred fire type showed no relationship to the size of charcoal peaks, suggesting that the quantity of charcoal observed in a sample does not provide information on fire severity. These results reveal the potential of examining fire regimes through time by combining sedimentary charcoal and pollen data, extending our interpretations of fire regimes deeper into the past.

*Keywords:* fire severity, historical range of variability, lodgepole pine, management, *Pinus contorta*, pollen analysis, succession

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### INTRODUCTION

Sedimentary records of fire occurrence have expanded our understanding of fire regimes beyond the observable record and the scope of physical evidence identified by dendroecology. These records have also contributed to our understanding of fire regimes in ecosystems (e.g. rainforests, grasslands) where

previous knowledge of fire frequency was limited (Long *et al.* 1998, Whitlock and Larsen 2001, Duffin 2008, Walsh *et al.* 2008, Conedera *et al.* 2009, Brunelle *et al.* 2010). Recent analyses of fire histories based on sedimentary charcoal have expanded the interpretation of these data to include some metrics of fire biomass consumption (Duffin 2008, Marlon *et al.* 2008, Higuera *et al.* 2009, Marlon *et al.* 2009).

For example, Duffin (2008) reported that increased fire intensity was associated with greater precipitation and resulted in greater herbaceous pollen abundance and charcoal abundance in African savanna lakes. Marlon *et al.* (2009) showed changes in charcoal abundance during the transition into and out of the Younger Dryas chronozone, 13 ka and 11.5 ka before present (ka BP). They inferred that abrupt climate change left a large amount of weakened or dead biomass on the landscape available for consumption by subsequent fire events.

The ecological role of fire in many forest systems has long been viewed as integral to the maintenance of forest form and function (Agee 1993, Kaufmann *et al.* 2007). Indeed, forest types can be differentiated in part by their fire regimes based on observed fire intensities, plant morphology, and reproductive histories (Kaufmann *et al.* 2007). The paleoenvironmental perspective of fire history has expanded our knowledge of the historical range of variability (Millar and Woolfenden 1999, Swetnam *et al.* 1999, Whitlock and Larsen 2001, Whitlock *et al.* 2004, Conedera *et al.* 2009); however, less is understood of the characteristics or ecological impact of pre-historic fires (e.g., Green 1981, 1982; Larsen and MacDonald 1998; Tinner *et al.* 1999, Tinner *et al.* 2006).

Analysis of macroscopic sedimentary charcoal has advanced significantly over the past two decades in the methodological and analytical approach of identification and quantification of charcoal particles (Clark 1988, Whitlock and Larsen 2001, Gavin *et al.* 2007, Higuera *et al.* 2007, Whitlock *et al.* 2008, Ali *et al.* 2009b, Conedera *et al.* 2009, Higuera *et al.* 2009). While it has been demonstrated that the numerous methods for quantifying charcoal abundance in a sample generally yield similar results (Ali *et al.* 2009b), most innovation has come in the statistical identification of fire events relative to the constant influx of charcoal particles into a basin (e.g., Clark

1990, Long *et al.* 1998, Mohr *et al.* 2000, Higuera *et al.* 2009, Higuera *et al.* 2010).

The methodology for conducting charcoal analysis has seen great development since the initial approach of identifying fire episodes as charcoal peaks that exceed a stationary, long-term time series mean (Clark 1990; for a complete review of methodology see Higuera *et al.* 2010). Subsequent models of analysis used charcoal “peaks” exceeding an iteratively determined universal threshold over a locally weighted mean “background” as indicative of fire episodes (Long *et al.* 1998, Mohr *et al.* 2000). The latest analytical method uses criteria identifying fires as those peaks that exceed the noise distribution of the raw data, locally determined through Gaussian mixture model of background charcoal influx at the 95% to 99% probability level (Higuera *et al.* 2010). The benefit of this latest iteration of fire episode identification is twofold. First, it is a relatively conservative estimator of fire activity based on probability function rather than researcher determined thresholds. Second, the locally determined peak identification allows for interpretation across vegetation changes and associated changes in fire regimes (Higuera *et al.* 2009, Higuera *et al.* 2010).

However, advances in sedimentary charcoal analysis for identifying fire has not been tracked by analysis of ecological effects of fire on ecosystems beyond the observable record despite the theoretical and empirical frameworks for doing so (Green 1981, 1982; Sugita *et al.* 1997, Larsen and MacDonald 1998, Tinner *et al.* 1999, Whitlock *et al.* 2004, Tinner *et al.* 2006, Higuera *et al.* 2011). Instead, fire severity is inferred from other sedimentary proxy, particularly magnetic susceptibility and grain size analysis, as high severity fire events often result in greater erosion rates and instantaneous sediment pulses within watersheds (Meyer and Pierce 2003, Pierce *et al.* 2004, Frechette and Meyer 2009, Colombaroli and Gavin 2010). Following the framework outlined by Sugita *et al.* (1997), large-scale fires,

characteristic of western North American forests, should result in temporary changes in pollen flux into a lake if the fire is several times the size of the lake basin (Sugita *et al.* 1997, Noss *et al.* 2006, Littell *et al.* 2009). As a result, changes in pollen flux of different taxa may be used as a tool to determine fire type and severity. Low to mid-severity fire events (i.e., surface fires not lethal to trees) should preferentially affect local understory taxa, resulting in relative increases in local arboreal pollen. Recovery from high severity fire, in contrast, should be reflected by an increase in pollen from understory vegetation first, with an increase in tree pollen lagging. Based on observed fire regimes in lodgepole pine (*Pinus contorta* Douglas ex Loudon var. *latifolia* Engelm. ex S. Watson) forests, this latter case should be most common in records from these environments (Baker 2009).

Lodgepole pine dominated forests are characterized as having mostly high severity fire regimes (Agee 1993, Schoennagel *et al.* 2004, Noss *et al.* 2006), suggesting that fires in these systems may be of the scale necessary to change pollen loadings deposited in lake sediments (Sugita *et al.* 1997). In addition, stand-replacing fires, which are the dominant fire type in these forests, should take multiple decades for forest recovery to pre-fire conditions, and thus may be evident in pollen data (however, see Kashian *et al.* 2005). Many studies have attempted to link long-term fire event frequency with vegetation or climate regimes (e.g., Carcaillet *et al.* 2001, Whitlock *et al.* 2008, Ali *et al.* 2009a). Here we focus on the local impacts of specific fires rather than associating long-term patterns of fire frequency with vegetation changes (e.g., Minckley *et al.* 2007). Such an analysis may be applicable to areas where fires are often much larger than lake basins and thus can affect pollen source areas.

In this study, 8000 years of post-fire vegetation data based on pollen analysis were compared to vegetation data from an unburned

subalpine forest in the southern Rocky Mountains. Fundamental questions of this study include: 1) are there statistically significant changes in pollen data after a fire event as inferred from the charcoal record?, and 2) are there statistically significant differences across post-fire pollen samples? We hypothesize that:

- 1) Fires change the vegetation for decades to centuries, and thus post-fire pollen samples should differ in composition from non-fire pollen samples.
- 2) Not all fires are the same (e.g., high severity, stand-replacing fires versus low severity, surface fires); thus, post-fire pollen samples should cluster into different groups.
- 3) Large charcoal peaks are produced by severe canopy fires; thus, they are followed by post-fire pollen samples consistent with severe canopy damage or mortality.

## METHODS

Little Windy Hill Pond (41.432928 N, 106.336342 W; elevation 2980 m), Carbon County, Wyoming, USA, is a small, ground-water-fed lake (1.32 m deep, 2.2 ha surface area) on the margin of a recessional moraine in the northern Medicine Bow Mountains with no in-flowing streams and an ephemeral outflow channel. The small watershed lies within the upper Medicine Bow River watershed, situated on Precambrian metasedimentary bedrock overlain by Pinedale age glacial till (Love and Christiansen 1985, Mears Jr. 2001). The watershed itself is relatively small (10.7 ha) with shallow slopes surrounding the lake basin.

The entire lake is currently fringed with a fen dominated by sedges (*Carex* spp. L.) with alpine laurel (*Kalmia microphylla* [Hook.] Heller), lousewort (*Pedicularis* sp. L.), lodgepole pine, and Engelman spruce (*Picea engelmannii* Parry ex Engelm.) interspersed on

raised surfaces. This fen would limit most coarse sands or macro-botanical remains from entering the lake via surface run-off, meaning that most large particles entering the basin are from wind-transport. However, persistence of this fringe feature over the period of record is doubtful given the evidence of past water-level changes (Shuman *et al.* 2009, Shinker *et al.* 2010). The upland vegetation is characterized by old-growth lodgepole pine and Englemann spruce with subdominant subalpine fir (*Abies bifolia* A. Murray) in the subcanopy. Constituents of the open understory include common juniper (*Juniperus communis* L. var. *depressa* Pursh.), sagebrush (*Artemisia* spp. L.), rose (*Rosa* spp. L.), currant (*Ribes* spp. L.), heather (*Ericaceae* spp.), and grasses and forbs (*Poaceae*, *Asteraceae*, and *Amaranthaceae*). Similar regional forests in the region have been characterized as having infrequent, high severity crown fires (Veblen 2000).

We collected a 3.45 m sediment core in July 2008 in three contiguous sections using a modified Livingstone piston corer with individual polycarbonate barrel sections. We detached the polycarbonate barrels from the piston device, capped them, and returned them to the University of Wyoming for description, sub-sampling, and analysis.

Accelerator Mass Spectrometry (AMS) radiocarbon dating was performed on the entire core to develop age-depth relationships (Table

1). Nine dates provided chronological control for the core. Age-depth estimations are based on overlapping linear regressions through consecutive sets of three calibrated radiocarbon ages. Best fit was determined by minimum differences between two overlapping regressions to minimize abrupt inflection points in the age-depth relationships. This method captures dates that fit within the errors of radiocarbon dating while providing age models that better approximate age-depth relationships than polynomials.

Charcoal analysis and fire history were based on 1 cm<sup>3</sup> samples contiguously sampled at 1 cm intervals along the entire length of the core. Samples were soaked in water, allowed to disaggregate, and sieved through 250 μm and 125 μm screens. The residuals were transferred to petri dishes, where macro-remains (>125 μm) were identified to the lowest taxonomic level and tallied using a stereo microscope at 25× to 50× magnification.

Fire history was determined using CharAnalysis (Higuera *et al.* 2009). Data were temporally binned using the value of the highest sedimentation rate determined in the age-depth model of the entire core (Mohr *et al.* 2000). CharAnalysis decomposes the charcoal count series into two components: 1) background accumulation of charcoal composed of residual materials from fire events stored in the watershed and transported into the sediment

**Table 1.** AMS radiocarbon dates used for determining age-depth relationships for Little Windy Hill Pond.

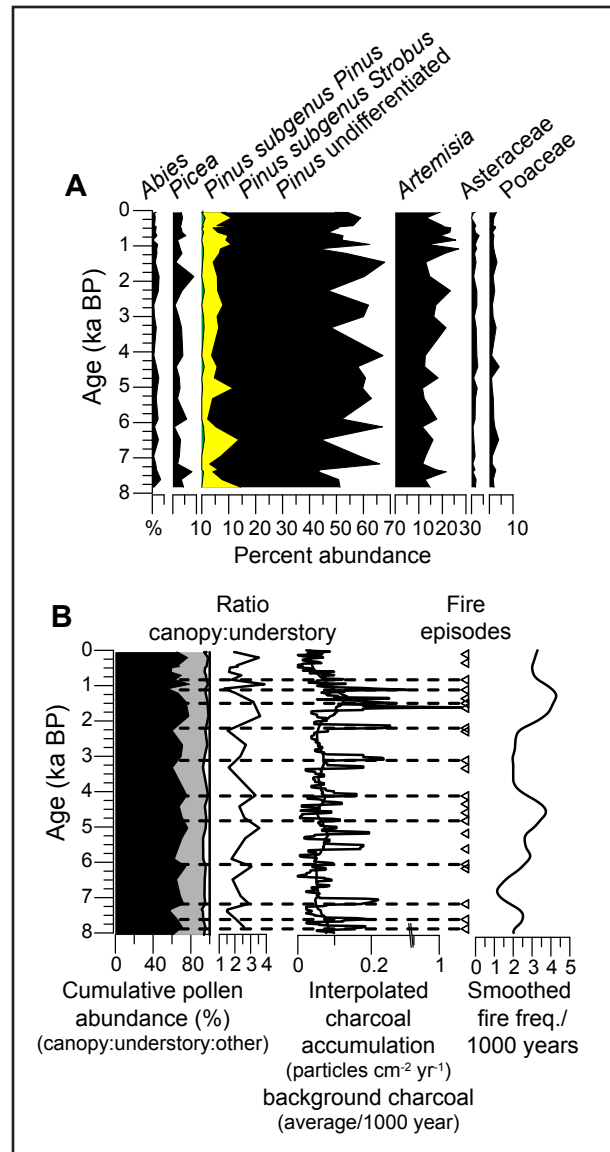
Lab code	Depth in core	Material	Age (yr)	Error	Calibrated age <sup>a</sup> (cal yr BP)
UCI 63879	NPD-LWH08 1A-1B; 53.5 cm	charcoal	1 735	20	1 613
UCI 58941	NPD-LWH08 1A-2B; 59.5 cm	charcoal	2 270	20	2 210
UCI 63880	NPD-LWH08 1A-1B; 69.5 cm	charcoal	3 040	20	3 218
UCI 63881	NPD-LWH08 1A-2B; 91.5 cm	charcoal	4 430	20	4 972
UCI 58940	NPD-LWH08 1A-2B; 105.5 cm	charcoal	6 640	25	7 506
UCI 63882	NPD-LWH08 1A-2B; 172.5 cm	charcoal	8 785	25	9 709
UCI 58938	NPD-LWH08 1A-3B; 195 cm	charcoal	9 235	45	10 297
UCI 63883	NPD-LWH08 1A-3B; 240.5 cm	charcoal	9 700	35	11 125
UGAMS 4602	NPD-LWH08 1A-3B; 333.5 cm	bulk	14 200	33	16 747

<sup>a</sup> Median age based on intcal04.14c Stuiver and Reimer.

from incidental aerial transport and surface run-off into the lake basin, and 2) charcoal peaks composed of rapidly deposited materials understood to indicate the occurrence of local fire within the lake watershed (Conedera *et al.* 2009). Background charcoal was established based on a 1000 yr lowess smoother, which is robust to outliers. Peak charcoal (total charcoal  $\div$  background charcoal) was identified as a fire event only when it exceeded the ninety-fifth percentile of the noise distribution of charcoal counts within 1000 years, based on a Gaussian mixture model (Higuera *et al.* 2009). Fire frequencies were smoothed over a 1000 yr moving window (Long *et al.* 1998).

Pollen sampling was conducted every  $\sim$ 4 cm. Pollen samples underwent standard acid-base digestion (Faegri *et al.* 1989). Minimums of 300 terrestrial pollen grains were tallied for each sample. Pollen proportions were calculated by dividing the individual pollen counts by the terrestrial pollen sum. We use proportional data for our analysis because: 1) our interest is in community-level responses to disturbance, so relative changes in pollen abundance best reflect community compositional changes; and 2) percentage data are less noisy than pollen influx data, not sensitive to changes in sedimentation rates, and thus most appropriate for determining ecological process in the case of our study (Moore *et al.* 1991, van der Knaap *et al.* 2010).

The unequal sampling strategy between the contiguously sampled fire record (charcoal) and intermittent sampling of the environment (pollen) results in a random sampling of post-fire and non-fire vegetation. Pollen data were binned into three categories: canopy, understory, and other (Figure 1; Table 2). The ratio of canopy to the understory was calculated for each sample to characterize vegetation composition of post-fire and non-fire samples. Pollen data were considered post-fire if they came from either the same or the following sample of an identified charcoal peak. Non-fire data were those that had no preceding significant or



**Figure 1.** **A:** Relative abundance of common pollen types for the past 8000 years at Little Windy Hill Pond. Shown are the relative abundances of taxa (*x*-axis) that had abundances of  $>4\%$  for at least one sample examined and are representative of canopy and understory dominants against time (*y*-axis). **B:** Cumulative pollen plot of canopy, understory, and other taxa and the ratio of canopy to understory taxa are plotted against the records of charcoal abundances interpolated into equal 19-year bins and the LOWESS background curve using a 1000 yr moving window. Fire episodes are shown for the entire record. Summary of fire frequency per 1000 yr is shown in last column. Dotted lines indicate those fire episodes with associated pollen data.

**Table 2.** Categorization of identified terrestrial pollen taxa used to determine the constituents of the canopy and understory vegetation. Types placed in the “other” category were either rare or considered regional taxa, not locally present.

Canopy	Understory	Other
<i>Abies</i>	<i>Artemisia</i>	<i>Acer</i>
<i>Picea</i>	Asteraceae	<i>Aceuthobium</i>
<i>Pinus</i> subgenus <i>Pinus</i>	<i>Cercocarpus</i>	<i>Alnus rubra</i> -type
<i>Pinus</i> subgenus <i>Strobilus</i>	Cupressaceae	<i>Amelanchier</i>
<i>Pinus</i> undifferentiated	Amaranthaceae	Apiaceae
	Ericaceae	<i>Betula</i>
	Liguliflorae	Brassicaceae
	Poaceae	Caryophyllaceae
	<i>Ribes</i>	<i>Ceanothus</i>
	Rosaceae	<i>Ephedra</i>
	<i>Shepherdia</i>	<i>Eriogonum</i>
		Fabaceae
		Lamiaceae
		Liliaceae
		Polygonaceae
		Polemoniaceae
		<i>Pseudotsuga</i>
		<i>Salix</i>
		<i>Sarcobatus</i>

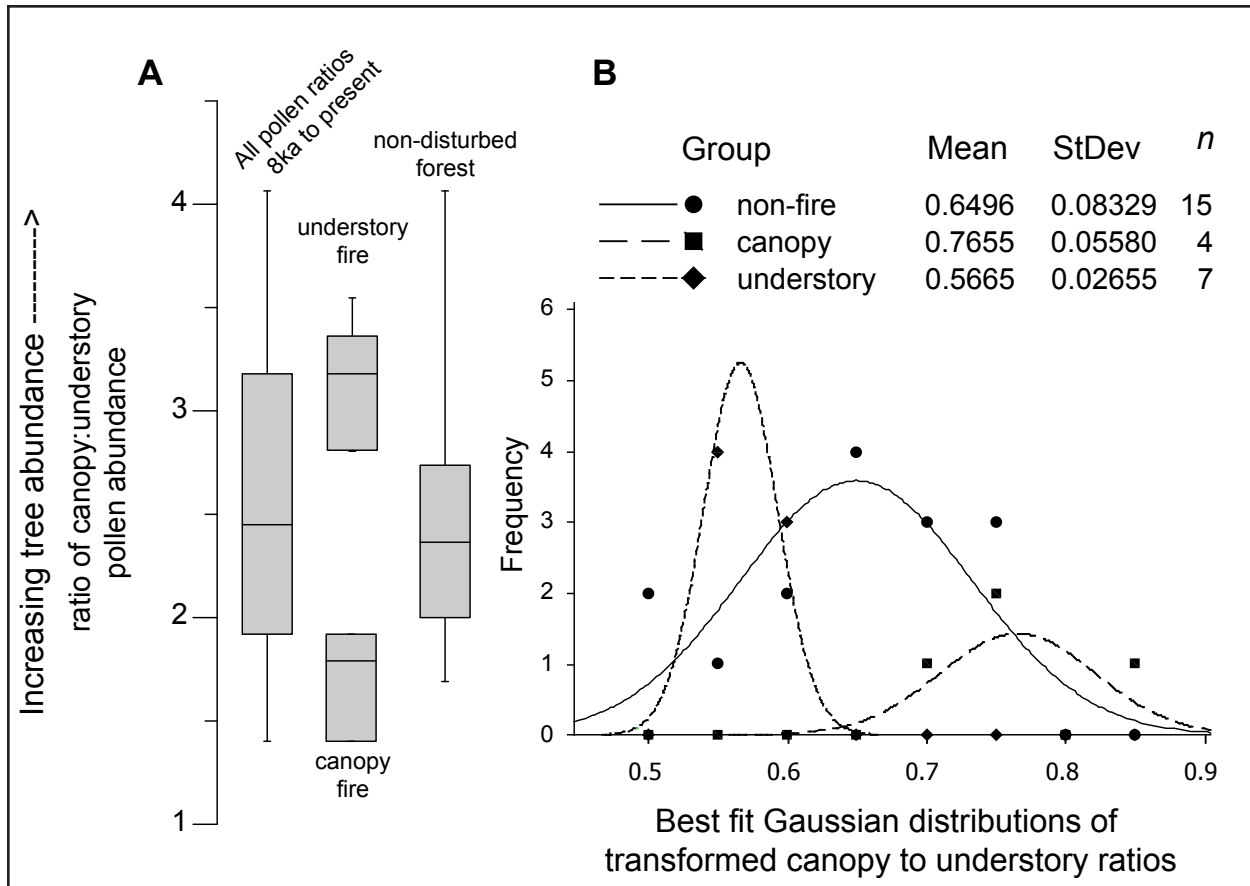
insignificant peak indication based on the CharAnalysis output (Higuera *et al.* 2009). These data were inverse square-root transformed to normalize their distribution for statistical analysis of fire type determination (Figure 2) (Box and Cox 1964). However, for discussion and box-plot presentation, we use non-transformed data. Pollen data following insignificant peaks were removed from non-fire data because of the inability to determine whether these peaks resulted from secondary transport of charcoal or a separate fire episode.

## RESULTS

The highest sedimentation rate was 19 yrs  $\text{cm}^{-1}$  (average 56 yr  $\text{cm}^{-1}$ ) at Little Windy Hill

Pond. Charcoal accumulation into the Little Windy Hill Basin was low throughout the record with the background influx averaging 0.03 particles  $\text{cm}^{-2} \text{yr}^{-1}$  from 8 ka BP to present, but rising to a distinct maximum (0.13 particles  $\text{cm}^{-2} \text{yr}^{-1}$ ) at around 1.3 ka BP (Figure 1). Charcoal peak frequency was initially low, ~2 fire per 1000 years at 8 ka BP, with the period of lowest inferred fire frequency (1.6 fires per 1000 years) centered on 6.5 ka BP. Charcoal peak frequency then rose to a peak of 3.7 fires per 1000 years by ~4.6 ka BP, but decreased to ~2 fires per 1000 years by 3.8 ka BP, and remained near this level until ~2.5 ka BP, when frequencies increased again (4.3 fires per 1000 years) at 1.2 ka BP. Since 1.2 ka BP, fire frequencies have decreased to the estimated present day values of ~3 fires per 1000 years. Over the past 8 ka, 22 significant charcoal peaks were identified, resulting in a fire return interval of approximately 364 years. This long-term fire frequency estimate is roughly twice that calculated from fire scarred trees, stand ages, and composite chronologies, which suggests a fire rotation of 187 years from similar forests northeast of Little Windy Hill Pond (Kipfmüller and Baker 2000).

The apparent discrepancy between sedimentary charcoal and dendroecological estimations may be attributable to physical site characteristics (i.e., elevation and aspect). However, the methods for determining fire return intervals differ as well, with fire episodes in sedimentary charcoal potentially representing multiple events within one or more contiguous samples (Whitlock and Larsen 2001, Conedera *et al.* 2009). Further, the sedimentation rate at Little Windy Hill Pond is relatively slow, averaging 56 yr  $\text{cm}^{-1}$  or about one-third the mean fire return interval calculated by Kipfmüller and Baker (2000), which is lower than the desirable resolution (one-fifth mean fire return interval) for matching these data (Clark 1988, Whitlock and Larsen 2001, Higuera *et al.* 2007, Higuera *et al.* 2010). However, our test is to identify pollen response



**Figure 2. A:** Boxplots comparing canopy:understory ratios from non-fire and post-fire pollen abundance data from 8 ka BP to present. Pollen data associated with fire events are split into canopy and understory type events. Higher values (y-axis) indicate greater tree pollen abundances in those samples. **B:** Best fit Gaussian distributions of inverse square transformed ratio data showing the frequency and range of distributions for non-fire and post-fire pollen ratios. Fire types were assigned post hoc based on the position of distributions.

to fire episodes, and thus is not contingent on capturing all potential events, particularly those misidentified because of changes in sedimentation rates, slow sedimentation rates, or combined in analysis of the charcoal time series. Further, using a conservative estimator of charcoal peaks in the sedimentary context rather than researcher-determined thresholds provides confidence that fire episodes identified in the Little Windy Hill dataset are those that are of the scale needed to identify changes in the vegetation composition (Sugita *et al.* 1997, Higuera *et al.* 2009).

Terrestrial vegetation was described by a total of 39 pollen types split into three groups:

canopy, understory, and other (rare or regional pollen types) (Table 2). Random sampling density of pollen data averages one observation every ~260 years since pine forest development (Figure 1). The temporal difference in the charcoal and pollen record is, however, negated by our use of these data as ecological observations of post-fire or non-fire vegetation composition (i.e., having no significant or insignificant peak associated in the same or preceding sample). The forest is dominated by pine pollen, most of which is likely derived from lodgepole pine (*Pinus* subgenus *Pinus*), though traces of *Pinus* subgenus *Strobus* suggest the presence of limber pine (*Pinus flexilis*

James). Spruce (*Picea* A. Dietr.) and fir (*Abies* Mill.) are also abundant over the last 8 ka. Understory constituents are dominated by sagebrush, which grows locally in openings and forest margins and from surrounding timberline and lower sagebrush steppe populations. Equally important to the understory are forbs and grasses, dominated by Asteraceae, Amaranthaceae, and Poaceae. Comparison of the ratio between the canopy and the understory was used as a metric of the ecological response of the forest to fires (Figure 2). Fifteen pollen samples were identified as non-fire following our criteria. Of the 22 identified fire events from 8 ka to present, 11 had pollen data associated with post-fire environments.

Grouping post-fire and non-fire pollen ratios revealed a two-mode distribution of the post-fire ratio of canopy to understory relative to the range of ratios for the non-fire data (Figures 2A and 2B). The lower distribution ( $n = 4$ , range = 1.4 to 1.9) represents post-fire samples where relative tree pollen abundance decreased, while the upper distribution ( $n = 7$ , range = 2.8 to 3.5) indicates that pollen from understory taxa relatively decreased (Figure 2). One post-fire observation was removed because its ratio value was the same as the mean of the non-fire data ( $n = 15$ , range = 1.7 to 4.0); it was not clear to which distribution it belonged, but inclusion in either group did not notably alter the statistical significance of the results.

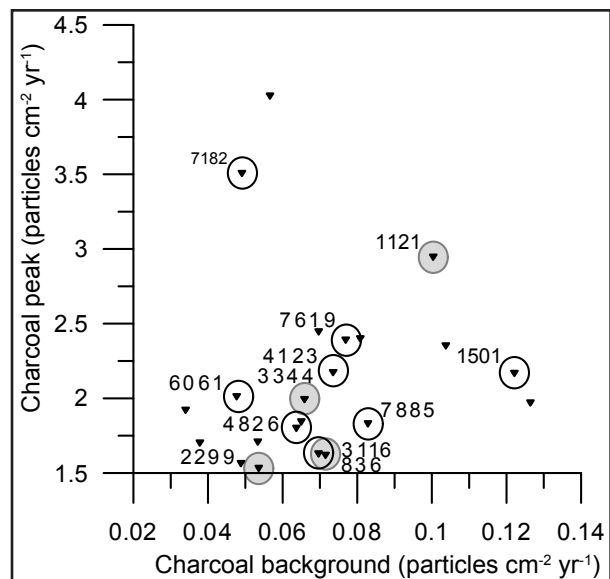
These results were used to classify inferred fire episodes as canopy (stand-replacing) fire or understory (surface) fire events following our hypothesis. A dichotomous classification was selected because stand-replacing and severe surface fires that killed canopy trees would yield the same response in the pollen data (Turner *et al.* 1997). Low severity fires preferentially cleared understory taxa, while maintaining the canopy structure. High severity fires affect both understory and canopy, but the understory recovers faster. While this di-

chotomy may not represent the full spectrum of fires found within this system, it provides useful insight into fire dynamics within the limits of paleoecological data.

Charcoal background was plotted against charcoal peak values to assess how the size of a charcoal peak relates to fire severity (Figure 3). All fires were plotted with those having associated pollen data circled and shaded by inferred fire type. The scatter diagram reveals no distinct pattern in terms of increases in background charcoal relative to charcoal peak or in terms of charcoal peak and fire type.

## DISCUSSION

Common forest associations in western North America are usually described by characteristic fire types, which provide expectations of fire regimes when developing management strategies (Agee 1993, Swetnam and Betancourt 1998, Noss *et al.* 2006). Further, these expectations form the basis for interpretation of an environmental or ecological histo-



**Figure 3.** Scatter diagram comparing charcoal background to peak magnitude for all fires since 8 ka BP. Circle events are those with pollen data associations. Shaded circles are interpreted canopy fire events.



ry, particularly beyond the observational record. In western North America, an increase in large fires caused primarily from climate variability has been observed despite nearly a century of suppression (Littell *et al.* 2009). The role of climate in determining frequency, severity, and spatial extent has been demonstrated on multiple temporal scales (Swetnam and Betancourt 1990, 1998; Marlon *et al.* 2008; Littell *et al.* 2009). Yet beyond the observational and dendroecological record, objective measures of vegetation and wildfire relations have not been established.

Contrary to the expectation of predominantly high severity fires in subalpine, lodgepole pine forests, changes in relative pollen abundance associated with fire episodes indicative of changes in fire type over the past 8 ka were observed (Figure 1B, Figure 2). Lodgepole pine forests in the northern Medicine Bow Mountains established and persisted with a relatively low severity fire regime (Figure 1B, Figure 3). Based on the pollen data, we assume that the forest structure was similar to that of the present; however, variability in early forest structure (i.e., a more open understory) may have facilitated this early period of low fire severity. Fire events in the early forest appear to be associated with consistent decreases in understory taxa and increases of canopy pollen abundance. Alternatively, slow sedimentation rates (Table 1) during the early forest period may have biased the records toward increases in forest pollen types, particularly pine. However, our hypothesis is that low severity fires preferentially cleared understory taxa, while maintaining the canopy structure. We feel that the increase in arboreal pollen loadings was caused by shrub, grass, and forb removal by fire, rather than short-term increases in tree density. This simple model must be applied to our interpretation, as stand structure directly prior to and after fire events is not known (Kashian *et al.* 2005). These low to medium severity fires have a median canopy to understory ratio of 3.2. Further sampling of

pollen data would be needed to determine how long after an event full recovery of the forest occurs (i.e., return of pre-fire pollen assemblage through superposed epoch analysis or other methodology [Genries *et al.* 2009, Blarquez and Carcaillet 2010]).

High severity fire events do appear to be biased toward the latter part of the record based on the random sampling of pollen data associated with charcoal peaks, consistent with the historical fire regime (Schoennagel *et al.* 2004). Ratios of canopy to understory pollen suggest an increase in canopy fires after 3.5 ka BP (Figure 1B, Figure 3). Assuming a true random sampling of fire events over the past 8 ka, the first canopy-type event identified occurred ca. 3.2 ka BP. Prior to that time, only understory events were observed, based on the pollen data. This is not to suggest that canopy fires could not occur prior to 3.2 ka, just that the data examined did not capture any of those events. In this latter period, four of the six fires sampled were considered high severity. The ratio of canopy to understory pollen (median = 1.8) for these high severity events is best explained by the assumed slow recovery rates of canopy relative to understory taxa (Figure 1, Figure 2, Table 2). Additionally, understory type vegetation may have become more dominant with an opened canopy, further lowering the relative abundance of tree pollen. If this pattern of high severity fires becoming more prevalent toward the latter part of the record is true, it suggests that stand-replacing fires were more common when conditions in western forests were generally wetter than previous (Shuman *et al.* 2009, Shinker *et al.* 2010). This paradox illustrates the importance of short-term climate variability to fires, superimposed on long-term climatic trends.

To change the composition of pollen deposited into a lake basin, we assume that a fire has to be at least 8 times larger than the surface area of the lake being studied (Sugita *et al.* 1997). The conservative method used to identify fire events from a single site likely under-

represents fires identified in more spatially explicit analyses as in dendroecology (Kipfmüller and Baker 2000, Whitlock and Larsen 2001, Higuera *et al.* 2009), or in compositing multiple sedimentary fire records from a region (Higuera *et al.* 2011). Important to the results of our study is that post-fire pollen data did capture changes in vegetation composition and potentially provided information on the type of fire occurrence. However, identified events are more likely those that were more similar to the larger fire events identified by Kipfmüller and Baker (2000), and proximal to, if not within, the watershed of Little Windy Hill Pond (e.g., Sugita *et al.* 1997). Our data are consistent with the idea that large fires cause changes in pollen composition within the limitations of paleoecological data; however, further study is needed to verify this conclusion. Independent proxy data of fire intensity to compare with vegetation records, such as increased magnetic susceptibility associated with greater slope wash, would provide opportunities to test these interpretations (Meyer and Pierce 2003, Pierce *et al.* 2004, Colombaroli and Gavin 2010).

Peak charcoal does not appear to relate to fire severity based on our study. Over the past 8 ka, background charcoal was relatively constant, except for the distinct increase centered near 1.2 ka BP (Figure 1A). Greater peak charcoal values should tend to increase the background charcoal values, particularly when large charcoal peaks are clustered (Figure 1A Figure 3). However, plots of charcoal background to peak charcoal show no clear trend, suggesting that peak magnitude does not provide information about fire size or intensity (Figure 3). Peak charcoal may be more representative of fire proximity to the shoreline of a lake, but that is a question that would be better addressed in paired dendro-lake sediment studies (e.g., Whitlock *et al.* 2004, Higuera *et al.* 2011). Canopy fires should deposit more charcoal onto a lake surface than understory fires because the charcoal would have greater lift and travel distances (Conedera *et al.* 2009).

Identifying the natural range of variability within a given ecosystem remains a challenge for natural resource managers (Millar and Woolfenden 1999, Gavin *et al.* 2007, Kaufmann *et al.* 2007, Jackson *et al.* 2009). Yet this challenge must be met in light of increasing urban-wildland interfaces and recent increases in fire activity in the Rocky Mountains and throughout the western United States (Noss *et al.* 2006, Littell *et al.* 2009). Prior to 3.5 ka, it is possible that the fire regime that we observe today was not in place in the subalpine forests of the Medicine Bow Mountains, and clearly more work is needed before this conclusion can be confirmed. Arguably, the fire regime of the subalpine, lodgepole dominated forests in the northern Medicine Bow Mountains has been in place for at least the past >3 ka years. This pattern is for relatively infrequent stand-replacing fires interspersed with low to mid-severity events. Lake level studies suggest that, while generally wetter, prolonged droughts lasting centuries in the Rocky Mountains may provide a mechanism for this change in fire regime in the latter part of the record (Shuman *et al.* 2009, Shuman *et al.* 2010). How climate changes and insect infestations may change this pattern is unclear; however, past prolonged droughts have not substantially changed the local vegetation (Shuman *et al.* 2009, Shinker *et al.* 2010, Shuman *et al.* 2010), suggesting some degree of resilience in these ecosystems.

Questions concerning the historical range of natural variability of fire regimes in western North American forests are relevant for the development of effective management strategies (Kaufmann *et al.* 2007). Perhaps even more fundamental to the historical range of natural variability is the examination of time periods relevant to management horizons to these analyses, such as characteristic fire frequencies over the past few millennia prior to modern management (e.g., Marlon *et al.* 2008). Defining relevant time periods and range of natural variability within ecosystems plays to the

strength of paleoenvironmental analyses (Millar and Woolfenden 1999, Gavin *et al.* 2007). However, the impact of those variations might be more difficult to ascertain.

We tested three hypotheses concerning 1) the ability of pollen data to detect vegetation changes after a disturbance like fire; 2) the assumption that fire severity or type could be identified by changes in canopy and understory pollen composition; and 3) the potential that sedimentary charcoal peak magnitudes are associated with fire severity. Our results suggest that pollen data does record changes in vegetation composition and can differentiate between high and medium to low severity fires, supporting our first two hypotheses. Our third hy-

pothesis was rejected, however, because large charcoal peaks were evident in both high and mid to low severity events. Specific to our study site, subalpine forests in the northern Medicine Bow Mountains of southeastern Wyoming have experienced changes in their fire regime over the past 8 ka years. Mid to low severity fires were most common with high severity events increasing over the past 3.5 ka when conditions appear to be relatively wet. These results suggest that while further studies are necessary to determine pollen data responses to fire disturbances, a temporal constraint may be appropriate for determining the natural range of variability in managing these forests.

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## LITERATURE CITED

- Agee, J. K. 1993. Fire ecology of Pacific Northwest forests. Island Press, Washington, D.C., USA.
- Ali, A.A., C. Carcaillet, and Y. Bergeron. 2009a. Long-term fire frequency variability in the eastern Canadian boreal forest: the influences of climate vs. local factors. *Global Change Biology* 15: 1230-1241. doi: [10.1111/j.1365-2486.2009.01842.x](https://doi.org/10.1111/j.1365-2486.2009.01842.x)
- Ali, A.A., P.E. Higuera, Y. Bergeron, and C. Carcaillet. 2009b. Comparing fire-history interpretations based on area, number and estimated volume of macroscopic charcoal in lake sediments. *Quaternary Research* 72: 462-468. doi: [10.1016/j.yqres.2009.07.002](https://doi.org/10.1016/j.yqres.2009.07.002)
- Baker, W.L. 2009. Fire ecology in Rocky Mountain landscapes. Island Press, Washington, D.C., USA.
- Blarquez, O., and C. Carcaillet. 2010. Fire, fuel composition and resilience threshold in subalpine ecosystem. *PLoS ONE* 5(8): e12480. doi: [10.1371/journal.pone.0012480](https://doi.org/10.1371/journal.pone.0012480)
- Box, G.E.P., and D.R. Cox. 1964. An analysis of transformations. *Journal of the Royal Statistical Society Series B (Methodological)* 26: 211-252.
- Brunelle, A., T.A. Minckley, S. Blissett, S.K. Cobabe, and B.L. Guzman. 2010. A ~8000 year fire history from an Arizona/Sonora borderland ciénega. *Journal of Arid Environments* 74: 475-481. doi: [10.1016/j.jaridenv.2009.10.006](https://doi.org/10.1016/j.jaridenv.2009.10.006)
- Carcaillet, C., Y. Bergeron, P.J.H. Richard, B. Fréchette, S. Gauthier, and Y.T. Prairie. 2001. Change of fire frequency in the eastern Canadian boreal forests during the Holocene: does vegetation composition or climate trigger the fire regime? *Journal of Ecology* 89: 930-946. doi: [10.1111/j.1365-2745.2001.00614.x](https://doi.org/10.1111/j.1365-2745.2001.00614.x)

- Clark, J.S. 1988. Particle motion and the theory of stratigraphic charcoal analysis: source area, transportation, deposition, and sampling. *Quaternary Research* 30: 67-80. doi: [10.1016/0033-5894\(88\)90088-9](https://doi.org/10.1016/0033-5894(88)90088-9)
- Clark, J.S. 1990. Fire and climate change during the last 750 years in northwestern Minnesota. *Ecological Monographs* 60: 135-159. doi: [10.2307/1943042](https://doi.org/10.2307/1943042)
- Colombaroli, D., and D.G. Gavin. 2010. Highly episodic fire and erosion regime over the past 2,000 y in the Siskiyou Mountains, Oregon. *Proceedings of the National Academy of Sciences* 107: 18909-18914. doi: [10.1073/pnas.1007692107](https://doi.org/10.1073/pnas.1007692107)
- Conedera, M., W. Tinner, C. Neff, M. Meurer, A.F. Dickens, and P. Krebs. 2009. Reconstructing past fire regimes: methods, applications, and relevance to fire management and conservation. *Quaternary Science Reviews* 28: 555-576. doi: [10.1016/j.quascirev.2008.11.005](https://doi.org/10.1016/j.quascirev.2008.11.005)
- Duffin, K.I. 2008. The representation of rainfall and fire intensity in fossil pollen and charcoal records from a South African savanna. *Review of Palaeobotany and Palynology* 151: 59-71. doi: [10.1016/j.revpalbo.2008.02.004](https://doi.org/10.1016/j.revpalbo.2008.02.004)
- Faegri, K., P.E. Kaland, and K. Kzywinski. 1989. *Textbook of pollen analysis*. Wiley, New York, New York, USA.
- Frechette, J.D., and G.A. Meyer. 2009. Holocene fire-related alluvial-fan deposition and climate in ponderosa pine and mixed-conifer forests, Sacramento Mountains, New Mexico, USA. *The Holocene* 19: 639-651. doi: [10.1177/0959683609104031](https://doi.org/10.1177/0959683609104031)
- Gavin, D.G., D.J. Hallett, F.S. Hu, K.P. Lertzman, S.J. Prichard, K. Brown, J.A. Lynch, P. Bartlein, and D.L. Peterson. 2007. Forest fire and climate change in western North America: insights from sediment charcoal records. *Frontiers in Ecology and the Environment* 5: 499-506. doi: [10.1890/060161](https://doi.org/10.1890/060161)
- Genries, A., L. Mercier, M. Lavoie, S.D. Muller, O. Radakovitch, and C. Carcaillet. 2009. The effect of fire frequency on local cembra pine populations. *Ecology* 90: 476-486. doi: [10.1890/07-1740.1](https://doi.org/10.1890/07-1740.1) PMID:19323231
- Green, D.G. 1981. Time series and postglacial forest ecology. *Quaternary Research* 15: 265-277. doi: [10.1016/0033-5894\(81\)90030-2](https://doi.org/10.1016/0033-5894(81)90030-2)
- Green, D.G. 1982. Fire and stability in the post-glacial forests of southwest Nova Scotia. *Journal of Biogeography* 9: 29-40. doi: [10.2307/2844728](https://doi.org/10.2307/2844728)
- Higuera, P.E., L.B. Brubaker, P.M. Anderson, F.S. Hu, and T.A. Brown. 2009. Vegetation mediated the impacts of postglacial climate change on fire regimes in the south-central Brooks Range, Alaska. *Ecological Monographs* 79: 201-219. doi: [10.1890/07-2019.1](https://doi.org/10.1890/07-2019.1)
- Higuera, P.E., D.G. Gavin, P.J. Bartlein, and D.J. Hallett. 2010. Peak detection in sediment-charcoal records: impacts of alternative data analysis methods on fire-history interpretations. *International Journal of Wildland Fire* 19: 996-1014. doi: [10.1071/WF09134](https://doi.org/10.1071/WF09134)
- Higuera, P.E., M.E. Peters, L.B. Brubaker, and D.G. Gavin. 2007. Understanding the origin and analysis of sediment-charcoal records with a simulation model. *Quaternary Science Reviews* 26: 1790-1809. doi: [10.1016/j.quascirev.2007.03.010](https://doi.org/10.1016/j.quascirev.2007.03.010)
- Higuera, P.E., C. Whitlock, and J.A. Gage. 2011. Linking tree-ring and sediment-charcoal records to reconstruct fire occurrence and area burned in subalpine forests of Yellowstone National Park, USA. *The Holocene* 21: 327-341. doi: [10.1177/0959683610374882](https://doi.org/10.1177/0959683610374882)
- Jackson, S.T., S.T. Gray, and B. Shuman. 2009. Paleoeecology and resource management in a dynamic landscape: case studies from the Rocky Mountain headwaters. Pages 61-80 in: G. Dietl and K.W. Flessa, editors. *Conservation Paleobiology Paleontological Society Papers* 15. The Paleontological Society, Boulder, Colorado, USA.

- Kashian, D.M., M.G. Turner, W.H. Romme, and C.G. Lorimer. 2005. Variability and convergence in stand structural development on a fire-dominated subalpine landscape. *Ecology* 86: 643-654. doi: [10.1890/03-0828](https://doi.org/10.1890/03-0828)
- Kaufmann, M.R., D. Binkley, P.Z. Fulé, M. Johnson, S.L. Stephens, and T.W. Swetnam. 2007. Defining old growth for fire-adapted forests of the western United States. *Ecology and Society* 12(2): 15.
- Kipfmüller, K.F., and W.L. Baker. 2000. A fire history of a subalpine forest in south-eastern Wyoming, USA. *Journal of Biogeography* 27: 71-85. doi: [10.1046/j.1365-2699.2000.00364.x](https://doi.org/10.1046/j.1365-2699.2000.00364.x)
- Larsen, C.P.S., and G.M. MacDonald. 1998. Fire and vegetation dynamics in a jack pine and black spruce forest reconstructed using fossil pollen and charcoal. *Journal of Ecology* 86: 815-828. doi: [10.1046/j.1365-2745.1998.8650815.x](https://doi.org/10.1046/j.1365-2745.1998.8650815.x)
- Littell, J.S., D. McKenzie, D.L. Peterson, and A.L. Westerling. 2009. Climate and wildfire area burned in western US ecoprovinces, 1916-2003. *Ecological Applications* 19: 1003-1021. doi: [10.1890/07-1183.1](https://doi.org/10.1890/07-1183.1)
- Long, C.J., C. Whitlock, P.J. Bartlein, and S.H. Millsaugh. 1998. A 9000-year fire history from the Oregon Coast Range, based on a high-resolution charcoal study. *Canadian Journal of Forest Research* 28: 774-787. doi: [10.1139/x98-051](https://doi.org/10.1139/x98-051)
- Love, J.D., and A.C. Christiansen. 1985. Geologic map of Wyoming. US Geological Survey, Reston, Virginia, USA.
- Marlon, J.R., P.J. Bartlein, C. Carcaillet, D.G. Gavin, S.P. Harrison, P.E. Higuera, F. Joos, M.J. Power, and I.C. Prentice. 2008. Climate and human influences on global biomass burning over the past two millennia. *Nature Geoscience* 1: 697-702. doi: [10.1038/ngeo313](https://doi.org/10.1038/ngeo313)
- Marlon, J.R., P.J. Bartlein, M.K. Walsh, S.P. Harrison, K.J. Brown, M.E. Edwards, P.E. Higuera, M.J. Power, R.S. Anderson, C. Briles, A. Brunelle, C. Carcaillet, M. Daniels, F.S. Hu, M. Lavoie, C. Long, T. Minckley, P.J.H. Richard, A.C. Scott, D.S. Shafer, W. Tinner, C.E. Umbanhowar, and C. Whitlock. 2009. Wildfire responses to abrupt climate change in North America. *Proceedings of the National Academy of Sciences* 106: 2519-2524. doi: [10.1073/pnas.0808212106](https://doi.org/10.1073/pnas.0808212106)
- Mears Jr., B. 2001. Glacial records in the Medicine Bow Mountains and Sierra Madre of southern Wyoming and adjacent Colorado, with a traveler's guide to their sites. Wyoming State Geological Survey, Laramie, USA.
- Meyer, G.A., and J.L. Pierce. 2003. Climatic controls on fire-induced sediment pulses in Yellowstone National Park and central Idaho: a long-term perspective. *Forest Ecology and Management* 178: 89-104. doi: [10.1016/S0378-1127\(03\)00055-0](https://doi.org/10.1016/S0378-1127(03)00055-0)
- Millar, C.I., and W.B. Woolfenden. 1999. The role of climate change in interpreting historical variability. *Ecological Monographs* 9: 1207-1216.
- Minckley, T.A., C. Whitlock, and P.J. Bartlein. 2007. Vegetation, fire, and climate history of the northwestern Great Basin during the last 14,000 years. *Quaternary Science Reviews* 26: 2167-2184. doi: [10.1016/j.quascirev.2007.04.009](https://doi.org/10.1016/j.quascirev.2007.04.009)
- Mohr, J.A., C. Whitlock, and C.N. Skinner. 2000. Postglacial vegetation and fire history, eastern Klamath Mountains, California, USA. *Holocene* 10: 587-601. doi: [10.1191/09596830067583767](https://doi.org/10.1191/09596830067583767)
- Moore, P.D., J.A. Webb, and M.E. Collinson. 1991. Pollen analysis. Second edition. Blackwell, London, United Kingdom.
- Noss, R.F., J.F. Franklin, W.L. Baker, T. Schoennagel, and P.B. Moyle. 2006. Managing fire-prone forests in the western United States. *Frontiers in Ecology and the Environment* 4: 481-487. doi: [10.1890/1540-9295\(2006\)4\[481:MFFITW\]2.0.CO;2](https://doi.org/10.1890/1540-9295(2006)4[481:MFFITW]2.0.CO;2)

- Pierce, J.L., G.A. Meyer, and A.J.T. Jull. 2004. Fire-induced erosion and millennial-scale climate change in northern ponderosa pine forests. *Nature* 432: 87-90. doi: [10.1038/nature03058](https://doi.org/10.1038/nature03058)
- Schoennagel, T., T.T. Veblen, and W.H. Romme. 2004. The interaction of fire, fuels, and climate across Rocky Mountain forests. *Bioscience* 54: 661-676. doi: [10.1641/0006-3568\(2004\)054\[0661:TIOFFA\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2004)054[0661:TIOFFA]2.0.CO;2)
- Shinker, J.J., B.N. Shuman, T.A. Minckley, and A.K. Henderson. 2010. Climatic shifts in the availability of contested waters: a long-term perspective from the headwaters of the North Platte River. *Annals of the Association of American Geographers* 100: 866-879. doi: [10.1080/00045608.2010.500196](https://doi.org/10.1080/00045608.2010.500196)
- Shuman, B., A.K. Henderson, S.M. Colman, J.R. Stone, S.C. Fritz, L.R. Stevens, M.J. Power, and C. Whitlock. 2009. Holocene lake-level trends in the Rocky Mountains, USA. *Quaternary Science Reviews* 28: 1861-1879. doi: [10.1016/j.quascirev.2009.03.003](https://doi.org/10.1016/j.quascirev.2009.03.003)
- Shuman, B., P. Pribyl, T.A. Minckley, and J.J. Shinker. 2010. Rapid hydrologic shifts and prolonged droughts in Rocky Mountain headwaters during the Holocene. *Geophysical Research Letters* 37: L06701. doi: [10.1029/2009GL042196](https://doi.org/10.1029/2009GL042196)
- Sugita, S., G.M. MacDonald, and C.P.S. Larsen. 1997. Reconstruction of fire disturbance and forest succession from fossil pollen in lake sediments: potentials and limitations. Pages 387-408 in: J.S. Clark, H. Cachier, and J.G. Goldammer, editors. *Sediment records of biomass burning and global change*. Springer-Verlag, Berlin, Germany.
- Swetnam, T.W., C.D. Allen, and J.L. Betancourt. 1999. Applied historical ecology: using the past to manage for the future. *Ecological Monographs* 9: 1189-1206.
- Swetnam, T.W., and J.L. Betancourt. 1990. Fire—southern oscillation relations in the southwestern United States. *Science* 249: 1017-1020. doi: [10.1126/science.249.4972.1017](https://doi.org/10.1126/science.249.4972.1017)
- Swetnam, T.W., and J.L. Betancourt. 1998. Mesoscale disturbance and ecological response to decadal-scale climate variability in the American Southwest. *Journal of Climate* 11: 3128-3147. doi: [10.1175/1520-0442\(1998\)011<3128:MDAERT>2.0.CO;2](https://doi.org/10.1175/1520-0442(1998)011<3128:MDAERT>2.0.CO;2)
- Tinner, W., F. Hu, R. Beer, P. Kaltenrieder, B. Scheurer, and U. Krähenbühl. 2006. Postglacial vegetational and fire history: pollen, plant macrofossil and charcoal records from two Alaskan lakes. *Vegetation History and Archaeobotany* 15: 279-293. doi: [10.1007/s00334-006-0052-z](https://doi.org/10.1007/s00334-006-0052-z)
- Tinner, W., P. Hubschmid, M. Wehrli, B. Ammann, and M. Conedera. 1999. Long-term forest fire ecology and dynamics in southern Switzerland. *Journal of Ecology* 87: 273-289. doi: [10.1046/j.1365-2745.1999.00346.x](https://doi.org/10.1046/j.1365-2745.1999.00346.x)
- Turner, M.G., W.H. Romme, R.H. Gardner, and W.W. Hargrove. 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. *Ecological Monographs* 67: 411-433. doi: [10.1890/0012-9615\(1997\)067\[0411:EOFSAP\]2.0.CO;2](https://doi.org/10.1890/0012-9615(1997)067[0411:EOFSAP]2.0.CO;2)
- van der Knaap, W., J. van Leeuwen, H. Svitavská-Svobodová, I. Pidek, E. Kvavadze, M. Chichinadze, T. Giesecke, B. Kaszewski, F. Oberli, L. Kalniņa, H. Pardoe, W. Tinner, and B. Ammann. 2010. Annual pollen traps reveal the complexity of climatic control on pollen productivity in Europe and the Caucasus. *Vegetation History and Archaeobotany* 19: 285-307. doi: [10.1007/s00334-010-0250-6](https://doi.org/10.1007/s00334-010-0250-6)
- Veblen, T.T. 2000. Disturbance patterns in southern Rocky Mountain forests. Pages 31-54 in: R.L. Knight, F.W. Smith, S.W. Buskirk, W.H. Romme, and W.L. Baker, editors. *Forest fragmentation in the southern Rocky Mountains*. University Press of Colorado, Boulder, USA.
- Walsh, M.K., C. Whitlock, and P.J. Bartlein. 2008. A 14,300-year-long record of fire-vegetation-climate linkages at Battle Ground Lake, southwestern Washington. *Quaternary Research* 70: 251-264. doi: [10.1016/j.yqres.2008.05.002](https://doi.org/10.1016/j.yqres.2008.05.002)

- Whitlock, C., and C. Larsen. 2001. Charcoal as a fire proxy. Pages 75-97 in: J.P. Smol, H.J.B. Birks, and W.M. Last, editors. *Tracking environmental change using lake sediments*. Kluwer Academic Publishers, Dordrecht, Netherlands.
- Whitlock, C., J. Marlon, C. Briles, A. Brunelle, C. Long, and P. Bartlein. 2008. Long-term relations among fire, fuel, and climate in the north-western US based on lake-sediment studies. *International Journal of Wildland Fire* 17: 72-83. doi: [10.1071/WF07025](https://doi.org/10.1071/WF07025)
- Whitlock, C., C.N. Skinner, P.J. Bartlein, T. Minckley, and J.A. Mohr. 2004. Comparison of charcoal and tree-ring records of recent fires in the eastern Klamath Mountains, California, USA. *Canadian Journal of Forest Research* 34: 2110-2121. doi: [10.1139/x04-084](https://doi.org/10.1139/x04-084)