



ELSEVIER

Available online at [www.sciencedirect.com](http://www.sciencedirect.com)

SCIENCE @ DIRECT®

Forest Ecology and Management 178 (2003) 5–21

Forest Ecology  
and  
Management

[www.elsevier.com/locate/foreco](http://www.elsevier.com/locate/foreco)

# The role of climate and vegetation change in shaping past and future fire regimes in the northwestern US and the implications for ecosystem management

Cathy Whitlock<sup>a,\*</sup>, Sarah L. Shafer<sup>b</sup>, Jennifer Marlon<sup>a</sup>

<sup>a</sup>*Department of Geography, University of Oregon, Eugene, OR 97403, USA*

<sup>b</sup>*U.S. Geological Survey, 200 SW 35th St., Corvallis, OR 97333, USA*

## Abstract

Fire is an important part of the disturbance regimes of northwestern US forests and its role in maintaining and altering forest vegetation is evident in the paleoecological record of the region. Long-term reconstructions of Holocene fire regimes, provided by the analysis of charcoal, pollen, and other fire proxies in a network of lake records, indicate that the Pacific Northwest and summer-dry regions of the northern Rocky Mountains experienced their highest fire activity in the early Holocene (11,000–7000 years ago) and during the Medieval Warm Period (ca. 1000 years ago) when drought conditions were more severe than today. In contrast, in summer-wet areas of the northern Rocky Mountains, the period of highest fire activity was registered in the last 7000 years when dry woodland vegetation developed. When synthesized across the entire northwestern US, the paleoecological record reveals that past and present fire regimes are strongly controlled by climate changes occurring on multiple time scales. The scarcity of fires in the 20th century in some northwestern US ecosystems may be the result of successful fire suppression policies, but in wetter forests this absence is consistent with long-term fire regime patterns. In addition, simulations of potential future climate and vegetation indicate that future fire conditions in some parts of the northwestern US could be more severe than they are today. The Holocene record of periods of intensified summer drought is used to assess the nature of future fire–climate–vegetation linkages in the region.

© 2003 Elsevier Science B.V. All rights reserved.

*Keywords:* Fire history; Charcoal records; Holocene climate change; Future fire conditions; Western US

## 1. Introduction

The role of fire as a driver of ecological change is widely recognized among researchers and managers. In forests of the western US much attention has focused on trying to identify and recreate the fire regimes that existed at the time of Euro-American settlement and before extensive fire suppression

efforts. The last 15 years have witnessed several large wildfires in western coniferous forests. In 2000, for example, over 3.5 million ha burned in western Montana, northern Idaho, and California despite over \$ 1.3 billion spent on fire fighting efforts ([National Interagency Fire Center, 2002](#)). These recent fire events are widely blamed on the build-up of fuels, in particular the “thickening” of the forest that has occurred in recent decades in the absence of fire. In 2001, over \$ 200 million was allocated as part of the National Fire Plan directed at fuel mitigation and our ability to suppress fires through such actions continues to

\* Corresponding author. Tel.: +1-541-346-4566;

fax: +1-541-346-2067.

E-mail address: [whitlock@oregon.uoregon.edu](mailto:whitlock@oregon.uoregon.edu) (C. Whitlock).

improve (USDA Forest Service, 2001). In the last 15 years, the western US has also experienced extreme fire-conducive climate conditions, including droughts that have been more severe than any previously recorded in the instrumental meteorological record (National Oceanic and Atmospheric Administration, 2002).

The co-occurrence of high fuel accumulation, low fuel moisture, and fire-conducive weather patterns has given rise to a national discussion about the causes and proper responses to wildland fires. The debate centers on some basic questions: to what extent is the current fire regime caused by forest management or is it a product of changing climate (both natural and human-induced changes)? Irrespective of the cause, do the environmental conditions supporting the current fire regimes exceed the range of conditions experienced in the past? Can intensive fuels management restore the pre-settlement fire regimes, given the potential magnitude of environmental changes projected for the future?

Answering these questions requires an understanding of the relationships among fire, climate, and vegetation, especially the dynamics of those relationships prior to extensive forest management activities. These questions also raise important management issues about future fire conditions that may occur as a result of potential future vegetation and climate changes. In this paper, we describe the methods used to study past fire, vegetation, and climate interactions in the northwestern US, an area that includes the Pacific Northwest and northern Rocky Mountains. These reconstructions provide an opportunity to examine both the pre-historical and historical range of variability of fire occurrence on multiple time scales. We also examine the potential future environmental changes in the region as simulated by climate and vegetation models and discuss the implications of these changes for future fire regimes and management responses to fire.

## 2. Tools for paleoenvironmental research

### 2.1. Fire-history reconstructions

Fire-history information is provided primarily by two types of data: (1) fire-scarred tree rings and stand-

age data, and (2) proxy data from sediment records (see Agee, 1993; Patterson et al., 1987; Whitlock and Larsen, 2002). These data sources describe fire regimes at multiple temporal and spatial scales. Tree-ring data and stand-age information provide short-term reconstructions of fire events, usually spanning the last 400 years or less. Fire-scars on tree rings register fire events that were not lethal to the tree, whereas stand establishment dates identify the minimum age of the last stand-replacement fire. In the northwestern US, the fire history of montane and subalpine forests is characterized by infrequent severe fires, as evidenced by the mosaic of stand ages in these forests (Arno and Sneek, 1977; Romme and Despain, 1989; Agee, 1993). The dominant conifer species of these forests, including subalpine fir (*Abies lasiocarpa* (*bifolia*)), whitebark pine (*Pinus albicaulis*), and Engelmann spruce (*Picea engelmannii*), are adapted to a long fire interval (i.e., a long time between subsequent stand-replacing fires). Other species, such as lodgepole pine (*Pinus contorta*), help maintain a stand-replacing fire regime as a result of their high flammability and serotinous cones. Lower elevation forests, dominated by ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*), are maintained by frequent ground fires, which are best measured by fire-scarred tree-rings. In between these two extremes are fire regimes in forests that feature mixtures of fire-resistant and fire-sensitive species, which result in a complex array of stand ages and species composition derived from both crown and ground fires. Most forested regions of the western US experience this mid-severity fire regime.

The second method of fire-history reconstruction, and the primary focus of this paper, involves the examination of paleoenvironmental data preserved in sediments, with most work focusing on lake sediments (although see Meyer and Pierce, 2003 for a discussion of fire records from alluvial fan and colluvial sediments and Gavin, 2000 for fire records from soils). Lake sediments serve as repositories of proxy data recording past environmental conditions within a watershed. Particulate charcoal, such as charred wood, bark, and leaves, is introduced into a lake through airborne fallout and delivery by streams and slope-wash. Intervals in sediment cores for which charcoal abundance exceeds a prescribed background level are considered evidence of a fire episode. The time series

of charcoal peaks from lake-sediment records provide information on long-term variations in fire frequency.

The tree-ring and lake-sediment records of past fire activity have strengths and weaknesses (see discussion in [Whitlock and Larsen, 2002](#)). Tree-ring records offer a high level of spatial resolution in a fire reconstruction, and it is possible to use tree-ring records to distinguish between locations that experienced high-severity and low-severity fires. The location of fire-scarred trees identifies the exact location of particular fires, and thus dendrochronological reconstructions provide spatially-specific information. They are also temporally precise in that the tree rings can be used to date a fire event to a particular year or even a particular season. Stand-age analysis is spatially-specific as well (i.e., the location of the fire can be identified), but it is temporally less precise because of the potential lag between the fire event and the first establishment of trees. Both methods also suffer from an “erasure effect” ([Agee, 1993](#)), which means that as old trees become progressively scarcer on the landscape the fire-history data they contain is essentially “erased”. This attenuation reduces the likelihood of identifying old fire events, and consequently most tree-ring studies show that fire events become less frequent as one goes back in time. Although tree-ring methods extend back to the age of the oldest living tree, this time span is not long enough to capture major changes in vegetation and climate, and the record is biased toward low-severity fire events that scar trees but do not kill them.

Charcoal records from lake sediments reconstruct past fires with less temporal and spatial precision than tree-ring records. Modern taphonomic studies have shown that charcoal accumulation into a lake continues for a few years after a fire because of transportation and redeposition of secondary charcoal within the watershed and the lake ([Millspaugh and Whitlock, 1995](#)). This process tends to blur the exact age of a fire, even when charcoal particles are directly dated by radiocarbon dating. Additionally, the charcoal deposited in a lake may represent more than one fire within the watershed, or fires from more than one year. As a result, lake-sediment researchers refer to a fire episode as one or more fires occurring in the time interval of interest, rather than individual fires. Ideally, lakes with annually laminated (i.e., varved) sediment permit the age of a fire to be established to the year

([Clark, 1990](#)), but such lakes are rare in the western US and the timing of charcoal deposition still post-dates the fire it represents. In non-laminated sediment records, the age of a fire event is established by interpolation from a series of radiometric ages determined by  $^{210}\text{Pb}$  and radiocarbon dating. The radiocarbon dates are converted to calendar years, and the possibility of multiple calendar ages for a single radiocarbon date introduces another source of error in the chronology. This lack of temporal precision, however, does not prevent the identification of individual fires in areas with long fire intervals. For example, fires in the coastal rainforests of the Pacific Northwest are infrequent enough to be distinguished in lakes with sedimentation rates of decades per centimeter; in contrast, dry-forest sites with frequent fires tend to produce less-discrete charcoal peaks.

Charcoal peaks in the uppermost sediments (dated with  $^{210}\text{Pb}$ ) can be calibrated by matching them against known fires. This modern calibration helps to establish a value that distinguishes background levels of charcoal from significantly higher amounts of charcoal, i.e., charcoal peaks. Background charcoal is the secondary material that is introduced into lakes during non-fire years and is present in measurable amounts in almost every centimeter of cores from the western US. Variations in background charcoal are thought to reflect changing levels of fuel biomass (see [Long et al., 1998](#); [Whitlock and Larsen, 2002](#)). In general, a region dominated by closed mixed-conifer forest with abundant woody fuel will produce higher background levels of charcoal than an open parkland with less woody fuels, although more research is needed to define the specific relationship between background charcoal and fuel biomass. The peaks above the background level represent the fire events and some component of natural variability.

Although not as precise as tree-ring records, charcoal records from lake sediments can provide some information on the spatial location and size of the fires represented by charcoal data. Records of macroscopic charcoal particles ( $>100\ \mu\text{m}$ ) are interpreted as resulting from a fire within the lake’s watershed, based on empirical evidence that particles of this size do not travel far from their source ([Whitlock and Millspaugh, 1996](#); [Clark et al., 1998](#); [Gardner and Whitlock, 2000](#)). In addition, local fires upwind of the lake are better recorded than those downwind ([Whitlock and Mill-](#)

spaugh, 1996; Gardner and Whitlock, 2000). Moreover, the size of a charcoal peak is not necessarily indicative of the size of the fire, because fires close to the lakeshore can deposit abundant charcoal into a lake even if a fire is relatively small. Identification of the potential fire source area rests on information about recent historical fires, either from documentary evidence or tree-ring studies.

## 2.2. *Vegetation history reconstructions*

In addition to charcoal, lake sediments also provide long-term records of vegetation change. Pollen in lake sediments is a primary tool for reconstructing past variations in vegetation and climate in the western US. The relationship between modern lake-sediment pollen and present-day vegetation and climate is used to reconstruct past vegetation–climate relationships, taking into consideration that pollen records are affected by the ability of some species to produce more pollen than others and that pollen of some taxa may travel very long distances (e.g., Fall, 1992; Davis, 1995; Minckley and Whitlock, 2000). Pollen is generally identified to the level of genus, but sometimes only family-level identification is possible. Pollen identifications are supplemented by the presence of seeds, leaves, and other plant macrofossils in the sediment, which can often be identified to species and provide information about local vegetation (Birks, 2002). These macrofossils can also be radiocarbon dated to provide a chronology for the sediment record.

## 2.3. *Fire-related erosion*

Past episodes of erosion into a lake can be measured by subtle increases in the sediment magnetic susceptibility, which is a proxy for the introduction of iron-bearing minerals from weathered bedrock, especially magnetite, or from soils that have burned and been thermally altered (Millsbaugh and Whitlock, 1995; Gedye et al., 2000). Non-destructive measurements of the magnetic susceptibility of sediments help to identify time periods when clastic material is mixed with autochthonous lake sediments. When pulses of clastic material are associated with charcoal peaks, they can provide evidence of local fires that were extensive and severe enough to trigger mass-wasting events within the watershed.

## 3. Modeling past and future fire conditions

### 3.1. *Models*

Our understanding of fire regimes gained from paleoecological data can be enhanced using a variety of climate, vegetation, and other physically-based process models. These numerical models can simulate the physical conditions supporting fire regimes and thus allow us to test hypotheses about the processes driving fire regimes at different times in the past. Models can also be used to simulate the potential future impacts of changing climate, vegetation, and fire on the landscape.

Coupled atmosphere–ocean general circulation models (AOGCMs) are used to identify the patterns and causes of climate change (COHMAP Members, 1988; Kutzbach et al., 1998), and they have been used to study past, present, and future climates (IPCC, 2001). AOGCMs typically have a coarse spatial resolution (a grid cell may span a few degrees of latitude and longitude) and a relatively crude representation of topography. They also often oversimplify the simulation of those climate variables that are most critical for understanding plant distributions and potential fire conditions, such as soil moisture. One of their strengths, however, is in demonstrating the potential effects of variations in the seasonal cycle of insolation, ice cover, atmospheric CO<sub>2</sub>, and topography on regional climate. Output from AOGCMs can be used as boundary conditions for regional, or mesoscale, climate models that offer a finer spatial resolution and more elaborate depictions of the climate processes that operate at the land surface (Giorgi and Mearns, 1991).

A variety of vegetation models have been used to simulate past and potential future changes in vegetation. These models range from statistical models (e.g., Iverson and Prasad, 1998; Shafer et al., 2001) to more mechanistic, process-based models (e.g., Haxeltine and Prentice, 1996). Most recent has been the development of dynamic global vegetation models (DGVMS), such as LPJ (Sitch et al., 2003) and IBIS (Foley et al., 1996), which simulate complex biogeochemical processes and vegetation dynamics including disturbance regimes. In addition to climate and vegetation models, other physically-based process models, such as water-balance models, can be used to simulate important fire-related properties, e.g., soil moisture.

### 3.2. Data-model comparisons as a research approach

When several paleoecological records are compared, it is possible to discern local, regional, and continental-scale patterns of fire and vegetation change. However, different physical processes may create similar patterns of change, and the same processes may interact differently at different temporal and spatial scales. Models can be used to test which processes are the most plausible controls of particular patterns, and data-model comparison efforts are increasingly common (e.g., COHMAP (COHMAP Members, 1988) and BIOME6000 (Prentice and Webb, 1998)). For example, climate reconstructions based on the paleoecological record can be compared with paleoclimate simulations produced by AOGCMs (Barnosky et al., 1987; Thompson et al., 1993; Bartlein et al., 1998). Such comparisons of data and model results highlight regions where the paleoclimate reconstructions seem well explained by a particular set of climate variables, and also identify regions where additional data and model development might be useful. Paleoecological databases also provide information on changing distributions and associations of plant and animal taxa through time (Webb, 1988; Delcourt et al., 1983; FAUNMAP Working Group, 1996). Paleoenvironmental databases for a variety of proxy data are now available through the NOAA World Data Center for Paleoclimatology (<http://www.ngdc.noaa.gov/paleo/paleo.html>).

## 4. Controls of long-term variations in fire history in the northwestern US

### 4.1. Large-scale controls of climate change

In the northwestern US, the long-term controls of climate change and how they influence regional environmental changes are relatively well known for the last 20,000 years—the time since the last ice age. By convention, the late-glacial period refers to the period from 16,000 to 11,000 cal year BP (i.e., calendar years before present) and the Holocene represents the last 11,000 cal years. Based on the timing of major environmental changes, we divide the Holocene into three periods for convenience of discussion: the early

Holocene (ca. 11,000–7000 cal year BP), middle Holocene (7000–4000 cal year BP), and late Holocene (4000 cal year BP to present). The actual timing of Holocene environmental changes varies somewhat from region to region.

In the last 20,000 years, the large-scale controls of climate included the size and position of the Laurentide and Cordilleran ice sheets and their influence on temperature gradients and the strength and position of the jet stream (and thus winter storm tracks; Thompson et al., 1993; Bartlein et al., 1998). The size of the ice sheets also determined the strength of the glacial anticyclone and the flow of surface winds off the ice sheet. Another important control of regional climate has been the variations in the amplitude of the seasonal cycle of insolation, which have occurred as a result of regular variations in the earth–sun orbital geometry, the tilt of the earth on its axis, and the timing of perihelion (the point in the earth's orbit when it is closest to the sun). These orbital variations occur on scales of  $10^4$  to  $10^5$  years, and they are considered the pacemaker of glacial–interglacial cycles (Imbrie et al., 1984). During the last glacial maximum approximately 20,000 cal year BP, summer and winter insolation were similar to their present values, but at 11,000 cal year BP summer insolation was 8% higher and winter insolation was 8% lower than at present at 45°N latitude. This increased seasonality led to increased summer temperatures and decreased effective moisture (i.e., precipitation minus evapotranspiration), and indirectly influenced the strength of the northeast Pacific subtropical high-pressure system and summer monsoons (Thompson et al., 1993; Whitlock and Bartlein, 1993). The fact that many types of paleoenvironmental records from the western US register a response to variations in insolation on orbital time scales attests to the importance of insolation variations in shaping regional climate and vegetation conditions during the late-glacial and Holocene periods.

The post-glacial vegetation history of the western US is described in several recent reviews (Baker, 1983; Adam, 1985; Mehringer, 1985; Barnosky et al., 1987; Anderson, 1990; Whitlock, 1992, 1993; Thompson et al., 1993; Fall et al., 1995). The late-glacial period was a time of biotic reorganization in the northwestern US as the influence of large ice sheets on climate was waning and summer insolation was increasing (Whitlock, 1992). Plant taxa colonized

regions vacated by glaciers, creating new pioneer communities. Regions outside the glacial limits were also undergoing rapid change, and in many areas the vegetation combined present-day subalpine and lowland taxa in assemblages that have no modern counterpart (e.g., Whitlock, 1992, 1993). As climate continued to warm, species distributions became arranged along gradients of latitude and elevation.

The seasonal cycle of insolation was greatest in the early Holocene and led to warmer summers and probably colder winters than at present throughout the region. The northeastern Pacific subtropical high-pressure system was stronger, and consequently the Pacific Northwest and much of the northern Rocky Mountains that are summer-dry (i.e., that receive most of their annual precipitation in winter) were even drier in summer in the early Holocene (Whitlock and Bartlein, 1993). Greater summer drought in the early Holocene is evidenced by the expansion of xerophytic communities, higher alpine treeline, and lower lake levels and stream activity. The summer monsoon of the southwestern US and parts of the Rocky Mountains also intensified in the early Holocene, and areas that today are summer-wet (i.e., that receive most of their annual precipitation in summer) were even wetter then, as indicated by the expansion of mesophytic plant taxa in those regions (Thompson et al., 1993; Whitlock and Bartlein, 1993).

Summer insolation decreased and winter insolation increased to present-day levels in the last 7000 years, and this attenuation of the seasonal cycle of insolation eventually led to the establishment of the modern vegetation, climate, and fire regimes. Cooler and effectively wetter conditions than before were established in the Pacific Northwest and Rocky Mountains between 5000 and 3000 cal year BP, as evidenced by increased mesophytic vegetation and downslope shifts in alpine treeline. Summer-wet regions record a decrease in summer precipitation in the middle and late Holocene as a result of reduced summer onshore flow of moisture. This drying led to the establishment of more-open xerophytic communities than before (Thompson et al., 1993).

Superimposed on climate changes driven by orbital variations are short-term variations in climate, such as the Medieval Warm Period (ca. 900–600 cal year BP; Gates, 1993) and the Little Ice Age (ca. 550–150 cal year BP; Gates, 1993). The cause of these variations is

not known, but changes in solar output and volcanic activity have been suggested (e.g., Crowley, 2000; Bond et al., 2001). Tree-ring and lake-sediment records in the Sierra Nevada (Stine, 1994; Hughes and Graumlich, 1996), for example, show evidence of drought during the Medieval Warm Period, and on many mountain ranges treeline lay above present levels (Leavitt, 1994). Cooler temperatures and expanded glacial activity are associated with the Little Ice Age in the northern Rocky Mountains and the Pacific Northwest (Davis, 1988), and this period seems to be the coldest of a series of cool oscillations in the late Holocene (e.g., Luckman, 1994).

#### 4.2. Long-term fire responses

A network of lake-sediment records provides a picture of changing fire activity in different parts of the northwestern US through the Holocene (Fig. 1). Various approaches have been used to reconstruct fire frequency (e.g., see Mehringer et al., 1977; Cwynar, 1987; Mehringer, 1985; Fall, 1997), but we explicitly consider sites where macroscopic charcoal was examined in contiguous samples. As noted above, such studies constrain the source of the fire and are calibrated based on a comparison with dendrochronological and historical records. Also, by distinguishing charcoal peaks from the slowly varying background trend, it is possible to examine changes in the frequency of fire episodes through time.

The records suggest that fire frequency (i.e., the return interval between fires) has changed continuously and no long-term stationarity is evident in the fire frequency record (Fig. 2). There are also distinct features in the spacing of fire episodes within regions that suggest spatial coherency in the disturbance regimes. Charcoal records from the summer-dry Klamath Mountains of northern California, for example, indicate that fires were frequent throughout the Holocene with little long-term trend in the data. Two sites from the Klamath region, Bluff and Crater lakes, suggest periods of frequent fire, such as at ca. 4000 and 1000 cal year BP. These periods may have been times of pronounced drought in northern California (Mohr et al., 2000). In contrast to the fire records, the pollen records from these sites record a large response to insolation-driven climate changes, and little change in association with the short-term variations in climate.

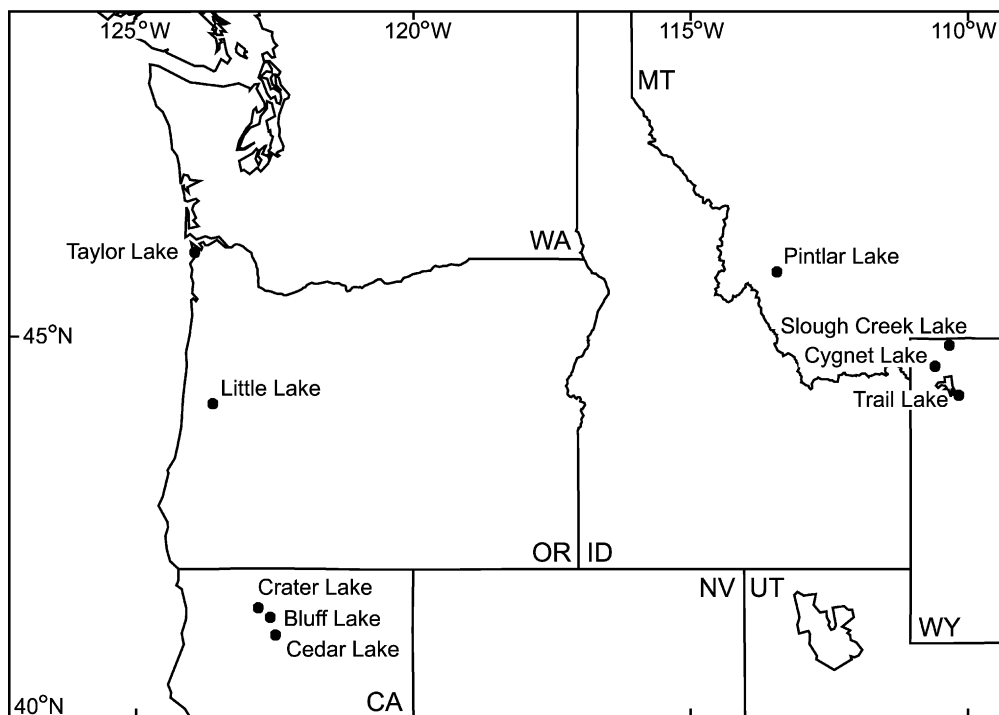


Fig. 1. Location of fire-history studies referred to in Fig. 2: Cedar Lake, CA (Whitlock et al., unpublished data); Bluff Lake and Crater Lake, CA (Mohr et al., 2000); Taylor Lake, OR (Long and Whitlock, 2002); Little Lake, OR (Long et al., 1998); Cygnet Lake, WY (Millsbaugh et al., 2000); Trail Lake, WY (Whitlock, unpublished data); Slough Creek Lake, WY (Millsbaugh and Whitlock, in press); Pintlar Lake, MT (Brunelle-Daines, 2002).

For example, an expansion of xerophytic taxa, most notably *Quercus* spp., is consistent with warmer drier conditions in the early Holocene, but no change in fire frequency is registered on this time scale (Mohr et al., 2000). In contrast, pollen data were not sensitive enough to detect vegetation changes on millennial and shorter time scales in this area, when the region has experienced elevated fire activity.

Data from the summer-dry Oregon Coast Range show high fire activity in the early Holocene and a trend towards fewer fires in the late Holocene (Long et al., 1998; Long and Whitlock, 2002). Fire-sensitive species, such as Douglas-fir, red alder (*Alnus rubra*), Oregon white oak (*Quercus garryana*), and bracken (*Pteridium* spp.), are well represented in the early Holocene interval. The decrease in fire activity correlates well with an expansion of mesophytic rainforest taxa, such as Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*), and provides

supporting evidence of cooling and increased moisture in the last few millennia.

Charcoal records from the summer-dry region of southern Yellowstone National Park also indicate increased fire activity associated with warmer and drier conditions in the early Holocene (Millsbaugh et al., 2000). Two sites, Cygnet and Trail lakes, register this fire response, and it occurs even where the vegetation has been relatively unresponsive to Holocene climate changes. At Cygnet Lake, for example, infertile, well-drained soils have maintained lodgepole pine forests over the last 11,000 years (Whitlock, 1993). In contrast, Trail Lake on andesitic terrain records an expansion of Douglas-fir and lodgepole pine in the early Holocene followed by increased spruce, fir, and whitebark pine in the late Holocene. At Cygnet Lake, the fire frequency was low prior to 11,000 cal year BP during an initial tundra-open meadow period. With the arrival of lodgepole pine,

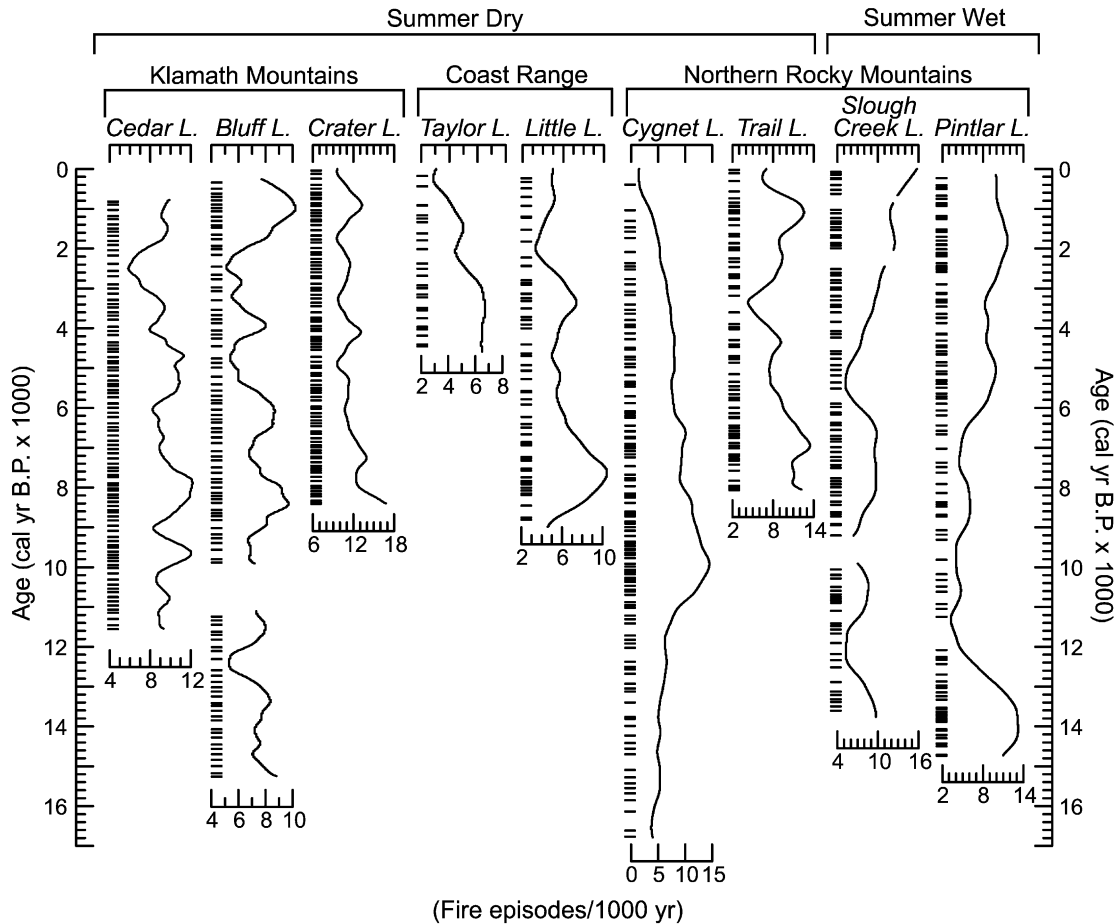


Fig. 2. Comparison of Holocene fire reconstructions from sites in different geographic and climatic locations in the western US (see Fig. 1 for site locations). The horizontal lines at each site represent past fire episodes, i.e., based on the age of peaks in the charcoal record obtained from radiocarbon-dated sediment cores (see Whitlock and Larsen, 2002). These peaks represent one or more fires occurring in a decade. The curves depict fire frequency, which is the number of fire episodes per 1000 years averaged over a moving window. Summer dry and summer wet refer to two different precipitation regimes evident in the western US (see text for discussion).

fire frequency increased and reached a maximum of 10–15 fires per 1000 years at 10,000–9000 cal year BP. In the last 7000 cal year BP the fire frequency declined to a modern return interval of 2–3 fires per 1000 years in the last two millennia, but lodgepole pine remained the dominant forest species at this site. This record shows that fire variations respond directly to climate even in areas where the vegetation is fairly unresponsive. Trail Lake indicates a decline in fire frequency from the early Holocene period, with an increase ca. 1000 cal years ago.

Records from summer-wet areas of the Rocky Mountains provide additional evidence of the strong

link between climate and fire conditions. These locations are areas that were influenced by increased summer precipitation in the early Holocene and have become progressively drier since then. Slough Creek Lake in northwestern Wyoming and Pintlar Lake in southwestern Montana register this response in their pollen and charcoal records (Brunelle-Daines, 2002; Millsbaugh and Whitlock, in press). Both sites have fire frequencies that were low in the early Holocene and became progressively more frequent in the late Holocene. At Slough Creek Lake, this increase in fire activity is associated with the expansion of Douglas-fir parkland at low elevations, replacing pine forest.



At Pintlar Lake, lodgepole pine forest replaced mixed-conifer forest.

Millsbaugh and Whitlock (in press) compare the Slough Creek Lake and Cygnet Lake records on shorter time intervals and show that, while the fire histories in summer-wet and summer-dry regions were out of phase on orbital time scales, they were occasionally synchronized on short time scales. For example, fire episodes at these sites are registered at ca. 1000, 2000, and 4000 cal year BP, and these particular events are associated with fire-related debris flow activity in northeastern Yellowstone National Park (Meyer et al., 1995). This synchronization of fires in the late Holocene may have been enhanced by the effect of decreasing summer insolation on atmospheric circulation and precipitation regimes. The climate of summer-wet and summer-dry regions became more similar in the late Holocene, as summer-dry areas became wetter and summer-wet areas became drier. During this period, the large-scale controls that cause different fire regimes on orbital time scales were overridden by widespread droughts and fires on shorter time scales. For example, fires have occurred in both summer-wet and summer-dry areas in recent years in the face of dry conditions.

## 5. Potential future fire conditions in the northwestern US

### 5.1. Fire regimes and climate change

The relationships among climate, vegetation, and fire regimes expressed in the paleoecological record, combined with model simulations of past, present, and potential future environmental changes, can help us understand how fire regimes may change in the future in the northwestern US. Projecting potential future fire regimes requires accurately simulating a myriad of complex ecological, physical, and human interactions, a task that is not yet possible. We can, however, examine the magnitude and direction of simulated changes in the physical and biotic environment and infer their potential impacts on fire regimes. This information, combined with an appreciation of the historical range of variability in fire occurrence, can help develop appropriate management strategies for the region.

Although there is still uncertainty in model simulations of future climate conditions, it is increasingly evident that human activities are contributing to climate changes that will significantly affect future fire regimes (IPCC, 2001). A recent study by Giorgi et al. (2001) compared the regional results of transient climate simulations from nine AOGCMs for the time period A.D. 2071–2100. Each AOGCM was run using two different greenhouse gas emission scenarios, with each scenario assuming different rates of increase in greenhouse gases (see Giorgi et al., 2001; IPCC, 2001 for descriptions of the emission scenarios). All of the AOGCMs simulated global warming with mean annual temperature increases ranging from approximately 0.9 to 4.5 °C among the models (Giorgi et al., 2001). Of particular significance is the general agreement of the AOGCM results—at least seven of the AOGCMs under each of the emission scenarios simulated warming in summer and winter for the northwestern US that was greater than the simulated global average annual warming. As Giorgi et al. (2001) note, the agreement of the model simulations under two different emission scenarios increases the confidence that can be ascribed to the simulations of regional warming. Although potential changes in precipitation are more difficult to simulate than those in temperature, at least seven of the AOGCM simulations for A.D. 2071–2100 also indicated slight increases in winter precipitation for the northwestern US. There was less agreement among the AOGCMs as to whether summer precipitation would increase or decrease in the region (Giorgi et al., 2001).

There are many ways in which these potential future climate changes could affect fire regimes. Significant increases in summer temperatures in the northwestern US without an accompanying increase in precipitation could increase summer drought stress on vegetation. If the drought stress was severe enough it could create vegetation conditions conducive to increased fire activity. Even if summer precipitation in the region increased significantly, greater evapotranspiration as a result of higher temperatures could still lead to increased drought stress. If drought stresses were large enough, they could affect riparian vegetation, which is often buffered from drought effects, particularly along perennial streams. Changes in temperature and the timing of precipitation would also affect fuel moisture levels, with drier fuels

increasing the potential for fires (Miller and Urban, 1999).

Increased temperatures could also result in an earlier and longer fire season (Flannigan et al., 2000; Gitay et al., 2001). Flannigan et al. (2000) evaluated simulations by two AOGCMs for 2060 using scenarios that assumed an approximate doubling of atmospheric CO<sub>2</sub> concentrations. They concluded that both AOGCMs simulated an increase in fire activity for the northwestern US based on an increase in the seasonal fire-severity rating index, which they defined as “a seasonal mean of the daily estimate of the control difficulty of a potential fire” (Flannigan et al., 2000, p. 222). Potential future changes in climate could also affect the frequency of natural ignition sources such as lightning. Although it is difficult to extrapolate from long-term climate changes simulated by AOGCMs to relatively short-term weather phenomena, such as thunderstorms, simulations of future climate change indicate a potential increase in atmospheric conditions that promote lightning-caused fires (e.g., Price and Rind, 1994).

As one measure of the potential impacts of future climate change on fire regimes in the northwestern US, we used a simple water-balance model to simulate

potential changes in summer soil moisture for A.D. 2050–2059. We also simulated summer soil moisture for 6000 cal year BP, a time period when many paleoecological records from the northwestern US register increased fire frequencies. Soil moisture is an important control on vegetation, and it integrates changes in temperature, precipitation, and evapotranspiration, providing a measure of potential drought stress. The simulations for 6000 cal year BP and A.D. 2050–2059 show similar patterns of soil moisture, particularly in the mountains of the northwestern US (Fig. 3). For 6000 cal year BP, the paleoecological record indicates that increased summer insolation resulted in higher-than-present summer temperatures, heightened drought, and drier soils and fuels. In turn, these changes led to fire frequencies that were greater than current levels in summer-dry regions. The simulated soil moisture anomalies for 6000 cal year BP (Fig. 3) are in agreement with the paleoecological record and indicate that much of the northwestern US had drier-than-present summer soil moisture at this time. Drier-than-present soils are also simulated for A.D. 2050–2059 as a result of simulated increases in summer temperatures and evapotranspiration, and, in some areas of the northwestern US, earlier snowmelt.

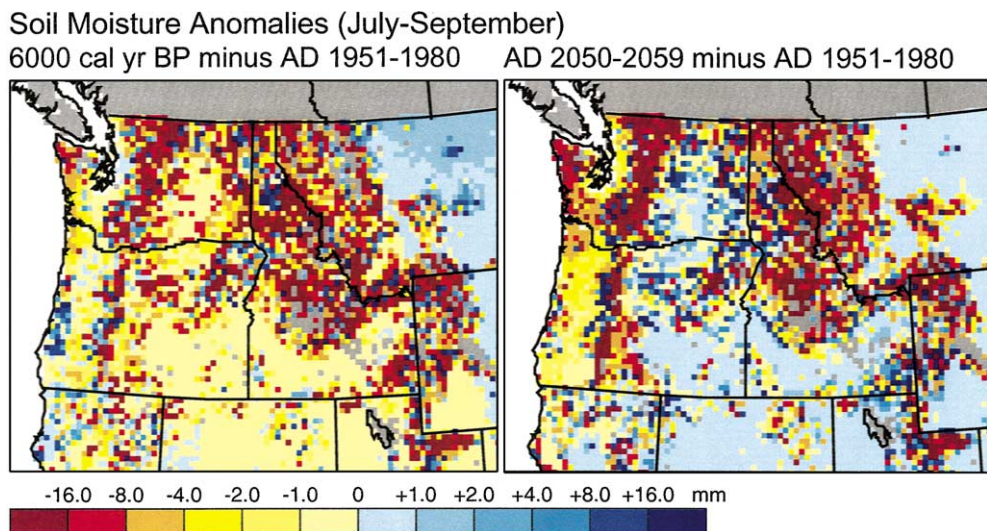


Fig. 3. Mean summer (July–September) soil moisture anomalies (mm) for 6000 cal year BP (left) and A.D. 2050–2059 (10-year mean) (right) compared to present (A.D. 1951–1980, 30-year mean) in the northwestern US. The Olympic Mountains, Cascade Range, and Rocky Mountains display similar patterns of negative summer soil moisture anomalies for both time periods, indicating slightly drier soils in summer in these regions as compared with present conditions. Climate data: A.D. 1951–1980 (Thompson et al., 1999); 6000 cal year BP, CCM3 (Bonan, 1996); A.D. 2050–2059, HADCM2 HCGSa (Mitchell and Johns, 1997). Soil data: CONUS-Soil (Miller and White, 1998).

There are also large areas of the interior northwestern US for which small increases in soil moisture are simulated as a result of simulated increases in summer precipitation.

The similar patterns of simulated summer soil moisture anomalies for 6000 cal year BP and A.D. 2050–2059 suggest that future climate changes could create soil moisture conditions similar to those that occurred during times in the Holocene when fire frequencies were higher. That the simulated patterns of soil moisture for the two time periods are similar does not mean that the response of the fire regime would be same in the future as at 6000 cal year BP, since other factors, including vegetation, affect fire regimes. However, by continuing to compare paleoecological data with model simulations of soil moisture and other variables, we can improve our understanding of both how and why interactions among climate, vegetation, and fire regimes have varied in the past, which in turn provides important information as to how these interactions may vary in the future.

## 5.2. Fire regimes and vegetation change

Future vegetation changes in the northwestern US will also affect fire regimes. Vegetation change can occur as a result of changes in climate, interactions among native and introduced species, and human activities, such as land use. Future changes in temperature and in the magnitude and frequency of precipitation events will have significant impacts on biotic communities in the northwestern US. Changes in seasonality will be particularly important. For example, warmer temperatures, if combined with increases in precipitation, could increase plant productivity in certain regions, providing more fuel during the fire season (Gitay et al., 2001). In addition to responding to future changes in temperature and precipitation, plants are also directly affected by increases in atmospheric concentrations of CO<sub>2</sub>, which increase the drought tolerance of some plant species by improving their water-use efficiency (Mooney et al., 1999; Simberloff, 2000). Vegetation models that incorporate anticipated increases in atmospheric CO<sub>2</sub> concentrations simulate an expansion of woody vegetation (e.g., Shafer, 2000), particularly in arid regions, that could potentially increase fuel biomass and fuel connectivity in these areas.

The paleoecological record indicates that plant taxa respond individually to climate change (Davis, 1981; Huntley, 1995; Webb, 1995) and this response is also observed in the modern record (e.g., Fitter and Fitter, 2002). As climate changes, the ranges of some plant species will expand and others will contract, altering the species composition of communities (Shafer et al., 2001). The potentially disparate response of species to changes in climate and atmospheric CO<sub>2</sub> concentrations will alter competitive interactions and affect the geographic distribution of fire-tolerant and fire-intolerant species. In turn, the changing mosaic of species on the landscape will alter the frequency and extent of future fires. In model simulations, Miller and Urban (1999) found that species composition also significantly affected fuel-bed bulk density, which in turn affects fire regimes.

Interactions of plant species with non-plant taxa will also affect fire regimes. For example, increases in potential winter temperatures will allow some insect species to significantly expand their ranges, while increased summer temperatures will increase the productivity of some species (Ayres and Lombardero, 2000). Potential increases in the frequency and magnitude of droughts could increase stress on trees making them more vulnerable to insect attack, and damage from insect outbreaks would leave stands more vulnerable to fire (Knight, 1987). The fire-insect outbreak feedback is one of the many climate–vegetation–fire interactions that will likely be more evident in the future.

Human activities, including the introduction of non-native invasive species, and land use changes, such as logging and habitat fragmentation, will affect the vulnerability of forest communities to climate change. Human introductions of certain non-native invasive species, such as cheatgrass (*Bromus tectorum*), have already altered fire regimes in portions of the northwestern US, and these plants are continuing to spread (Mack, 1981). The invasion of cheatgrass in intermountain regions of the western US has created a continuous cover of fine fuels in some areas that were formerly covered by patchy bunchgrasses, allowing fires to spread more easily (West and Young, 2000). Fires also create opportunities for invasive species to establish (D'Antonio, 2000).

The paleoecological record and future vegetation simulations suggest that certain plant species are relatively resistant to climate changes, while others respond

to climate change with major geographic readjustments. Lodgepole pine, for example, may be relatively resistant to projected changes in climate and fire frequency just as it has shown little response to warming in the past (Whitlock, 1993; Bartlein et al., 1997). With increasing fire activity in the future, the structure of lodgepole pine forests may shift to younger age classes and a finer-grained mosaic (Romme and Turner, 1991), but the forest dominant could remain the same. In contrast, Douglas-fir, which did well during periods of warmer-than-present summer conditions and higher fire frequencies in the past, may be especially vulnerable to projected climate changes that include warm winters. Warmer winter temperatures could reduce the competitiveness of its seedlings by not providing a sufficient period of winter cold temperatures to meet the chilling requirement of this species (McCreary et al., 1990; Kirschbaum et al., 1996). Moreover, Douglas-fir persisted during times of increased fire occurrence, but model projections suggest that it will decline if frequencies exceed 1 fire per 20 years (Keane et al., 1990).

The simulated distribution of Douglas-fir for A.D. 2090–2099 (Fig. 4) illustrates the potential spatial complexity of the vegetation response. The response surface model used in this simulation identifies areas in the northwestern US where potential future bioclimatic conditions are similar to those currently occupied by Douglas-fir, as well as areas where future bioclimatic conditions are sufficiently different from current conditions that they may no longer be suitable for the species. The model results indicate a potential reduction in suitable bioclimatic conditions for Douglas-fir along the Pacific slope and western margins of its range, with potential new areas of suitable bioclimatic conditions along the eastern margins of its range. There are a number of caveats that accompany this model simulation, including the recognition that there are many processes that will affect the response of Douglas-fir to future climate change that are not simulated by the response surface model. These processes include the response of the species to changing atmospheric CO<sub>2</sub> concentrations, interactions with other species, and the

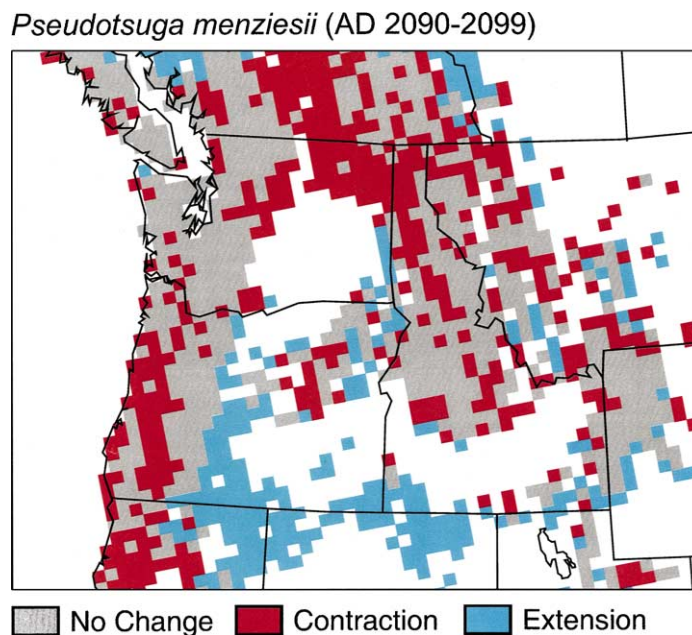


Fig. 4. Potential future distribution of *P. menziesii* (Douglas-fir) in the northwestern US, simulated using climate scenarios for A.D. 2090–2099 (10-year mean) generated by the HADCM2 AOGCM (Mitchell and Johns, 1997). “No change” indicates where *P. menziesii* is observed at present and is simulated to occur under future climate conditions; “contraction” indicates where *P. menziesii* is observed at present but is simulated to be absent under future climate conditions; and “extension” indicates where *P. menziesii* is not observed at present but is simulated to occur under future climate conditions. Climate data: A.D. 2090–2099 HADCM2 HCGSa (Mitchell and Johns, 1997). See Shafer et al. (2001) for methods and additional species. Modified from Shafer et al. (2001).

effects of changes in disturbance regimes, such as fire (Shafer et al., 2001). Thus, the response surface model results are not predictions of range changes at any particular location on the ground. Rather, the results suggest that bioclimatic conditions over large areas of its current range may become unsuitable as a result of projected climate changes. Future fires in these areas could initiate the conversion of Douglas-fir forests to those dominated by different species if future bioclimatic conditions limit the establishment and viability of Douglas-fir seedlings.

Finally, a critical point to remember in assessing the potential future impacts of climate change on fire regimes and vegetation is that climate change is transient—as global warming continues to increase the interactions among climate, vegetation and fire regimes will also change. Increased winter precipitation, for example, is simulated to increase snowpack in the Yellowstone region of the northwestern US for A.D. 2050–2059. As winter temperatures continue to warm, however, a point will be reached where less precipitation will occur as snow, and snowpack will begin to decrease. These changes will affect the timing and quantity of snowmelt, which in turn will affect soil moisture, streamflow, and upland and riparian vegetation in certain areas. The transient nature of climate change greatly increases the difficulty for managers of developing appropriate responses to future climate change.

## 6. Relevance to ecosystem management

An understanding of climate, vegetation, and fire interactions in the past provides important perspectives for management efforts promoting future sustainability of forests and riparian ecosystems. First, the paleoecological record from the northwestern US shows that fire frequency has continually changed during the Holocene in response to climate change. Periods of intense drought in the past featured more fires and fire-adapted vegetation, and wet conditions were associated with fewer fire events and the establishment of more fire-sensitive forests. The timing of drought and high fire activity has varied from region to region, reflecting the spatial heterogeneity of the seasonal patterns of precipitation at any particular time (Mock, 1996). Of importance for ecosystem management is the lack of a fire cycle or recurrent

fire interval at centennial and millennial time scales based on charcoal data. Likewise, tree-ring studies in the Pacific Northwest and northern Rocky Mountains show considerable temporal variability in fire occurrence on decadal time scales (Heyerdahl et al., 1998; Weisberg and Swanson, 2003).

The variability recorded in the fire-history record is important because it contradicts the notion of a static fire return interval that is often referred to in ecosystem management plans. Although mean fire interval may be a useful concept for management planning in certain instances, such as in defining an envelope of natural variability (Swetnam et al., 1999), this concept should be used cautiously. The fire activity of the last few centuries in many areas of the western US is not typical of the longer record. Overcoming the effects of fire suppression in recent decades is a worthy goal, but it is important to remember that even our best efforts cannot reproduce pre-Euro-American settlement fire regimes. The climate, vegetation, and fire conditions that existed then do not exist today and are not likely to exist in the near future. Although the past does not provide a perfect analog for the future, knowledge of previous fire regimes, combined with our understanding of modern fire–climate relations, can help us anticipate future changes in fire regimes. For example, projections of increased summer drought suggest that fire frequency or fire severity could increase in most western US forests (see also Meyer and Pierce, 2003).

Second, northwestern US forests, including riparian forest communities, are relatively young. Present communities have formed only in the last few millennia as the region's climate became cooler and wetter (Whitlock, 1992). Old-growth riparian communities may have established during a cooler wetter period of generally low fire activity during the Little Ice Age or following particularly widespread fires in the late 1500s (Weisberg and Swanson, 2003). Thus, the forests that greeted early Euro-American settlers to the region would be difficult to recreate under present climate and fire conditions.

Third, the individualistic behavior of the region's dominant tree species has led to range contractions and expansions as well as entire shifts in species distributions. Given the magnitude of projected climate changes, individualistic responses of species may be more pronounced in the future. The paleoecological record reveals that shifts in fire regimes have

sometimes been the catalyst of rapid vegetation changes in the past, and it is likely that disturbance will influence how vegetation adjust to future climate changes. Certain species have persisted in the past under higher fire frequencies than they experience today, and these species may be able to compete favorably if fire frequencies increase in the future.

Fourth, different sources of fire-history data help us to evaluate fire–vegetation–climate relationships on multiple time scales and across landscapes. Fire reconstructions based on lake-sediment records, dendrochronological data, and documentary evidence help disclose the temporal and spatial variability of fire in ecosystems. For example, in low-elevation forests that experienced frequent fires in recent times, the effects of fire suppression and other management practices are well recorded in tree-ring data (e.g., [Hessburg and Agee, 2003](#)). Charcoal records from such forests (although currently not available) would disclose the frequency of stand-replacing events that are lethal to the trees, information that the tree-ring record is unable to provide. In montane and subalpine forests, current fire regimes include mixed- to high-severity infrequent fires. Dendrochronological data poorly reconstruct the frequency of such events, whereas the charcoal data provide information on stand-replacing fires spanning several millennia.

Fifth, an understanding of the spatial heterogeneity of precipitation regimes in the northwestern US in the past offers another tool for forward-looking ecosystem management. Future fire conditions in summer-dry regions may be best described by an examination of the early Holocene, when drier-than-present summers resemble those of future projections. In summer-wet sites, the last few millennia are the time of highest fire occurrence and may be the best analog for the future (although this assertion is based on very few records and needs further testing). Future trade-offs in the spatial distribution of precipitation will particularly alter riparian ecosystems by affecting the timing and magnitude of discharge, including snowmelt and storm events; the frequency and severity of fire on riparian communities; and the potential for invasion by non-native species ([Dunham et al., 2003](#)). Our ability to describe the spatial extent and character of future conditions will continue to improve as climate and vegetation models increase in resolution and complexity, and disturbance regimes are more explicitly addressed.

Finally, an important challenge is to incorporate the complexity of climate–vegetation–fire relationships into a conceptual framework of fire management. In protecting areas of special concern, such as riparian buffers, we must recognize the dynamic nature of ecosystems in the past and the complexity of potential future responses. Fire management activities that alter the fire regime directly or indirectly may collide with future vegetation and climate changes that are not under management control. These interactions have the potential to produce unexpected and undesirable consequences.

Thus, ecosystem planning and management must be adaptive enough to incorporate flexibility in the face of environmental change. Adaptive management requires clearly defined goals predicated on information gained from research that is scientifically sound, comprehensive, and multidisciplinary ([National Research Council, 2002](#)). Long-term monitoring is necessary to determine the successes and consequences of management decisions in the light of the complex ecological responses that are likely in the future. The different configurations of climate, hydrology, vegetation, and fire in the paleoecological record provide an important tool for delineating the magnitude of possible future responses of fire regimes to climate and vegetation changes, and help to identify those variables that should be part of future ecosystem monitoring efforts.

## Acknowledgements

Support for this research was provided by NASA Earth System Science Fellowship 97/0281, and US National Science Foundation grants ATM-9910638, EAR-9906100, and ATM-0117160. We thank Patrick Bartlein for assistance with data and figures, and Grant Meyer, Daniel Muhs, Laura Strickland, and one anonymous reviewer for their comments on the manuscript.

## References

- Adam, D.P., 1985. Quaternary pollen records from California. In: Bryant Jr., V.M., Holloway, R.G. (Eds.), *Pollen Records of Late-Quaternary North American Sediments*. American Association of Stratigraphic Palynologists Foundation, Austin, TX, pp. 125–140.

- Agee, J.K., 1993. *Fire Ecology of Pacific Northwest Forests*. Island Press, Washington, DC, 493 pp.
- Anderson, R.S., 1990. Holocene forest development and paleoclimates within the central Sierra Nevada, California. *J. Ecol.* 78, 470–489.
- Arno, S.F., Sneek, K.M., 1977. A method for determining fire history in coniferous forests in the mountain West. USDA Forest Service General Technical Report No. INT-42.
- Ayres, M.P., Lombardero, M.J., 2000. Assessing the consequences of global change for forest disturbance from herbivores and pathogens. *Sci. Total Environ.* 262, 263–286.
- Baker, R.G., 1983. Holocene vegetational history of the western United States. In: Wright Jr., H.E. (Eds.), *Late-Quaternary Environments of the United States*. University of Minnesota Press, Minneapolis, MN, pp. 109–127.
- Barnosky, C.W., Anderson, P.M., Bartlein, P.J., 1987. The northwestern US during deglaciation; vegetational history and paleoclimatic implications. In: Ruddiman, W.F., Wright Jr., H.E. (Eds.), *North America and Adjacent Oceans During the Last Deglaciation*. Geology of North America, vol. K-3. Geological Society of America, Boulder, CO, pp. 289–321.
- Bartlein, P.J., Whitlock, C., Shafer, S.L., 1997. Future climate in the Yellowstone National Park region and its potential impact on vegetation. *Conserv. Biol.* 11, 782–792.
- Bartlein, P.J., Anderson, K.H., Anderson, P.M., Edwards, M.E., Mock, C.J., Thompson, R.S., Webb, R.S., Webb III, T., Whitlock, C., 1998. Paleoclimate simulations for North America over the past 21,000 years: features of the simulation climate and comparisons with paleoenvironmental data. *Quat. Sci. Rev.* 17, 549–585.
- Birks, H.H., 2002. Plant macrofossils. In: Smol, J.P., Birks, H.J.B., Last, W.M. (Eds.), *Tracking Environmental Change Using Lake Sediments*, vol. 3: Terrestrial, Algal, and Siliceous Indicators. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 49–74.
- Bonan, G.B., 1996. A land surface model (LSM version 1.0) for ecological, hydrological, and atmospheric studies: technical description and user's guide. NCAR Technical Note No. NCAR/TN-417 + STR, Boulder, CO, 150 pp.
- Bond, G., Kromer, B., Beer, J., Muscheler, R., Evans, M.N., Showers, W., Hoffmann, S., Lotti-Bond, R., Hajdas, I., Bonani, G., 2001. Persistent solar influence on North Atlantic climate and deep-ocean flow south of Iceland. *Nature* 297, 515–517.
- Brunelle-Daines, A., 2002. Holocene changes in fire, climate, and vegetation in the northern Rocky Mountains of Idaho and western Montana. Ph.D. Dissertation. University of Oregon, Eugene, OR, 178 pp.
- Clark, J.S., 1990. Fire and climate change during the last 750 years in northwestern Minnesota. *Ecol. Monogr.* 60, 135–159.
- Clark, J.S., Lynch, J., Stocks, J.B., Goldammer, J., 1998. Relationships between charcoal particles in air and sediments in west-central Siberia. *Holocene* 8, 19–29.
- COHMAP Members, 1988. Climate changes of the last 18,000 years: observations and model simulations. *Science* 241, 1043–1052.
- Crowley, T.J., 2000. Causes of climate change over the last 1000 years. *Science* 289, 270–277.
- Cwynar, L.C., 1987. Fire and the forest history of the North Cascade Range. *Ecology* 68, 791–802.
- D'Antonio, C., 2000. Fire, plant invasions, and global changes. In: Mooney, H.A., Hobbs, R.J. (Eds.), *Invasive Species in a Changing World*. Island Press, Washington, DC, pp. 65–93.
- Davis, M.B., 1981. Quaternary history and the stability of forest communities. In: West, D.C., Shugart, H.H., Botkin, D.B. (Eds.), *Forest Succession: Concepts and Application*. Springer, New York, pp. 132–153.
- Davis, P.T., 1988. Holocene glacier fluctuations in the American cordillera. *Quat. Sci. Rev.* 7, 129–158.
- Davis, O.K., 1995. Climate and vegetation patterns in surface samples from arid western USA: application to Holocene climatic reconstructions. *Palynology* 19, 95–117.
- Delcourt, H.R., Delcourt, P.A., Webb III, T., 1983. Dynamic plant ecology: the spectrum of vegetational change in time and space. *Quat. Sci. Rev.* 1, 153–175.
- Dunham, J.B., Young, M.K., Rieman, B.E., Gresswell, R.E., 2003. Effects of fire on fish populations: landscape perspectives on persistence of native fishes and non-native fish invasions. *For. Ecol. Manage.* 178 (1–2), 183–196.
- Fall, P.L., 1992. Pollen accumulation in a montane region of Colorado, USA: a comparison of moss polsters, atmospheric traps, and natural basins. *Rev. Palaeobot. Palynol.* 72, 162–197.
- Fall, P.L., 1997. Fire history and composition of the subalpine forest of western Colorado during the Holocene. *J. Biogeogr.* 24, 309–325.
- Fall, P.L., Davis, P.T., Zielinski, G.A., 1995. Late Quaternary vegetation and climate of the Wind River Range, Wyoming. *Quat. Res.* 43, 393–404.
- FAUNMAP Working Group, 1996. Spatial response of mammals to late Quaternary environmental fluctuations. *Science* 272, 1601–1605.
- Fitter, A.H., Fitter, R.S.R., 2002. Rapid changes in flowering time in British plants. *Science* 296, 1689–1691.
- Flannigan, M.D., Stocks, B.J., Wotton, B.M., 2000. Climate change and forest fires. *Sci. Total Environ.* 262, 221–229.
- Foley, J.A., Prentice, I.C., Ramankutty, N., Levis, S., Pollard, D., Sitch, S., Haxeltine, A., 1996. An integrated biosphere model of land surface processes, terrestrial carbon balance, and vegetation dynamics. *Glob. Biogeochem. Cy.* 10, 603–628.
- Gardner, J.J., Whitlock, C., 2000. Charcoal accumulation following a recent fire in the Cascade Range, northwestern USA, and its relevance for fire-history studies. *Holocene* 5, 541–549.
- Gates, D.M., 1993. *Climate Change and its Biological Consequences*. Sinauer Associates, Massachusetts.
- Gavin, D.G., 2000. Holocene fire history of a coastal temperate rain forest, Vancouver Island, British Columbia, Canada. Ph.D. Dissertation. University of Washington, Seattle, WA, 131 pp.
- Gedye, S.J., Jones, R.T., Tinner, W., Ammann, B., Oldfield, F., 2000. The use of mineral magnetism in the reconstruction of fire history: a case study from Lago di Origlio, Swiss Alps. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 164, 101–110.
- Giorgi, F., Mearns, L.O., 1991. Approaches to the simulation of regional climate change: a review. *Rev. Geophys.* 29, 191–216.
- Giorgi, F., Whetton, P.H., Jones, R.G., Christensen, J.H., Mearns, L.O., Hewitson, B., vonStorch, H., Francisco, R., Jack, C.,

2001. Emerging patterns of simulated regional climatic changes for the 21st century due to anthropogenic forcings. *Geophys. Res. Lett.* 28, 3317–3320.
- Gitay, H., Brown, S., Easterling, W., Jallow, B., 2001. Ecosystems and their goods and services. In: McCarthy, J.J., Canziani, O.F., Leary, N.A., Dokken, D.J., White, K.S. (Eds.), *Climate Change 2001: Impacts, Adaptation, and Vulnerability. Contribution of Working Group II to the Third Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, pp. 235–342.
- Haxeltine, A., Prentice, I.C., 1996. BIOME3: an equilibrium terrestrial biosphere model based on ecophysiological constraints, resource availability, and competition among plant functional types. *Glob. Biogeochem. Cy.* 10, 693–709.
- Hessburg, P., Agee, J.K., 2003. An environmental narrative of Inland Northwest US forests, 1800–2000. *For. Ecol. Manage.* 178 (1–2), 23–59.
- Heyerdahl, E.K., Brubaker, L.B., Agee, J.K., 1998. Spatial controls on historical fire regimes: a multiscale example from the interior West, USA. *Ecology* 72, 660–679.
- Hughes, M.K., Graumlich, L.J., 1996. *Climatic Variations and Forcing Mechanisms of the Last 2000 Years*, vol. 141. *Multi-millennial Dendroclimatic Studies from the Western United States*. NATO ASI Series, pp. 109–124.
- Huntley, B., 1995. How vegetation responds to climate change: evidence from palaeovegetation studies. In: Pernetta, J.C., Leemans, R., Elder, D., Humphrey, S. (Eds.), *Impacts of Climate Change on Ecosystems and Species: Environmental Context*. IUCN, Gland, Switzerland, pp. 43–63.
- Imbrie, J., Hays, J.D., Martinson, D.G., McIntyre, A., Mix, A.C., Morley, J.J., Pisias, N.G., Prell, W.L., Shackleton, N.J., 1984. The orbital theory of Pleistocene climate: support from a revised chronology of the marine  $\delta^{18}\text{O}$  record. In: Berger, A., Imbrie, J., Kukla, G., Saltzman, B. (Eds.), *Milankovitch and Climate*. Reidel, Dordrecht, The Netherlands, pp. 269–305.
- IPCC, 2001. *Climate change 2001: The scientific basis*. Houghton, J.T., Ding, Y., Griggs, D.J., Noguer, M., van der Linden, P.J., Dai, X., Maskell, K., Johnson, C.A. (Eds.), *Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK, 881 pp.
- Iverson, L.R., Prasad, A.M., 1998. Predicting abundance of 80 tree species following climate change in the eastern United States. *Ecol. Monogr.* 68, 465–485.
- Keane, R.E., Arno, S.F., Brown, J.K., 1990. Simulating cumulative fire effects in Ponderosa pine/Douglas-fir forests. *Ecology* 71, 189–203.
- Kirschbaum, M.U.F., Fischlin, A., Cannell, M.G.R., Cruz, R.V.O., Galinski, W., Cramer, W.P., 1996. Climate change impacts on forests. In: Watson, R.T., Zinyowera, M.C., Moss, R.H. (Eds.), *Climate Change 1995: Impacts, Adaptations and Mitigation of Climate Change*. Cambridge University Press, Cambridge, UK, pp. 95–129.
- Knight, D.H., 1987. Parasites, lightning, and the vegetation mosaic in wilderness landscapes. In: Turner, M.G. (Ed.), *Landscape Heterogeneity and Disturbance*. Springer, New York, pp. 59–83.
- Kutzbach, J., Gallimore, R., Harrison, S., Behling, P., Selin, R., Laarif, F., 1998. Climate and biome simulations for the past 21,000 years. *Quat. Sci. Rev.* 17, 473–506.
- Leavitt, S.W., 1994. Major wet interval in White Mountains medieval warm period evidenced in  $\delta^{13}\text{C}$  of bristlecone pine tree rings. *Clim. Change* 26, 299–307.
- Long, C.J., Whitlock, C., 2002. Fire and vegetation history from the Coastal rain forest of the Western Oregon Coast Range. *Quat. Res.* 58, 215–225.
- Long, C.J., Whitlock, C., Bartlein, P.J., Millspaugh, S.H., 1998. A 9000-year fire history from the Oregon Coast Range, based on a high-resolution charcoal study. *Can. J. For. Res.* 28, 774–787.
- Luckman, B.H., 1994. Evidence for climatic conditions between ca. 900–1300 A.D. in the southern Canadian Rockies. *Clim. Change* 26, 171–182.
- Mack, R.N., 1981. Invasion of *Bromus tectorum* L. into western North America: an ecological chronicle. *Agro-Ecosystems* 7, 145–165.
- McCreary, D.D., Lavender, D.P., Hermann, R.K., 1990. Predicted global warming and Douglas-fir chilling requirements. *Ann. Sci. For.* 47, 325–330.
- Mehring Jr., P.J., 1985. Late-Quaternary pollen records from the interior Pacific Northwest and northern Great Basin of the United States. In: Bryant Jr., V.M., Holloway, R.G. (Eds.), *Pollen Records of Late-Quaternary North American Sediments*. American Association of Stratigraphic Palynologists Foundation, Austin, TX, pp. 167–189.
- Mehring Jr., P.J., Arno, S.F., Peterson, K.L., 1977. Postglacial history of Lost Trail Pass bog, Bitterroot Mountains, Montana. *Arctic Alpine Res.* 9, 345–368.
- Meyer, G.A., Pierce, J., 2003. Climatic control of fire-induced sediment pulses in Yellowstone National Park and Central Idaho: a long-term perspective. *For. Ecol. Manage.* 178 (1–2), 89–104.
- Meyer, G.A., Wells, S.G., Jull, A.J.T., 1995. Fire and alluvial chronology in Yellowstone National Park: climatic and intrinsic controls on Holocene geomorphic processes. *Geol. Soc. Am. Bull.* 107, 1211–1230.
- Miller, C., Urban, D.L., 1999. Forest pattern, fire, and climatic change in the Sierra Nevada. *Ecosystems* 2, 76–87.
- Miller, D.A., White, R.A., 1998. A conterminous United States multilayer soil characteristics dataset for regional climate and hydrology modeling. *Earth Interact.* 2, 1–26.
- Millspaugh, S.H., Whitlock, C., 1995. A 750-year fire history based on lake sediment records in central Yellowstone National Park, USA. *Holocene* 5, 283–292.
- Millspaugh, S.H., Whitlock, C., in press. Postglacial fire, vegetation, and climate history of the Yellowstone-Lamar and Central Plateau provinces, Yellowstone National Park. In: Wallace, L. (Ed.), *After the Fires: The Ecology of Change in Yellowstone National Park*. Yale University Press, New Haven, CT.
- Millspaugh, S.H., Whitlock, C., Bartlein, P.J., 2000. Variations in fire frequency and climate over the last 17,000 years in central Yellowstone National Park. *Geology* 28, 211–214.
- Minckley, T., Whitlock, C., 2000. Spatial variation of modern pollen in Oregon and southern Washington, USA. *Rev. Palaeobot. Palynol.* 112, 97–123.



- Mitchell, J.F.B., Johns, T.C., 1997. On modification of global warming by sulphate aerosols. *J. Clim.* 10, 245–267.
- Mock, C.J., 1996. Climatic controls and spatial variations of precipitation in the western United States. *J. Clim.* 9, 1111–1125.
- Mohr, J.A., Whitlock, C., Skinner, C.J., 2000. Postglacial vegetation and fire history, eastern Klamath Mountains, California. *Holocene* 10, 587–601.
- Mooney, H.A., Canadell, J., Chapin III, F.S., Ehleringer, J.R., Körner, Ch., McMurtrie, R.E., Parton, W.J., Pitelka, L.F., Schulze, E.-D., 1999. Ecosystem physiology responses to global change. In: Walker, B., Steffen, W., Canadell, J., Ingram, J. (Eds.), *The Terrestrial Biosphere and Global Change: Implications for Natural and Managed Ecosystems*. Cambridge University Press, Cambridge, UK, pp. 141–189.
- National Interagency Fire Center, 2002. <http://www.nifc.gov/fire-info/2000/index.html>.
- National Research Council, Committee on Ungulate Management in Yellowstone National Park, 2002. *Ecological Dynamics on Yellowstone's Northern Range*. National Academy Press, Washington, DC.
- National Oceanic and Atmospheric Administration, 2002. <http://www.noaa.gov>.
- Patterson III, W.A., Edwards, K.J., MacGuire, D.J., 1987. Microscopic charcoal as a fossil indicator of fire. *Quat. Sci. Rev.* 6, 3–23.
- Prentice, I.C., Webb III, T., 1998. BIOME6000: reconstructing global mid-Holocene vegetation patterns from paleoecological records. *J. Biogeogr.* 25, 997–1005.
- Price, C., Rind, D., 1994. The impact of a  $2\times$  CO<sub>2</sub> climate on lightning-caused fires. *J. Clim.* 7, 1484–1494.
- Romme, W.H., Despain, D.G., 1989. Historical perspective on the Yellowstone fires of 1988. *Bioscience* 39, 695–698.
- Romme, W.H., Turner, M.G., 1991. Implications of global climate change for biogeographic patterns in the Greater Yellowstone ecosystem. *Conserv. Biol.* 5, 373–386.
- Shafer, S.L., 2000. Potential vegetation response to future climate change in western North America and its implications for biological conservation and geographical conceptualizations of place. Ph.D. Dissertation. University of Oregon, Eugene, OR.
- Shafer, S.L., Bartlein, P.J., Thompson, R.S., 2001. Potential changes in the distributions of western North America tree and shrub taxa under future climate scenarios. *Ecosystems* 4, 200–215.
- Simberloff, D., 2000. Global climate change and introduced species in United States forests. *Sci. Total Environ.* 262, 253–261.
- Sitch, S., Smith, B., Prentice, I.C., Arneeth, A., Bondeau, A., Cramer, W., Kaplan, J.O., Levis, S., Lucht, W., Sykes, M.T., Thonicke, K., Venevsky, S., 2003. Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. *Global Change Biology* 9, 161–185.
- Stine, S., 1994. Extreme and persistent drought in California and Patagonia during medieval time. *Nature* 269, 546–549.
- Swetnam, T., Allen, C., Betancourt, J., 1999. Applied historical ecology: using the past to manage for the future. *Ecol. Appl.* 9, 1189–1206.
- Thompson, R.S., Whitlock, C., Bartlein, P.J., Harrison, S.P., Spaulding, W.G., 1993. Climatic changes in the western United States since 18,000 year BP. In: Wright Jr., H.E., Kutzbach, J.E., Webb III, T., Ruddiman, W.F., Street-Perrott, F.A. (Eds.), *Global Climates Since the Last Glacial Maximum*. University of Minnesota Press, Minneapolis, MN, pp. 468–513.
- Thompson, R.S., Anderson, K.H., Bartlein, P.J., 1999. Atlas of relations between climatic parameters and distributions of important trees and shrubs in North America. US Geological Survey Professional Paper No. 1650 A&B.
- USDA Forest Service, 2001. [http://www.fireplan.gov/FS\\_Prog\\_RPT\\_July\\_30.cfm](http://www.fireplan.gov/FS_Prog_RPT_July_30.cfm).
- Webb III, T., 1988. Eastern North America. In: Huntley, B., Webb III, T. (Eds.), *Vegetation History*. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 385–414.
- Webb III, T., 1995. Pollen records of late Quaternary vegetation change: plant community rearrangements and evolutionary implications. In: National Research Council Commission on Geosciences, Environment, and Resources. *Effects of Past Global Change on Life*. National Academy Press, Washington, DC, pp. 221–232.
- Weisberg, P.J., Swanson, F.J., 2003. Regional synchronicity in fire regimes of western Oregon and Washington, USA. *For. Ecol. Manage.* 172, 17–28.
- West, N.E., Young, J.A., 2000. Intermountain valleys and lower mountain slopes. In: Barbour, M.G., Billings, W.D. (Eds.), *North American Terrestrial Vegetation*. Cambridge University Press, Cambridge, UK, pp. 255–284.
- Whitlock, C., 1992. Vegetational and climatic history of the Pacific Northwest during the last 20,000 years: implications for understanding present-day biodiversity. *Northw. Environ. J.* 8, 5–28.
- Whitlock, C., 1993. Postglacial vegetation and climate of Grand Teton and southern Yellowstone National Parks. *Ecol. Monogr.* 63, 173–198.
- Whitlock, C., Bartlein, P.J., 1993. Spatial variations of Holocene climatic change in the Yellowstone region. *Quat. Res.* 39, 231–238.
- Whitlock, C., Larsen, C.P.S., 2002. Charcoal as a fire proxy. In: Smol, J.P., Birks, H.J.B., Last, W.M. (Eds.), *Tracking Environmental Change Using Lake Sediments*, vol. 3: Terrestrial, Algal, and Siliceous Indicators. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 74–97.
- Whitlock, C., Millsbaugh, S.H., 1996. Testing assumptions of fire history studies: an examination of modern charcoal accumulation in Yellowstone National Park. *Holocene* 6, 7–15.