Forest fires have swept into public and policy awareness over the past several decades, with an increase in the frequency of large fires in western North America (Westerling et al. 2006). At the same time, human settlement and other infrastructure are impinging on the wildland interface at an unprecedented rate, resulting in annual US federal suppression costs exceeding $1 billion in 3 of the past 6 years (OIG 2006). These recent, large fires have been attributed to a variety of processes, from local increases in fuel loads and shifts in stand composition to regional and global changes in climate (Schoennagel et al. 2004). In some regions, such as the southwestern US, historical fire suppression has been blamed for increases in stand density and fire severity (Allen et al. 2002). In contrast, climate change explains recent patterns in fire occurrence over broad areas of western North America (Fauria and Johnson 2006; Trouet et al. 2006). The few forecasts that exist indicate that the trend toward increased incidence of fires will continue (eg McKenzie et al. 2004; Flannigan et al. 2005).

To place modern fire processes in a meaningful context, scientists and policy makers need a long-term view of fire variability. Fossil records describing past ecosystems (paleoecological records) can quantify the historical range of variability of fire occurrence. They can therefore provide an important reference for ecosystem-based strategies aimed at maintaining ecological processes, habitats, and species (eg Willis and Birks 2006; Figure 1). It should be made clear, however, that application of paleoecological data to forecasting the future is complicated by the fact that the future may not resemble any time in the past (Jackson and Williams 2004), particularly with respect to the climatic and fuel controls of fire. While this may limit the potential for the past to serve as an analog for the future, there is an important need for a mechanistic understanding of the processes that pro-
In this review, we highlight several paleo-fire records from western North America and explain their relevance in the reconstruction of historical forest dynamics, fire–climate relationships, and feedbacks between vegetation and fire under climate change. We also emphasize the importance of paleo-records for validating dynamic ecosystem models designed to project future fire regimes (Panel 1).

Millennial-scale variability in fire regimes

Knowledge of long-term forest disturbance rates is essential for answering basic questions related to forest dynamics, such as the predominant mode of tree recruitment (following large fires, small-scale tree deaths, or wind disturbances) over periods spanning more than a single tree generation. If forest management is to be based on the context defined by their historical dynamics (eg simulating patch size and intensity of typical forest disturbances), disturbance histories are crucial sources of information (Swetnam et al. 1999). In regions where fire is rare, disturbance histories must be long enough to characterize the frequency and range of variability of fire occurrence if we are to understand the development of the current vegetation and fire regime. One such region is the cool and wet coastal rainforest of the Pacific Northwest of North America, where fires have lasting effects on the ecosystem, due to the longevity of the trees (> 400 years) and the slow rates of decay. For example, it is common to find evidence of recent disturbance, possibly fire, in the form of shade-intolerant tree species of a single age embedded within old-growth forest (Agee 1993). In these regions, paleoecological studies represent a key approach to understanding the natural variability of fire regimes.

Paleo-fire studies from the coastal rainforest of southwestern British Columbia, Canada, show how the spatial and temporal patterns of fire have shaped the diversity of current forest structure. Radiocarbon-dated soil charcoal along an 11-km valley on Vancouver Island indicated that 20% of the sampled sites, mostly terraces or north-facing slopes, had not burned in over 6000 years (Gavin et al. 2003; Figure 5a). A lake-sediment record from similar forests also suggests multi-millennial periods with limited fire, preceded by greater fire activity during the early Holocene (11 700–7000 years ago), when forests were dominated by fire-adapted species (Brown and Hebda 2002; Figure 5b). In contrast, soil charcoal and tree-ring evidence on dry, south-facing slopes show that nearly all such sites burned within

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**Figure 1.** High-severity fires, such as this one in central Alaska, result in the mortality of most canopy trees. Such fires are typical over broad areas of western North America. The return intervals between high-severity fires typically range from decades to millennia, due to the time required to renew fuel loads and the rarity of ignition and fire weather. Because of the lack of a tree-ring record pre-dating the most recent high-severity fire, the only source of information on the long-term variability of fire in these regions is the paleoecological record. As these fires deposit abundant wood charcoal into soils and lake sediments, an increasing number of charcoal records are clarifying the connections among climate change, vegetation change, and fire.
the past 1000 years. These sites have shallow soils and stunted forests consistent with the cumulative impact of multiple fires on the soil resource. Further inland, in southwestern British Columbia and at high elevations, sub-alpine meadows and adjacent forests experienced greater fire frequency than sites on similar terrain on the coast (Hallett et al. 2003; Figure 5c). Despite the presence of early summer snowpacks that could have reduced fire occurrence, these sites have more frequent lightning ignitions compared to coastal areas and are more likely to be influenced by blocking ridges of high pressure that dry fuels across British Columbia and Alberta. However, the soil charcoal record from this forest–meadow parkland indicates that fire intervals at specific points were of sufficient length (> 400 years) to support widespread old-growth conditions (Lertzman et al. 2002; Figure 5d). Together, these studies show huge spatial and temporal variability in past fire regimes in southwestern British Columbia, and help to reveal the processes that generated today’s ecosystems.

### Comparing fire histories to assess the role of climate

A simple principle underlying most fire-history studies is that the direct impacts caused by climate should result in spatially synchronous fire activity across sites (Swetnam 1993). Consistent with this expectation, recent paleo-fire syntheses revealed the synchrony of millennial-scale trends in fire relative to long-term changes in climate and forest composition (Whitlock et al. 2003). At this time scale (> 14 000 years), paleo-records encompass major changes in the climatic boundary conditions, including orbital geometry affecting the seasonal distribution of solar energy, extent of ice sheets, and CO$_2$ concentrations. These forcing mechanisms exert the clearest “controls” over the nature of fire regimes and can provide explanations for past patterns in fire activity. For example, syntheses by Whitlock et al. (2003) and Brunelle et al. (2005) show that, while there is considerable local variability, fire history over the past 12 000 years follows different trajectories of summer moisture in distinct climatic regions of western North America.

During the late Holocene (4000 years ago until present), the large-scale controls of climate, and presumably the range of climatic variability, were approaching those of the last few centuries. This period is therefore highly relevant in determining a background reference for many current fire management issues. Gavin et al. (2006) explicitly tested the degree of synchrony of fire episodes between two 5000-year-long fire records in southern British Columbia. The results showed very little common timing of fire episodes, even though the sites were only ~ 10 km apart and both located in spruce–fir sub-alpine forest. Differences in ignition histories and post-fire fuel dynamics probably outweighed the synchronizing effect of climate, even over millennia. However, the effect of climate on fire regimes may become evident with an increasing number of sites that, together, represent a sizeable area (Gavin et al. 2006). For example, century-scale patterns of synchrony are emerging in areas with a high density of accurately dated paleo-fire records, such as southern British Columbia (Hallett et al. 2003). The finding of increasing synchrony with increasing area sampled is to be expected from a spatially distributed phenomenon such as fire. Such comparisons suggest that even millennial-scale patterns from a single site should not be generalized to a large area.

### Fire, climate, and changing forest composition

Fire mediates the responses of forests to climate change, either by accelerating species turnover or by selecting for fire-adapted species (Overpeck et al. 1990). In the same way, changes in species composition may alter fire occurrence by changing the concentration and arrangement of flammable fuels (Bond and Keeley 2005). The strong potential for interactions and feedbacks between fire and

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**Figure 2.** The spatial and temporal domains of fire history methods span several orders of magnitude. Vertical lines extend from the finest temporal accuracy to the maximum temporal depth of a particular method. Horizontal lines extend from estimates of the finest spatial accuracy of individual records to the combined spatial extent of all existing North American records. A terminal circle represents an insurmountable constraint on a particular method. Dashed lines represent the potential to extend fire history further back in time, although this is contingent upon discovering such records. Arrows represent the potential for more spatial coverage with future work. While tree-ring and sediment paleo-fire records may be compared from sites separated by hundreds of kilometers, the aggregated area represented by these records is quite small. Modified from Swetnam et al. (1999).
its controls suggest that fire occurrence over long periods may reflect indirect (ie vegetation and human land use) as well as direct climatic controls (Bergeron et al. 2004). Paleo-fire records, in conjunction with independent evidence of past vegetation and climate, can help to clarify the links between fire, fuel, and climate through periods of substantial climate change, revealing which processes are most important in controlling fire occurrence.

A recent synthesis of 15 paleo-fire records in the western US revealed that biomass burning, as estimated from charcoal accumulation in sediments, and tree cover, as estimated from pollen records, have steadily increased over the past 11 000 years (Marlon et al. 2006). The parallel increase in the amount of biomass and biomass burning suggests that, at a regional scale and over millennia, fuel loads have acted as an important control of the degree of burning. This pattern of increasing biomass burning emerges only after compositing many records and does not address substantial between-site variation in the influence of forest composition on fire. To illustrate such differences, we compare three records with contrasting fire–vegetation–climate relationships.

On the Central Plateau of Wyoming’s Yellowstone National Park, due to the presence of infertile rhyolitic...
soils, the vegetation was dominated by fire-prone lodgepole pine forests throughout the Holocene (Millspaugh et al. 2000; Figure 6b). With little vegetation change to confound a fire–climate relationship, fire frequency decreased gradually with generally decreasing summer temperature over this period. As most pollen records from western North America show substantial changes in forest composition, this record provides a valuable “control” for the direct role of climate on fire occurrence.

In the Alaskan boreal forest, Holocene changes in species composition had a major effect on fire occurrence. Here, a striking increase in fire occurred approximately 6000 years ago, coincident with the establishment of black-spruce dominated forests, as the regional climate became cooler and wetter than previously (Lynch et al. 2002; Figure 6c). Compared to white spruce, the conifer that dominated prior to 6000 years ago, black spruce forests are composed of more widely spaced trees, occur on deep, peaty soils, and produce abundant fine crown fuels. These are all conditions that favor dry fuel and fire spread. Several records show a consistent association between fire and black spruce (such as in Figure 6), regardless of the timing of the increase in black spruce (Hu et al. 2006). Thus, the strong differences in flammability of boreal tree species may exert a more important control of fire than regional climate change. However, in areas where black spruce is less common, or during periods dominated by similar vegetation, climate is probably an important control of fire history (Lynch et al. 2004; Anderson et al. 2006).

The role of forest composition in fire occurrence is also evident in a montane forest of North Cascades National Park in northern Washington State, where two major vegetation shifts occurred during the Holocene (Prichard 2003; Figure 6d). At ca 8000 years ago, fire frequency decreased in conjunction with a replacement of lodgepole pine by western white pine and Douglas-fir, indicating the onset of moister conditions; this has been widely documented at other sites in the region (Walker and Pellatt 2003). Then, approximately 4500 years ago, the establishment of the modern, diverse western hemlock and western redcedar forest was followed by a return to more frequent, and possibly more severe, fires. This increase in fire frequency is unexpected because hemlock and redcedar establishment suggests a mild, wet winter climate with earlier, cooler summers – conditions that are not conducive to fire initiation.

As in the North Cascades, a late-Holocene increase in fire occurrence also took place in southwestern British Columbia (Figure 5d), indicating that regional rather than local factors affected fire regimes. The counterintuitive pattern in late-Holocene fire history may reflect an incomplete understanding of climate and/or vegetation on long time scales. One possibility is that the preceding period was rela-

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**Figure 5.** Two types of paleoecological records of fire incidence in low fire frequency coastal ecosystems of southwestern British Columbia. These records provide complementary information on the spatial and temporal patterns of fire. (a) The time elapsed since the most recent fire (the time-since-fire) over a network of 83 sites in a watershed on the west coast of Vancouver Island, British Columbia (Gavin et al. 2003). Fire ages were determined using soil-charcoal radiocarbon dates and tree-ring records. (b) A lake-sediment charcoal record from the west coast of Vancouver Island showing long periods with little to no fire (Pixie Lake; Brown and Hebda 2002). CHAR is charcoal accumulation rate, as in Figure 4, but sampled at 5-cm intervals. (c) Intervals between fires inferred from dated charcoal layers in deep organic sub-alpine meadow soils (Hallett et al. 2003). (d) A lake-sediment charcoal record from southwest British Columbia sub-alpine forest (Hallett et al. 2003).
Fire and parallel vegetation histories can provide reference conditions for forests prior to large-scale changes, including land use and fire suppression (Swetnam et al. 1999). In regions where fire suppression has greatly altered fire intervals, tree-ring evidence may supplant charcoal records in defining reference conditions, because of their increased resolution. Nevertheless, charcoal records may extend the tree-ring record to broaden such reference periods. Care must be taken when defining reference periods, because long-term paleoecological records may extend back to periods when the range of variability in climate, fire, or other ecosystem properties would have limited relevance to the present.

**Mechanistic controls of fire**

Dynamic interactions among vegetation, fuels, physical landscape, climate, and humans can provide a perspective on mechanistic controls of fire unavailable through other approaches. For example, there has often been a dichotomy between fire ecologists who view local factors (patterns of vegetation and fuels) as dominant controls of fire regimes and those who view climatic variation as pre-eminent. This dichotomy reflects different scales of focus. Sub-continental fire climatology analyses tend to emphasize the dominant controls of seasonal to decadal climatic variation (eg Hessl et al. 2004), while managers are often focused on short-term and local ecological phenomena that drive management debates (eg Peterson et al. 2005). In contrast, the paleoecological perspective shows that climate and site ecology are important controls of fire regimes. As shown in this paper (eg Figure 6), such insights are region-specific and require detailed analyses of multiple proxy indicators of past climate, fire, and vegetation, as well as comparisons of historical records from the same region.

**Ecological modeling**

Long-term fire histories may be used to aid development of ecosystem models that will allow managers to con-
struct many “what if” forecasts of fire under a range of future fuel and climate scenarios. One means of predicting fire is through statistical modeling of the relationship between historical fire occurrence and different climatic variables. For example, McKenzie et al. (2004) quantified relationships between area burned and climatic parameters for the 11 large states in the contiguous western US and projected area burned using a climate model scenario for future climate. Should these relationships hold in the future, this analysis predicted 100–200% increases in annual area burned, but with considerable regional variation due to different relative climatic controls of fire.

Although statistical models provide a straightforward approach to projecting fire occurrence, the effects of changing vegetation are not explicitly modeled. Given that projected future climate changes are of a scale similar to or greater in amplitude than those during the Holocene (IPCC 2007), future fire occurrence may be greatly affected by changes in vegetation and climate. If vegetation changes substantially under future climate, existing statistical models may not reliably predict concomitant changes in fire regimes.

To project fire in a system with changing vegetation requires a mechanistic approach with a dynamic vegetation model. Such models have only recently been modified to simulate fire and feedbacks between fire and vegetation (e.g., Arora and Boer 2005). These models also address the effects of increases in atmospheric CO₂ on vegetation (e.g., by increasing water-use efficiency). Furthermore, they are able to examine how the specific sequence of climatic variations that ultimately occur affects the dynamics of vegetation and fire over time, toward some future condition.

Paleoecological records provide data at the spatial and temporal scales (stands to landscapes, over centuries to millennia) in which vegetation models operate. Model “hindcasts” of vegetation and fire during past climates can therefore be compared to paleoecological records. These data–model comparisons may be used to evaluate the predictive power of models and, when validated, the models can provide mechanistic explanations for patterns in the data. Few studies have yet used paleo-fire data in this way (Spessa et al. 2003). Flannigan et al. (2001) carried out one such study, in which paleo-fire data from 6000 years before present was used as an analog for future warming to test predicted changes in fire regimes. With further contributions of paleo-fire records to a growing dataset, and with the concurrent development of vegetation models that include fire processes, we expect paleo-fire records to play a major role in projecting future patterns in vegetation and fire.

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References


WebPanel 1. The development of paleo-fire records

Lake sediment charcoal
The quantity of charcoal in lake sediments is related to fire activity: the frequency of fire, and/or the amount of biomass consumed in fire (Whitlock and Larsen 2002). Thus, the amount of charcoal is not necessarily linearly related to fire frequency if there is a concurrent change in flammable biomass. For example, it is conceivable that a switch between fire regimes of infrequent, stand-replacing fires to frequent, small, surface fires could result in less charcoal being delivered to a lake (Power et al. 2006). To improve the interpretation of charcoal records, many researchers quantify the charcoal stratigraphy from sediment cores and then identify individual charcoal peaks (sometimes called “fire episodes” to acknowledge that one or more fires may be embedded in one peak). One method is to sieve contiguous samples and isolate the charcoal of a relatively large size (Long et al. 1998; WebFigures 1 and 2), while others quantify charcoal in the same sediment sample prepared for pollen analysis (Tinner and Hu 2003). In order to identify peaks in charcoal, the entire stratigraphy must be quantified at a resolution sufficient to distinguish the low-charcoal periods between peaks.

There are several critical research needs related to interpreting charcoal records.

• Not all records contain the stratigraphic resolution to allow identification of charcoal peaks, but there are currently no criteria for making such an assessment.

• The statistical treatment of charcoal records to isolate charcoal peaks is based on some poorly understood assumptions regarding the processes that govern peak formation. Understanding these processes may help us to interpret situations where charcoal peaks are difficult to identify objectively (Higuera et al. 2007).

• Sediment records integrate fire over an area of unknown size, and thus fire intervals from sediment records may be shorter than intervals at specific points. Research is needed to help determine the size of this “charcoal source area”.

The method of quantifying charcoal, either by surface area, volume, or particle counts, remains at issue among researchers. Some have found different measures to be strongly correlated, obviating the work required to measure particle sizes (Tinner and Hu 2003).

Charcoal in soils and other depositional environments
Soil charcoal studies may be conducted in regions that lack lake sediments because charcoal persists in soils for thousands of years. A major advantage of determining fire dates from radiocarbon-dated soil charcoal is that fire locations are known (except where substantial soil movement occurs). Some disadvantages are that radiocarbon dating is expensive and that dates may overestimate the actual age of a fire if the charcoal was derived from wood that was already old at the time of the fire. Furthermore, soils are often mixed, making it difficult to assess fire intervals except in undisturbed organic soils (or peats) in cool, humid climates (Lertzman et al. 2002). Other settings where charcoal may not be mixed include small basins (termed small hollows) that contain a meter or more of sediment (Higuera et al. 2005) and alluvial or colluvial fans that accumulate loose material at the base of a hill (Sanborn et al. 2006). Debris flows (downslope movement of water-saturated sediment) are strongly associated with severe, tree-killing fires, such that charcoal records of debris flows may reveal how often severe fires occur in a region currently in a low-severity fire regime (Pierce et al. 2004).

References