



Climatic Change, Wildfire, and Conservation

DONALD MCKENZIE,*§ ZE'EV GEDALOF,† DAVID L. PETERSON,* AND PHILIP MOTE‡

*U.S. Department of Agriculture Forest Service, Pacific Wildland Fire Sciences Lab, 400 N 34th Street #201, Seattle, WA 98103, U.S.A.

†University of Victoria Tree-Ring Laboratory, Box 3050, Station CSC, Victoria, British Columbia, V8W 3P5, Canada

‡JISAO/SMA Climate Impacts Group, University of Washington, Seattle, WA 98195, U.S.A.

Abstract: *Climatic variability is a dominant factor affecting large wildfires in the western United States, an observation supported by palaeoecological data on charcoal in lake sediments and reconstructions from fire-scarred trees. Although current fire management focuses on fuel reductions to bring fuel loadings back to their historical ranges, at the regional scale extreme fire weather is still the dominant influence on area burned and fire severity. Current forecasting tools are limited to short-term predictions of fire weather; but increased understanding of large-scale oceanic and atmospheric patterns in the Pacific Ocean (e.g., El Niño Southern Oscillation, Pacific Decadal Oscillation) may improve our ability to predict climatic variability at seasonal to annual leads. Associations between these quasi-periodic patterns and fire occurrence, though evident in some regions, have been difficult to establish in others. Increased temperature in the future will likely extend fire seasons throughout the western United States, with more fires occurring earlier and later than is currently typical, and will increase the total area burned in some regions. If climatic change increases the amplitude and duration of extreme fire weather, we can expect significant changes in the distribution and abundance of dominant plant species in some ecosystems, which would thus affect habitat of some sensitive plant and animal species. Some species that are sensitive to fire may decline, whereas the distribution and abundance of species favored by fire may be enhanced. The effects of climatic change will partially depend on the extent to which resource management modifies vegetation structure and fuels.*

Key Words: climatic change, conservation, fire history, general circulation models, wildfire

Cambio Climático, Incendios y Conservación

Resumen: *La variabilidad climática es un factor dominante que afecta a incendios mayores en el oeste de Estados Unidos, observación sustentada por datos paleoecológicos de carbón en sedimentos lacustres y reconstrucciones de árboles con cicatrices de fuego. Aunque la gestión actual de incendios se centra en la reducción de combustibles para que las cargas de combustible retornen a sus valores históricos, en la escala regional el clima ígneo extremo aun es la influencia dominante del área quemada e intensidad del fuego. Las herramientas predictivas actuales están limitadas a pronósticos de clima ígneo a corto plazo, pero mejorar nuestra habilidad para predecir la variabilidad climática desde estacional a anualmente podría mejorar con mayor conocimiento de los patrones oceánicos y atmosféricos a gran escala en el Océano Pacífico (por ejemplo, Oscilación Meridional El Niño, Oscilación Decadal del Pacífico). La asociación entre estos patrones cuasi-periódicos y la ocurrencia de incendios, aunque evidente en algunas regiones, ha sido difícil de establecer en otras. El futuro incremento de temperatura probablemente extenderá las temporadas de incendios en el oeste de Estados Unidos, con más incendios antes y después de lo típico actualmente, e incremento en la superficie quemada en algunas regiones. Si el cambio climático incrementa la amplitud y duración de clima ígneo extremo, podemos esperar cambios significativos en la distribución y abundancia de especies de plantas dominantes en algunos ecosistemas, lo cual afectaría el hábitat de algunas especies de animales y plantas sensibles. Algunas especies sensibles al fuego pueden declinar, mientras que puede aumentar la distribución*

§email donaladmckenzie@fs.fed.us

Paper submitted October 28, 2003; revised manuscript accepted December 4, 2003.

y abundancia de especies favorecidas por el fuego. Los efectos del cambio climático dependerán parcialmente de la medida en que la gestión de recursos modifique la estructura de la vegetación y los combustibles.

Palabras Clave: cambio climático, conservación, incendios no controlados, GCM, historia de incendios

Introduction

Vegetation dynamics, disturbance, climate, and their interactions are key ingredients in predicting the future condition of ecosystems and landscapes and the vulnerability of species and populations to climatic change (Lenihan et al. 1998; Keane et al. 1999; Schmoldt et al. 1999). Wildfire is the most important natural ecological disturbance in western North America; hence, understanding the associations between climatic influences and characteristics of fire regimes is essential. Fire presents a particular challenge for conservation because it is stochastic in nature and is highly variable temporally and spatially (Agee 1998; Lertzman et al. 1998).

Historical fire regimes varied widely across North America, before extensive fire suppression began in the early twentieth century. Fire frequency ranged from fire-return intervals (FRIs) of 2–5 years in dry forests and grasslands of the Southwest (Baisan & Swetnam 1990; Grissino-Mayer 1995; Fulé et al. 1997) to multiple centuries in temperate rainforests of the Pacific Northwest or subalpine forests of the Cascade Range and Rocky Mountains (Romme & Knight 1981; Agee 1993). Low-severity fire regimes were typical in arid and semiarid forests; fires normally occurred frequently enough that only understory trees were killed and an open-canopy savanna was maintained. These systems have been altered the most by fire exclusion, such that the canopy is now often closed, fuel loads are both higher and more contiguous, and fire-return intervals are longer.

High-severity fire regimes are typical in subalpine forests and in low-elevation forests with high precipitation and high biomass; fires occur infrequently and often involve crown fuels, with the potential for high mortality in mature trees. Because of their longer fire-return intervals, these systems have been proportionally less affected by twentieth-century fire exclusion.

Mixed-severity fire regimes are typical in montane forests with intermediate precipitation and moderately high fuel accumulations; fire behavior varies from low to high intensity, often causing a mosaic of ground and crown fire with patchy distribution of tree mortality (Taylor 1993; Agee 1998). Fire severity also varies in non-forested ecosystems, from light surface fires in dry woodlands that cause little mortality in woody plant species to stand-replacing fires in chaparral and shrub ecosystems (Zedler et al. 1983; Christensen 1985; Keeley & Fotheringham 2003).

The effects of a particular fire can be inferred from antecedent climate, weather at the time of the fire, vegetation structure and composition, and the abundance and distribution of live and dead fuels (Reinhardt et al. 1997). Similarly, fire-regime characteristics are often inferred from climate, coarse-scale vegetation classifications, biophysical variables (elevation, slope, aspect), and geographic location (McKenzie et al. 2000). The relative influence of climate and fuels on fire behavior and effects varies regionally and subregionally across the western United States. In wet forests and subalpine forests with high fuel accumulations, climatic conditions are usually limiting and fuels are rarely limiting (Bessie & Johnson 1995). Prolonged drought of one or more years combined with extreme fire weather (high temperature, high wind, low relative humidity) is required to carry fire. In drier forests, ignition and fire behavior at small spatial scales were historically limited by fuels. Large fires—especially those involving crown fuels—typically required extreme fire weather governed by specific types of synoptic climatology (Z.G., unpublished data). Current fuel conditions differ across much of the western United States, however, such that large, intense fires may occur under less severe weather (Agee 1997).

We reviewed the extensive and diverse literature that links climatic variability to fire regimes in western North America. We show how three types of fire records—charcoal sediments, fire history from fire-scarred trees and stand-age structures, and twentieth-century fire records and observations—are associated with time series from climate reconstructions and the contemporary instrumental record. These associations can be used to infer how fire regimes may be altered under climatic-change scenarios, with increasing quantitative rigor and confidence but with decreasing temporal extent. We focused on forest and shrubland ecosystems that are important for conservation and restoration and for fire management and explored the potential for altered fire regimes associated with anticipated changes in climate through statistical models that combine climate projections from general circulation models (GCMs) with an 87-year record of fire extent for the western United States. These are equilibrium, or stationary, models, meaning that no dynamic vegetation changes are projected in conjunction with them. Finally, we address the effects of climatically induced changes in fire regimes on both threatened or vulnerable species and invasive or exotic species and note the increased difficulties ahead for management.

Climatic Variability and Historical Fire Regimes

Palaeoecological Records

Estimates of the temporal variability in fire regimes throughout the Holocene are possible through the collection and dating of charcoal fragments (Clark & Royall 1996). Sediment-core charcoal dates are established and the charcoal-accumulation rate (CHAR) over time is computed via statistical relationships between a fragment's depth in the core and sedimentation rates. When pulses in CHAR can be separated from background levels associated with region-wide sources, the pulses are presumed to represent individual fires, but accurate spatial resolution (area burned) is not possible because of uncertainties in local dispersal mechanisms. Pollen and macrofossils from the same lake sediments can be used to infer patterns of vegetation (tree-species) composition associated with CHAR. Temporal resolution is typically coarse (≥ 10 years; Prichard 2003), but record length can exceed 10,000 years (Millspaugh et al. 2000; Prichard 2003).

Independent estimates of global climatic variability during the Holocene are based on oxygen isotope studies of ocean sediment and high-latitude ice cores (Imbrie et al. 1989; Petit et al. 1999), back calculation of orbitally induced variations in solar insolation (Berger 1978), reconstructions of lake levels (e.g., Benson et al. 1996), and simulations based on global circulation models (GCMs) (Webb & Kutzbach 1998). Comparisons among the three types of time series—CHAR, vegetation, climate variables—allow for statistical inferences about the effects of climate on fire regimes and vegetation and the direct effects of fire on vegetation.

Coarse-scale temperature reconstructions suggest that increased CHAR is associated with warmer temperatures in sites throughout western North America (Long et al. 1998; Mensing et al. 1999; Millspaugh et al. 2000; Hallett et al. 2003; Prichard 2003). Fire-return intervals throughout the Holocene are generally inferred to have been shorter during periods of warmer, drier climate (e.g., 6–10,000 years before the present), based on direct evidence in charcoal in lake sediments and soil. Fire severity is similarly inferred to have been lower in most areas during these periods, based on two indirect arguments: (1) species currently associated with lower-severity fire regimes increased in abundance relative to species associated with stand-replacing fire regimes today and (2) at least in forested ecosystems, there is a roughly inverse relationship within regions between fire frequency and fire severity (McKenzie et al. 2000).

Reconstructions from Fire-Scarred Trees

Fire scars on trees, in conjunction with counts of annual growth rings, provide annual and sometimes intra-annual resolution of fire dates. Individual trees may exhibit a large

number of surface fires, preserving a history of fire at a particular point in space, and with a large number of accurately dated fire-scar samples it is possible to characterize past surface-fire regimes. The percentage of fire-sensitive trees scarred by fire in a given year provides a surrogate for the percentage of a study area burned. Methods borrowed from survival analysis (Hosmer & Lemeshow 2002) can be used to estimate the statistical properties of low-severity fire regimes (Grissino-Mayer 1999; Heyerdahl et al. 2001).

The extent of a fire-scar record depends on the longevity of the tree species recording fire. Typically, the length of a record is <700 years, but it may extend to 3000 years (Swetnam 1993). Fire-scar records can be compared to climate reconstructions from tree-ring time series from dominant trees of drought-sensitive species on sites that have not experienced obvious disturbance (McKenzie et al. 2001). With broadly distributed data records (e.g., Cook et al. 1999), robust reconstructions are possible for annual temperature and precipitation, drought indices such as Palmer Drought Severity Index (PDSI; Alley 1984), and quasi-periodic patterns such as the El Niño/Southern Oscillation (ENSO) and the Pacific Decadal Oscillation (PDO) (Mantua et al. 1997).

Stand-Age Reconstructions of High-Severity Fire Regimes

Techniques for estimating the frequency of stand-replacing fires differ from those in low-severity regimes because no single tree has scars from multiple fires. By careful reconstruction of stand-age or “time-since-fire” maps, it is possible to estimate the statistical properties of fire regimes (Heinselman 1973; Morrison & Swanson 1990; Johnson & Gutsell 1994). Cumulative probability distributions from the exponential family are fit to “survivorship curves”—monotonic functions representing the proportion of a landscape that did not experience fire up to a certain age—to estimate mean fire frequency (Johnson & Gutsell 1994). Up to this point, statistical methods are analogous to those for low-severity fires, but because fires are generally infrequent, little can be inferred from stand-age reconstructions about the association between fire occurrence and extent and short-term climatic variability. With a long enough record, however, estimates of changing fire frequency can be made at multidecadal scales (Reed et al. 1998; Reed 2002). In forests characterized by mixed-severity fire regimes, stand-age maps may be combined with fire-scar reconstructions to characterize both high-severity and low-severity fire cycles (Baker & Ehle 2001).

Historical Fires in Nonforested Ecosystems

Shrublands and grasslands lack the residual structures (fire-scarred trees) for recording multiple fire events at the same location; thus, before the contemporary period

no annual record of fires in these systems is possible. Although annual precision has been achieved in sediment charcoal from ocean-bottom waters for twentieth-century records, precision deteriorates as one moves back through the historical period (before 1900) (Schimmelmann et al. 1992; Mensing et al. 1999). Thus, there is a gap of extent and resolution in nonforested systems between the palaeoecological record (from charcoal sediments, where they exist) and the contemporary record.

Climatic Variability and Fire at Regional Scales

Large, severe fires account for most of the area burned in a given year, and considerable resources have been devoted to quantifying associations between climate and fire extent, both in the western United States and Canada (Haines 1988; Swetnam & Betancourt 1990; Johnson & Larsen 1991; Balling et al. 1992; Johnson & Wowchuk 1993; Werth & Ochoa 1993). Contemporary studies have the advantage of fire maps or fire atlases with which to estimate annual area burned directly, whereas historical (fire-scar) studies must rely on surrogates such as the percentage of sites that exhibit signs of fire in a given year.

Regional-scale relationships between climate and fire vary, depending on seasonal and annual variability in key climatic drivers, fire frequency and severity, and the legacy of the previous years' climate in live and dead fuels (Grissino-Mayer & Swetnam 2000; Veblen et al. 2000; Heyerdahl et al. 2002; Baker 2003; Hessler et al. 2003). In most regions, current-year drought is associated with increased area burned, but the effects of antecedent conditions vary owing to the complex interactions among climatic effects. In the American Southwest, for example, large fire years are associated with current-year drought but wetter-than-average conditions in the five previous years, whereas small fire years are strongly associated with drought in the previous year (Swetnam & Betancourt 1990). In contrast, in Washington state, Hessler et al. (2004) and Wright and Agee (2004) found direct associations only between fire extent and current-year drought. Synchronous fire years are associated with the ENSO cycle in the Southwest and southern Rocky Mountains (Swetnam & Betancourt 1990; Veblen et al. 2000), less so in eastern Oregon (Heyerdahl et al. 2002), and not at all in Washington (Hessler et al. 2003; Z.G., unpublished data), although Hessler et al. (2003) did identify coherence between the spectral signatures of the percentage scarred from fire and ENSO and PDO. The ability of ENSO events to affect fire regimes may depend both on the timing of the onset of phase shifts between El Niño and La Niña and on their relationship to the timing and duration of the fire season in different regions (Kitzberger & Veblen 2003).

Results from the Canadian Rocky Mountains generally support the inference that fires are more frequent in warmer climates. Fire cycles in these forests were longer during than prior to the Little Ice Age (Masters 1990;

Johnson & Larsen 1991), corroborating inferences made for modern and future climates, for which it is difficult to discriminate management-related changes in the fire cycle from climatically induced changes. Results from elsewhere, however, suggest that fire cycles may have been shorter during the Little Ice Age than either prior to or since, complicating simple interpretation of climate change (Bergeron & Archambault 1993; Weir et al. 2000).

In regions such as the Canadian boreal forest and Pacific Northwest, where fine-fuel production is not limited by climatic variability, short-term (i.e., synoptic) fluctuations in atmospheric conditions play an important role in forcing extreme wildfire years (Johnson & Wowchuk 1993; Agee 1997; Skinner et al. 1999; Gedalof et al. 2004). Although there are subtle differences in the structure of the atmospheric anomalies that characterize extreme wildfire years, they generally consist of anomalous "blocking" ridges of high pressure that divert precipitation away from the region in the days to weeks preceding wildfire occurrence. When the blocking ridge has been especially strong and persistent, the extreme pressure gradient associated with cyclonic storms produces strong winds that, in conjunction with lightning, cause wildfires of unusual severity (Countryman et al. 1969; Finklin 1973). These conditions are mitigated by fuel conditions in some ecosystems, however. For example, in open ponderosa pine (*Pinus ponderosa* Dougl. ex Laws) and Douglas-fir forests (*Pseudotsuga menziesii* [Mirb]) with sparse surface fuels, even extreme weather coupled with ignition may not produce severe fires. In contrast, in high-elevation forests, moisture levels in fine fuels (foliage and fine branches), sensitive to short-term weather, are critical for determining the intensity of crown fires (Bessie & Johnson 1995).

Effects of Climatic Change on Fire

The combination of a warmer climate with carbon dioxide fertilization may cause more frequent and more severe fires in the western United States (Price & Rind 1994; Lenihan et al. 1998). Global circulation models suggest that the length of the fire season, as expressed by measures such as temperature, drought indices, degree-days, and fire weather indices, will likely be longer (Wotton & Flannigan 1993). These changes suggest that we can expect more fires to occur during a given year, but the question remains whether we can quantify the changes and account for the very different fire regimes that exist in different parts of the western United States.

Projections of the effects of climatic change on fire regimes have been of two types: mechanistic models that explicitly represent fire weather, fire behavior, and fire effects at subregional scales (Keane et al. 1999; Miller & Urban 1999; Keane & Finney 2003), and statistical models at regional to continental scales, often linked to output from global circulation models (Flannigan et al. 2001,

2003). The mechanistic approach provides a much more thorough prognosis for the potential effects of fire on vegetation and fuel succession (Keane et al. 1996, 1999; Miller & Urban 1999) but is limited in spatial extent by its computational load and need for detailed input data (McKenzie et al. 2003). However, Lenihan et al. (1998) and Bachelet et al. (2001) combined mechanistic ecosystem modeling with a threshold response for fire events to project increased fire frequency and extent in a warmer world. In either case, global circulation models reliably predict large-scale circulation and temperature (and to a lesser extent precipitation) at annual or longer scales but cannot reliably simulate short-term fire weather.

A third approach, which we use here, is to develop statistical relationships between observed climate and fire extent during the twentieth century and to use those relationships in conjunction with projections of future temperature and precipitation to infer the sign and magnitude of future changes in fire activity. This approach assumes that broad-scale statistical relationships between climatic variables and fire extent will be robust to extrapolation to future climate even if the mechanisms that drive synoptic patterns are not linearly associated with those climatic variables.

We built statistical models of the associations between seasonal and annual precipitation and temperature and fire extent for the period 1916–2002 on a state-by-state scale for each of the 11 western states (Washington, Idaho, Montana, Oregon, California, Nevada, Utah, Wyoming, Colorado, Arizona, New Mexico; data from multiple sources). Although ideally the geographic partition employed would be more ecologically meaningful (e.g., ecosystem provinces; Bailey 1996), no data exist at that scale for anywhere near the record length available for the states. In every state but California, the data are left-skewed (area burned in most years was below the mean), but in California the data are almost normally distributed. In a few states, one or a few fire years stand far above the rest, usually characterized by pronounced antecedent drought and fire weather of unusual severity (2002 in Arizona, Colorado, and Oregon; 1988 in Wyoming; 1983 in Utah).

Using state averages of temperature and precipitation from the U.S. Climate Division data set (<http://www.cdc.noaa.gov/usclimate/usclimdivs.html>), we calculated linear correlations of \log_{10} (area burned) with mean summer (June, July, August) temperature and precipitation. For most of the states, the highest correlations are with positive temperature anomalies and negative precipitation anomalies in the months June through August. In some states (Montana, Nevada, and Utah), area burned is positively correlated with the previous summer's precipitation, and for others (Idaho, New Mexico) area burned is positively correlated with spring temperature more than summer temperature (results not shown). All computations were programmed in the Matlab and Interactive Data Language environments.

These analyses reveal two important relationships. First, the association between area burned and climate is highly nonlinear. The distribution of annual area burned by wildfire spans several orders of magnitude and is dominated by individual large fires that burn under extreme conditions. Given the importance of individual extreme events and the extreme nonlinearity in the record of area burned, these results suggest that relatively modest changes in mean climate could lead to substantial increases in area burned, particularly in crown-fire ecosystems in which distinct thresholds of fuel moisture and fire weather are known to exist.

Second, in most states there is a greater range of values for area burned under hot, dry conditions than under cool, wet conditions. That is, whereas unfavorable (i.e., cool, wet) conditions nearly always lead to reductions in area burned, favorable conditions do not necessarily lead to increases. This difference in response is due to the specific sequence of events that is typically required to cause large increases in area burned: although drought appears to be an important precondition for the occurrence of large fires, these fires will not occur unless the drought is accompanied by a source of ignition (usually lightning) and a mechanism for rapid spread (strong winds). Furthermore, as long as weather conditions do not become unfavorable for wildfire, forests will remain flammable, and ignition and rapid spread can occur at any point during the fire season. Consequently, critical fire-weather events may not be readily apparent in seasonal or even monthly means.

To determine the dependence of area burned on climate, we performed multiple regression of $f = \log_{10}$ (area burned) on summer temperature and precipitation, which yields a bilinear fit to the climate data:

$$f(T, p) = f_0 + a_0T + a_1p,$$

where f_0 is the mean area burned and a_0 (a_1) are the coefficients of regression of area burned against summer temperature (precipitation). If the regression for a variable was not statistically significant, then the regression coefficient a_0 or a_1 was set to zero. This only applied in California (T) and Nevada (both T and P). Contours of f against summer temperature and precipitation anomalies are shown in Fig. 1. The slopes of the contours give an indication of which climate variable has more influence over area burned, and the spacing indicates overall sensitivity to changes in these variables. The years with the largest area burned usually had summers that were warmer and drier than average. In very few cases were cool or wet summers associated with large area burned. Montana is the most sensitive, with a 50-fold increase in mean area burned over the observed range in climate. California and Nevada are the least sensitive. In many cases the data indicate a sharp increase in mean area burned for positive temperature (Arizona, New Mexico,

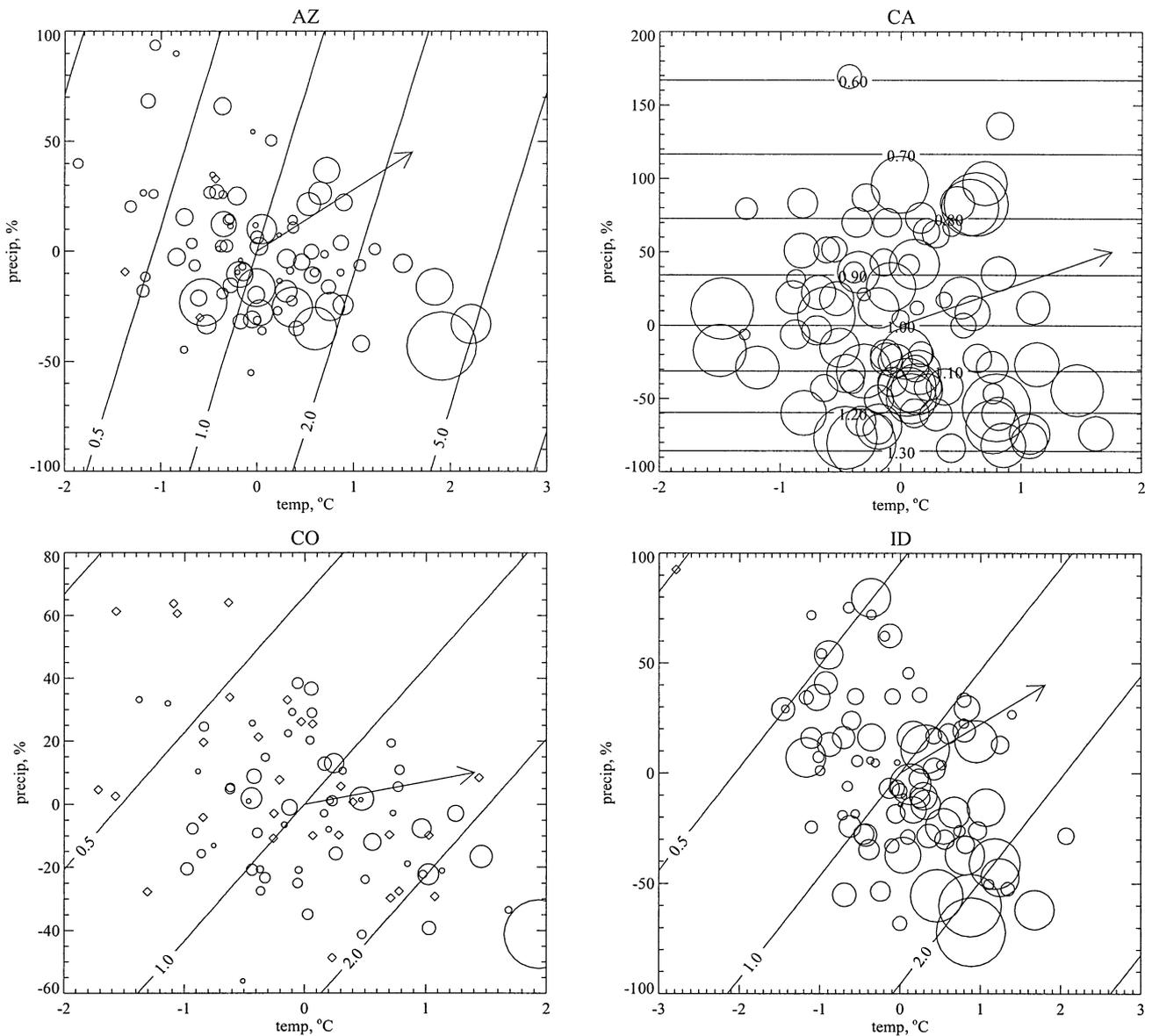


Figure 1. Area burned for each of the 11 states in the western United States. In each panel, data for 1 year are represented by a circle whose position indicates the summer temperature (x-axis) and precipitation (y-axis) anomalies and whose area is proportional to area burned. The size of the largest circle is the same in each panel, and years in which area burned was <math>< 1/16</math> of that of the largest year are indicated by small diamonds. Largest circles tend to appear in the lower right of each panel (warm, dry summers). Contour lines indicate the mean area burned from multiple regression, as a ratio to the value at the origin; contours are at 0.1, 0.2, 0.5, 1, 2, 5, and so forth, except for California. The arrow shows the direction of climatic change for each state indicated by the PCM-B2 simulation; one should imagine a collection of arrows representing various climate scenarios projected by other global circulation models, all pointing farther to the right (but some farther down, a few farther up) than the ones shown here, hence indicating a larger mean area burned. Abbreviations: precip, precipitation; temp, temperature, AZ, Arizona; CA, California; CO, Colorado; ID, Idaho; MT, Montana; NV, Nevada; NM, New Mexico; OR, Oregon; UT, Utah; WA, Washington; WY, Wyoming. (continued)

Utah, Wyoming) or negative precipitation (Idaho, Montana, Wyoming) anomalies.

We used these regressions with new climate statistics for 2070–2100 represented by output from two state-of-the-art global climate models. The HadCM3 of the Hadley

Center for Climate Prediction (Gordon et al. 2000), United Kingdom, with socioeconomic scenario A2, features relatively high CO₂ concentrations by 2100, whereas the Parallel Climate Model (PCM) of the U.S. National Center for Atmospheric Research (Washington et al. 2000),

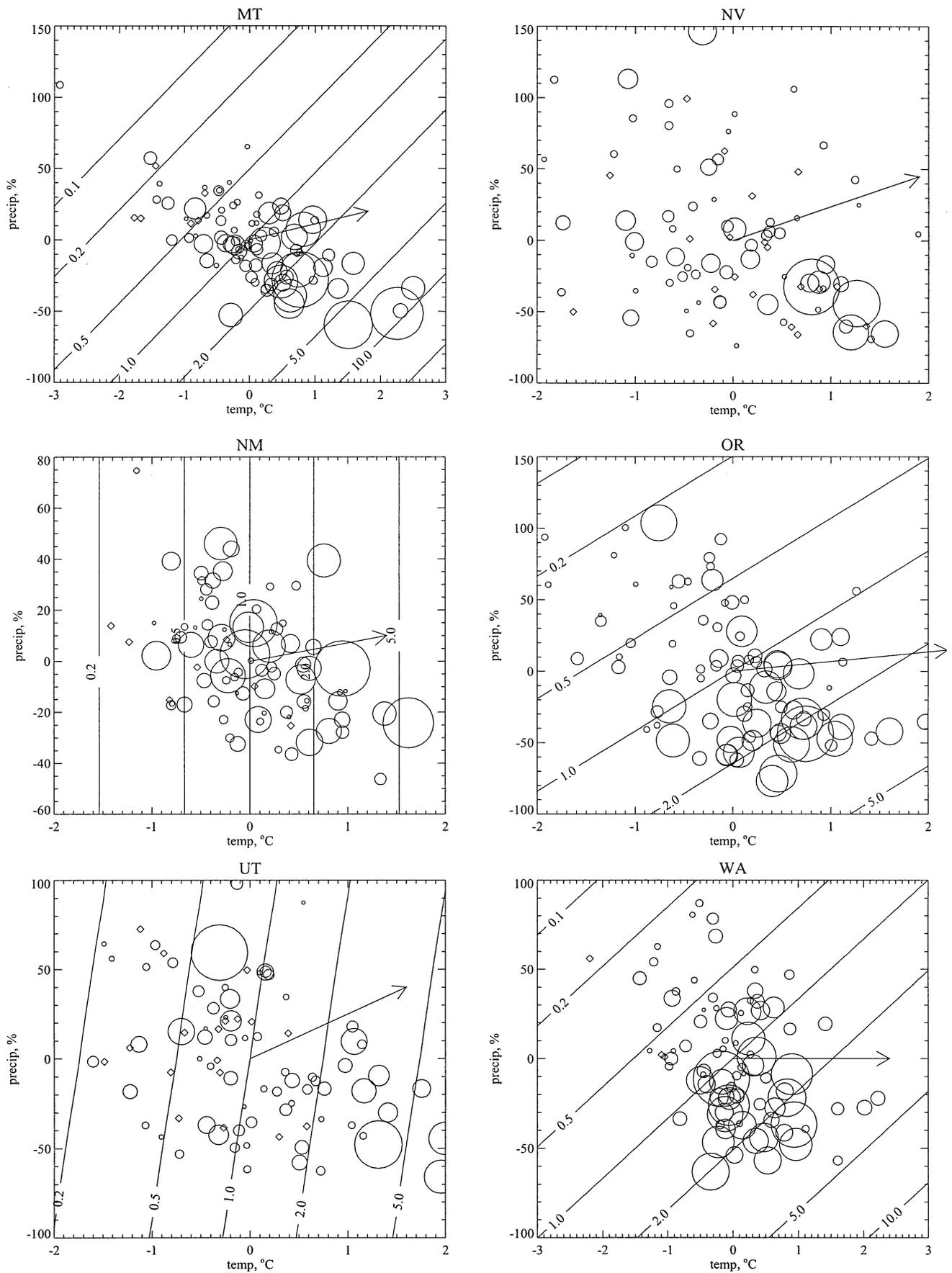


Figure 1. (continued).

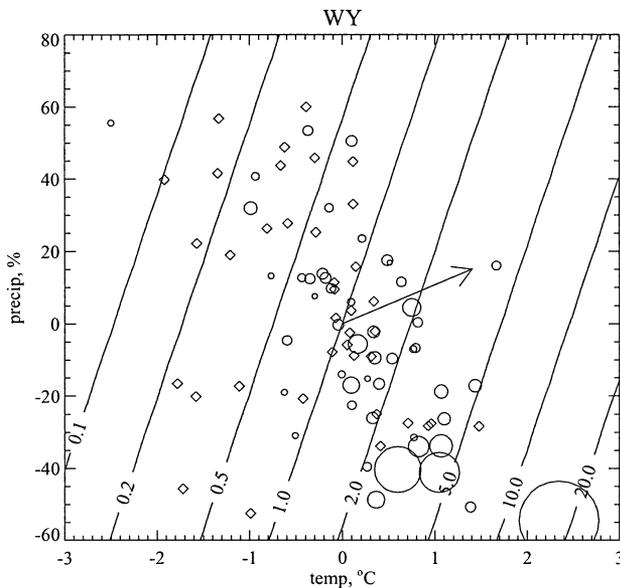


Figure 1. (continued).

with socioeconomic scenario B2, features relatively low CO₂ concentrations by 2100. The PCM-B2 and HadCM3 project very different changes in summer climate for the West in the period 2070–2100 relative to that of 1970–2000 (+1.6° and +6.3° C for temperature and +11% and +8% for precipitation, respectively) and effectively represent best-case and worst-case scenarios.

We combined the regression analysis with the projected changes in summer temperature and precipitation according to the PCM-B2 scenario (indicated by the arrows for each state; Fig. 1) (HadCM3 predictions were too far outside current levels.) The tip of the arrow shows the ratio in area burned for late-twenty-first-century climate to that for twentieth-century climate. For all states but California and Nevada, this method projected an increase in the mean area burned by a factor of 1.4 to 5, with the largest increases in New Mexico and Utah. For the HadCM3-A2 scenario, the Northwest suffered a large decline (34%) in precipitation, which would augment the very large temperature increases to produce a change in mean area burned so large that it could not be estimated by this method. The regression analysis certainly suggests that the temperature effect predominates, which renders irrelevant the disagreement between the two climate models on the sign of the precipitation change.

There are three limitations to this approach. First, we used the interannual variability of area burned to infer changes over much longer time scales, whereas the response of forest ecosystems to climatic variations and to altered fire regimes might be very different on centennial time scales. Second, we used a linear approach to extrapolate from the center of a probability-distribution function to and in some cases beyond its edge, so the results are somewhat crude. Confidence intervals are wider

at extremes, meaning that prediction of means, though less critical for some applications than for forecasting extremes, is more robust than the latter. More sophisticated approaches such as simulations of forest dynamics under a changed climate (Bachelet et al. 2001) produce more precise quantitative results but are also necessarily extrapolating beyond twentieth-century experience. Other inferred variables, such as 500-millibars height and spatial patterns of fuel moisture (Flannigan et al. 2003), also would compound the potential error in extrapolation from current conditions (McKenzie et al. 1996b). Third, the history of fire in the western United States during the twentieth century was affected as much by management practices as by climate, and the large fire years from 1988 to 2002 were, though climatically unusual, probably enhanced by fire suppression in the mid-twentieth century.

Nonetheless, three important lessons emerge from this analysis. First, even for a very low-end climatic-change scenario (the PCM-B2), it seems likely that area burned will at least roughly double by the end of this century in most western states, and there seems to be no reason to believe it will decrease. Second, it appears that the most important variable in determining future area burned will be summer temperature, which improves confidence in predictions because climate models simulate temperature (and presumably project it into the future) with greater fidelity than precipitation. Third, our analysis has revealed state-by-state variations in the sensitivity of fire to climate. At the low end, fire in California and Nevada appears to be relatively insensitive to changes in summer climate, and area burned in these states might not respond strongly to changed climate. At the other extreme, Montana, Wyoming, and New Mexico appear to be acutely sensitive, especially to temperature changes, and may respond dramatically to global warming.

Implications for Conservation

A coarse-scale view suggests that multiple transitions are possible for dominant vegetation types in response to the changes in fire regimes expected with climatic change (Fig. 2), with overall diversity of vegetation decreasing (McKenzie et al. 1996a). Although there is much uncertainty as to potential changes in fire regimes, the preponderance of prehistoric, historic, and contemporary evidence of fire-climate interactions and our understanding of vegetation dynamics in response to fire suggest that the following four changes have implications for fire-sensitive species.

Warmer, drier summers, on average, will produce more frequent, more extensive fires in forest ecosystems, likely reducing both the extent and connectivity of late-successional refugia. For example, isolated stands of older

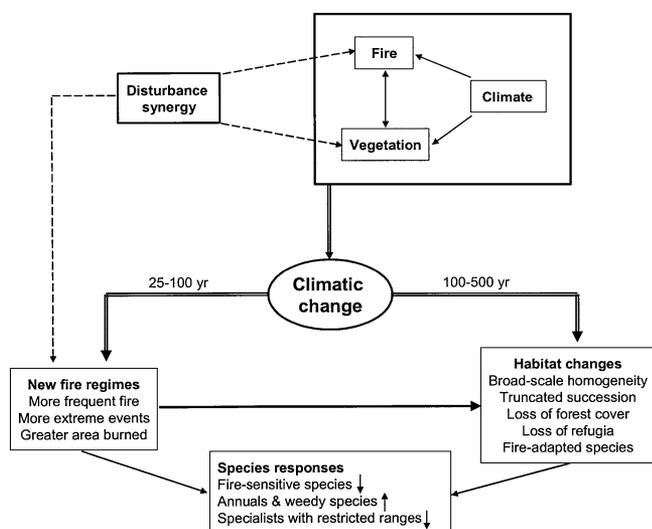


Figure 2. Interactions among climate, vegetation, and fire will shift with global climatic change. Fire will provide the main constraints on vegetation in the western United States because fire regimes will change more rapidly than vegetation can respond to climate alone (numbers are approximate). Species responses will vary, but the synergistic effects of climatic change and fire are expected to encourage invasive species.

ponderosa pine and Douglas-fir, especially in mesic sites (e.g., riparian areas) have survived past disturbances (Camp et al. 1997). Increased fire extent and severity would increase the risk of mortality in these stands. This change would threaten the viability of species restricted to habitat in open-canopy old forest (Northern Spotted Owl [*Strix occidentalis* subsp. *Caurina*], Northern Goshawk [*Accipiter gentiles*]; Graham et al. 1999) and in dense, multistory, closed-canopy forest (Flammulated Owl [*Otus flammeolus*]; Johnson & O'Neil 2001), whereas species dependent on early-successional habitat (e.g., northern pocket gopher [*Thomomys talpoides*]) would increase. The loss of late-successional habitat would create a challenging management issue on federal lands where late-seral species are a priority for protection. Increased emphasis on fire being included as a natural process in the management of dry forests compounds the difficulty of managing for processes at coarse scale and for species at fine scale.

Reduced snowpack and earlier snowmelt in mountains will extend the period of moisture deficits in water-limited systems, increasing stress on plants and making them more vulnerable to multiple, often synergistic disturbances. Trees are continually subject to an environmental stress complex and are rarely killed by a single agent, with the notable exception of fire. Multiple stresses on ecosystems often have cumulative effects that are more than additive, with one stress predisposing organisms to another stress (Paine et al. 1998). In the Inter-

mountain West, long periods of low precipitation deplete soil moisture, in turn causing water stress and low xylem pressure in trees, which allows beetles (especially *Dendroctonus* spp.) to colonize cambial tissue. An outbreak of beetles in stressed trees can spread to healthy trees, causing significant mortality over thousands of hectares. Areas with high mortality accumulate woody fuels, which greatly increases the hazard of a stand-replacing fire and subsequent beetle attack on dead and damaged trees (Gara et al. 1985). Such a cascade of spatial and temporal patterns of disturbance makes it difficult to achieve conservation goals for plant and animal species, especially those associated with late-successional forest structure.

Fire-return intervals are likely to be shorter in savanna, shrublands, and chaparral, increasing their vulnerability to invasion by weedy or annual species adapted to frequent fire. For example, in southwestern chaparral and throughout the Intermountain West, shorter fire-return intervals facilitate invasion by exotic annuals, whose continuous cover provides positive feedback for yet more frequent and widespread fires (Zedler et al. 1983; Harrod & Reichard 2001; Keeley & Fotheringham 2003). In addition to significant loss of shrub ecosystems, habitat would be lost for obligate sagebrush species such as the Sage Grouse (*Centrocercus* spp.; Connelly et al. 1991; Pedersen et al. 2003), and multiple species of passerine birds might also be compromised (Knick & Rotenberry 1995). The expected shorter return time of extreme fire events could increase the rate of habitat conversion.

In the cases of many rare taxa that are adapted to specific habitats, any significant alteration of the fire regime may pose a serious threat. For example, amphibian declines are of particular concern to the conservation community, though a direct relationship with climatic change has been difficult to identify (Carey & Alexander 2003; Collins & Storfer 2003). However, more frequent or widespread fires could produce significant habitat loss through region-wide declines in large woody debris, particularly in advanced decay classes, thereby compromising the viability of some species indirectly (Gustafson et al. 2001). Similarly, species in sky-island ecosystems may lose habitat from both the advance of lower tree-line from warming and increased fire in isolated forests (Lomolino et al. 1989; Folliott et al. 1996).

On the other hand, in ecosystems whose fire regimes have recently been altered by fire exclusion, climatic change may accelerate the restoration of historic fire regimes, thereby reducing threats to vulnerable species. For example, species that are adapted to stand-replacing fires, such as the Black-backed Woodpecker (*Picoides arcticus*), may increase under altered fire regimes (Hutto 1995; Murphy & Lehnhausen 1998).

Although it appears that, in general, climatic change and altered fire regimes will exacerbate rather than alleviate threats to vulnerable species, because many are associated with specialized and fragmented habitat, threats and

potential mitigation must be assessed on a case-by-case basis. Moreover, threats to multiple species may demand conflicting paradigms for management. For example, in the southern portion of the range of Canada lynx (*Lynx canadensis*) in western North America, its preferred habitat is mature forest with large downed wood for denning and cover, adjacent to brushy, early successional habitat favored by snowshoe hare (*Lepus americanus*), a primary prey of lynx (Ruggiero et al. 2000). In a greenhouse climate with larger and more severe fires, this juxtaposition of older and younger stands will become less common for dry forests with high-frequency and low-intensity fire regimes, although habitat may improve in fire regimes of moderate frequency and intensity and low frequency and high intensity.

Conclusions

Because ecosystems are dynamic, species currently at risk that are restricted to isolated, undisturbed habitats are already living on borrowed time, even if current fire regimes were to be maintained (Boughton & Malvadkar 2002). Anticipating the changing hazards in dynamic ecosystems that are responding to climatic change will be a formidable task for conservation managers, considering the high level of uncertainty about the magnitudes and rates of climatic change, especially for precipitation. In addition, given the complexity of ecosystem function and processes and the stochasticity of ecological disturbance, it is difficult to predict the effects of climatic change on natural resources. Our understanding of the effects of climatic variability, particularly temperature and drought, on fire occurrence provides some predictability to the potential for large and severe fires. Although associations between fire and quasi-periodic patterns (PDO and ENSO) have been identified, we have little understanding of how these indices will respond to climate warming. Thus, our ability to extrapolate these latter associations into the future is poor.

If longer or more severe fire seasons are indeed an outcome of climate warming, the probability of losing local populations of species that depend on late-seral habitat will increase. Obviously most species have persisted despite many millennia of natural and human-caused fire, but contemporary landscapes have been altered by timber extraction, agriculture, and human settlements. Options for suitable postfire habitat have been reduced, creating the potential for severe "bottlenecks" in space and time, particularly for species that have narrow habitat requirements, restricted distributions, or low mobility. At any particular location, say a national forest or national park, there may be few options for providing sufficient habitat to mitigate these bottlenecks.

Climatic change, fire policy, and fuel-treatment strategies are complex biosocial issues, and integrating them

with wildlife conservation objectives is challenging. Conservation of taxa that live in late-seral forest and riparian habitat has been a dominant management paradigm for the past two decades, but this emphasis is often incompatible with increased use of fire and mechanical thinning for ecosystem restoration (Cissel et al. 1999). For example, fuel treatments and natural fires that remove a portion of the overstory, understory, and surface fuels reduce the risk of subsequent crown fire but also preclude habitats required for some plant and animal species. Public distrust of motivations for conducting fuel treatments and agency frustration with appeals and litigation create a challenging ecological and social context for decision making. Reasoned discussions among decision makers, public-land managers, and stakeholders at local and regional scales can help in the development of resource management strategies that mitigate risk to ecosystems and sensitive species.

Acknowledgments

We thank A. Morgan for assembling the fire data and A. Bayard for help with graphics. Comments from J. Agee, R. Harrod, T. MacCulloch, K. Miyanishi, and an anonymous reviewer improved the manuscript. This research was funded by the U.S. Department of Agriculture Forest Service Pacific Northwest Research Station and the Joint Institute for the Study of the Atmosphere and Ocean under cooperative agreement NA178RG11232 of the National Oceanic and Atmospheric Administration.

Literature Cited

- Agee, J. K. 1993. Fire ecology of Pacific Northwest forests. Island Press, Washington, D.C.
- Agee, J. K. 1997. The severe weather wildfire: too hot to handle? *Northwest Science* 71:153-157.
- Agee, J. K. 1998. The landscape ecology of western fire regimes. *Northwest Science* 72:24-34.
- Alley, W. 1984. The Palmer drought severity index: limitations and assumptions. *Journal of Climate and Applied Meteorology* 23:1100-1109.
- Bachelet, D., R. P. Neilson, J. M. Lenihan, and R. J. Drapek. 2001. Climate change effects on vegetation distribution and carbon budget in the United States. *Ecosystems* 4:164-185.
- Bailey, R. G. 1996. *Ecosystem geography*, Springer-Verlag, New York.
- Baisan, C. H., and T. W. Swetnam. 1990. Fire history on a desert mountain range: Rincon Mountain Wilderness, Arizona, USA. *Canadian Journal of Forest Research* 20:1559-1569.
- Baker, W. L. 2003. Fire and climate in forested landscapes of the U.S. Rocky Mountains. Pages 120-157 in T. T. Veblen, W. L. Baker, G. Montenegro, and T. W. Swetnam, editors. *Fire and climatic change in temperate ecosystems of the western Americas*. Springer-Verlag, New York.
- Baker, W. L., and D. Ehle. 2001. Uncertainty in surface-fire history: the case of ponderosa pine forests in the western United States. *Canadian Journal of Forest Research* 31:1205-1226.
- Balling, R. C., G. A. Meter, and S. G. Wells. 1992. Relation of surface climate and area burned in Yellowstone National Park. *Agricultural and Forest Meteorology* 60:285-293.

- Benson, L. V., J. W. Burdett, M. Kashgarian, S. P. Lund, F. M. Phillips, and M. O. Rye. 1996. Climatic and hydrologic oscillations in the Owens Lake Basin and adjacent Sierra Nevada, California. *Science* **274**:746-749.
- Berger, A. L. 1978. Long-term variations of daily insolation and Quaternary climatic change. *Journal of Atmospheric Sciences* **35**:2362-2367.
- Bergeron, Y., and S. Archambault. 1993. Decrease of forest fires in Quebec's southern boreal zone and its relation to global warming since the end of the Little Ice Age. *Holocene* **3**:255-259.
- Bessie, W. C., and E. A. Johnson. 1995. The relative importance of fuels and weather on fire behavior in subalpine forests. *Ecology* **76**:747-762.
- Boughton, D., and U. Malvadkar. 2002. Extinction risk in successional landscapes subject to catastrophic disturbances. *Conservation Ecology* **6**(2): <http://www.cosecol.org/vol6/iss1/art2>.
- Brown, R., J. K. Agee, and J. F. Franklin. 2004. Forest restoration and fire: principles in the context of place. *Conservation Biology* **18**:000-000
- Camp, A., C. Oliver, P. Hessburg, and R. E. Everett. 1997. Predicting late-successional fire refugia pre-dating European settlement in the Wenatchee Mountains. *Forest Ecology and Management* **95**:63-77.
- Carey, C., and M. A. Alexander. 2003. Climate change and amphibian declines: is there a link? *Diversity and Distributions* **9**:111-121.
- Christensen, N. L. 1985. Shrubland fire regimes and their evolutionary consequences. Pages 85-100 in S. T. A. Pickett and P. S. White, editors. *The ecology of natural disturbance and patch dynamics*. Academic Press, San Diego.
- Cissel, J. H., F. J. Swanson, and P. J. Weisberg. 1999. Landscape management using historical fire regimes: Blue River, OR. *Ecological Applications* **9**:1217-1231.
- Clark, J. S., and P. D. Royall. 1996. Local and regional sediment charcoal evidence for fire regimes in presettlement north-eastern North America. *Journal of Ecology* **84**:365-382.
- Collins, J. P., and A. Storfer. 2003. Global amphibian declines: sorting the hypotheses. *Diversity and Distributions* **9**:89-98.
- Connelly, J. W., W. L. Wakkinen, A. D. Apa, and K. P. Reese. 1991. Sage grouse use of nest sites in southeastern Idaho. *Journal of Wildlife Management* **55**:521-524.
- Cook, E. R., D. M. Meko, D. W. Stahle, and M. K. Cleveland. 1999. Drought reconstructions for the continental United States. *Journal of Climate* **4**:1145-1162.
- Countryman, C. M., M. H. McCutchan, and B. C. Ryan. 1969. Fire weather and fire behavior at the 1968 Canyon fire. U.S. Department of Agriculture Forest Service, Berkeley, California.
- Finklin, A. I. 1973. Meteorological factors in the Sundance fire run. Report. U.S. Department of Agriculture Forest Service, Ogden, Utah.
- Flannigan, M., I. Campbell, M. Wotton, C. Carcaillet, P. Richard, and Y. Bergeron. 2001. Future fire in Canada's boreal forest: paleoecology results and general circulation model: regional climate model simulations. *Canadian Journal of Forest Research* **31**:854-864.
- Flannigan, M. D., B. J. Stocks, and M. Weber. 2003. Fire regimes and climatic changes in Canadian forests. Pages 97-119 in T. T. Veblen, W. L. Baker, G. Montenegro, and T. W. Swetnam, editors. *Fire and climatic change in temperate ecosystems of the western Americas*. Springer-Verlag, New York.
- Folliott, P. F., L. F. DeBano, M. B. Maker Jr., G. J. Gottfried, G. Solis-Garza, C. B. Edminster, D. G. Neary, L. S. Allen, and R. H. Hamre, technical coordinators. 1996. Effects of fire on Madrean Province ecosystems: a symposium proceedings. General technical report RM-GTR-289. U.S. Department of Agriculture Forest Service, Fort Collins, Colorado.
- Fulé, P. Z., W. W. Covington, and M. M. Moore. 1997. Determining reference conditions for ecosystem management of southwestern ponderosa pine. *Ecological Applications* **7**:895-908.
- Gara, R. I., W. R. Littke, J. K. Agee, D. R. Geiszler, J. D. Stuart, and C. H. Driver. 1985. Influences of fires, fungi, and mountain pine beetles on development of a lodgepole pine forest in south-central Oregon. Pages 153-162 in D. M. Baumgartner, editor. *Lodgepole pine: the species and its management*. Washington State University, Pullman.
- Gordon, C., C. Cooper, C. A. Senior, H. T. Banks, J. M. Gregory, T. C. Johns, J. F. B. Mitchell, and R. A. Wood. 2000. Simulation of SST, sea ice extents, and ocean heat transports in a version of the Hadley Centre coupled model without flux adjustments. *Climate Dynamics* **16**:147-168.
- Graham, R. T., R. L. Rodriguez, K. M. Paulin, R. L. Player, A. P. Heap, and R. Williams. 1999. The Northern Goshawk in Utah: habitat assessment and management recommendations. General technical report RMRS-GTR-22. U.S. Department of Agriculture Forest Service Rocky Mountain Research Station, Ogden, Utah.
- Grissino-Mayer, H. D. 1995. Tree-ring reconstructions of climate and fire history at El Malpais National Monument, New Mexico. Ph.D. dissertation. University of Arizona, Tucson.
- Grissino-Mayer, H. D. 1999. Modelling fire interval data from the American Southwest with the Weibull distribution. *International Journal of Wildland Fire* **9**:37-50.
- Grissino-Mayer, H. D., and T. W. Swetnam. 2000. Century-scale climatic forcing of fire regimes in the American Southwest. *Holocene* **10**:213-220.
- Gustafson, E. J., N. L. Murphy, and T. R. Crow. 2001. Using a GIS model to assess terrestrial salamander response to alternative forest management plans. *Journal of Environmental Management* **63**:281-292.
- Haines, D. A. 1988. A lower atmospheric severity index for wildland fire. *National Weather Digest* **13**:23-27.
- Hallett, D. J., D. S. Lepofsky, R. W. Mathewes, and K. P. Lertzman. 2003. 11000 years of fire history and climate change in the mountain hemlock rain forests of southwestern British Columbia based on sedimentary charcoal. *Canadian Journal of Forest Research* **31**:292-312.
- Harrod, R. J., and S. Reichard. 2001. Fire and invasive species within the temperate and boreal coniferous forests of western North America. Pages 95-101 in K. E. M. Galley and T. P. Wilson, editors. *Proceedings of the invasive species workshop: the role of fire in the control and spread of invasive species*. Miscellaneous publication 11. Tall Timbers Research Station, Tallahassee, Florida.
- Heinselman, M. L. 1973. Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. *Quaternary Research* **3**:329-32.
- Hessl, A. E., D. McKenzie, and R. Schellhaas. 2004. Drought and Pacific Decadal Oscillation affect fire occurrence in the inland Pacific Northwest. *Ecological Applications* **14**:425-442.
- Heyerdahl, E. K., L. B. Brubaker, and J. K. Agee. 2001. Spatial controls of historical fire regimes: a multiscale example from the interior West, USA. *Ecology* **82**:660-678.
- Heyerdahl, E. K., L. B. Brubaker, J. K. Agee. 2002. Annual and decadal climate forcing of historical fire regimes in the interior Pacific Northwest, USA. *The Holocene* **12**:597-604.
- Hosmer, D. W., and S. Lemeshow. 2002. *Applied logistic regression*. 2nd edition. Wiley, New York.
- Hutto, R. L. 1995. Composition of bird communities following stand-replacement fires in northern Rocky Mountain (U.S.A.) conifer forests. *Conservation Biology* **9**:1041-1058.
- Imbrie, J., A. McIntyre, and A. C. Mix. 1989. Oceanic response to orbital forcing in the Late Quaternary: observational and experimental strategies. Pages 121-164 in A. Berger, S. H. Schneider, and J. C. Duplessy, editors. *Climate and geosciences, a challenge for science and society in the 21st century*. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Johnson, D. H., and T. A. O'Neil, editors. 2001. *Wildlife-habitat relationships in Oregon and Washington*. Oregon State University Press, Corvallis.
- Johnson, E. A., and C. P. S. Larsen. 1991. Climatically induced change in fire frequency in the southern Canadian Rockies. *Ecology* **72**:194-201.
- Johnson, E. A., and D. R. Wowchuk. 1993. Wildfires in the southern Canadian Rocky Mountains and their relationships to mid-tropospheric

- anomalies. *Canadian Journal of Forest Research* **23**:1213–1222.
- Johnson, E. A., and S. L. Gutsell. 1994. Fire frequency models, methods, and interpretations. *Advances in Ecological Research* **25**: 239–287.
- Keane, R. E., and M. A. Finney. 2003. The simulation of landscape fire, climate, and ecosystem dynamics. Pages 32–68 in T. T. Veblen, W. L. Baker, G. Montenegro, and T. W. Swetnam, editors. *Fire and climatic change in temperate ecosystems of the western Americas*. Springer-Verlag, New York.
- Keane, R. E., K. Ryan and S. W. Running. 1996. FIRE-BGC: a mechanistic ecological process model for simulating fire succession on coniferous forest landscapes of the Northern Rocky Mountains. Research paper INT-484. U.S. Department of Agriculture Forest Service Rocky Mountain Research Station, Fort Collins, Colorado.
- Keane, R. E., P. Morgan, and J. D. White. 1999. Temporal patterns of ecosystem processes on simulated landscapes in Glacier National Park, Montana, USA. *Landscape Ecology* **14**:311–329.
- Keeley, J. E., and C. J. Fotheringham. 2003. Impact of past, present, and future fire regimes on North American Mediterranean shrublands. Pages 218–262 in T. T. Veblen, W. L. Baker, G. Montenegro, and T. W. Swetnam, editors. *Fire and climatic change in temperate ecosystems of the western Americas*. Springer-Verlag, New York.
- Kitzberger, T., and T. T. Veblen. 2003. Influences of climate on fire in Northern Patagonia, Argentina. Pages 296–321 in T. T. Veblen, W. L. Baker, G. Montenegro, and T. W. Swetnam, editors. *Fire and climatic change in temperate ecosystems of the western Americas*. Springer-Verlag, New York.
- Knick, S. T., and J. T. Rotenberry. 1995. Landscape characteristics of fragmented shrubsteppe habitats and breeding passerine birds. *Conservation Biology* **9**:1059–1071.
- Lenihan, J., C. Daly, D. Bachelet, and R. P. Neilson. 1998. Simulating broad-scale fire severity in a dynamic global vegetation model. *Northwest Science* **72**:91–103.
- Lertzman, K., J. Fall, and B. Dorner. 1998. Three kinds of heterogeneity in fire regimes: at the crossroads of fire history and landscape ecology. *Northwest Science* **72**:4–23.
- Lomolino, M. V., J. H. Brown, and R. Davis. 1989. Island biogeography of montane forest mammals in the American Southwest. *Ecology* **70**:180–194.
- Long, C. J., C. Whitlock, P. J. Bartlein, and S. H. Millspaugh. 1998. A 9000-year history from the Oregon coast range, based on a high-resolution charcoal study. *Canadian Journal of Forest Research* **28**:774–787.
- Mantua, N. J., S. R. Hare, Y. Zhang, J. M. Wallace, and R. C. Francis. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. *Bulletin of the American Meteorological Society* **78**:1069–1079.
- Masters, A. M. 1990. Changes in forest fire frequency in Kootenay National Park, Canadian Rockies. *Canadian Journal of Botany* **68**:1763–1767.
- McKenzie, D., D. L. Peterson, and E. Alvarado. 1996a. Predicting the effect of fire on large-scale vegetation patterns in North America. Research paper PNW-489. U.S. Department of Agriculture Forest Service Pacific Northwest Research Station, Portland, Oregon.
- McKenzie, D., D. L. Peterson, and E. Alvarado. 1996b. Extrapolation problems in modeling fire effects at large spatial scales: a review. *International Journal of Wildland Fire* **6**:165–176.
- McKenzie, D., D. L. Peterson, and J. K. Agee. 2000. Fire frequency in the Columbia River Basin: building regional models from fire history data. *Ecological Applications* **10**:1497–1516.
- McKenzie, D., A. Hessel, and D. L. Peterson. 2001. Recent growth in conifer species of western North America: assessing the spatial patterns of radial growth trends. *Canadian Journal of Forest Research* **31**:526–538.
- McKenzie, D., S. Prichard, A. E. Hessel, and D. L. Peterson. 2004. Empirical approaches to modelling wildland fire in the Pacific Northwest, USA: methods and applications to landscape simulations. Pages 85–97 in A. J. Perera and L. Buse, editors. *Emulating natural forest landscape disturbances: concepts and applications*. Columbia University Press, New York.
- Mensing, S. A., J. Michaelsen, and R. Byrne. 1999. A 560-year record of Santa Ana fires reconstructed from charcoal deposited in the Santa Barbara Basin, California. *Quaternary Research* **51**:295–305.
- Miller, C., and D. Urban. 1999. Forest pattern, fire, and climatic change in the Sierra Nevada. *Ecosystems* **2**:76–87.
- Millspaugh, S. H., C. Whitlock, and P. J. Bartlein. 2000. Variations in fire frequency and climate over the past 17,000 yr in central Yellowstone National Park. *Geology* **28**:211–214.
- Morrison, P. H., and F. J. Swanson. 1990. Fire history and pattern in a Cascade Range landscape. General technical report PNW-254. U.S. Forest Service Pacific Northwest Research Station, Portland, Oregon.
- Murphy, E. C., and W. A. Lehnhausen. 1998. Density and foraging ecology of woodpeckers following a stand-replacement fire. *Journal of Wildlife Management* **62**:1359–1372.
- Paine, R. T., M. J. Tegner, and E. A. Johnson. 1998. Compounded perturbations yield ecological surprises. *Ecosystems* **1**:535–545.
- Pedersen, E. K., J. W. Connelly, J. R. Hendrickson, and W. E. Grant. 2003. Effect of sheep grazing and fire on sage grouse populations in southeastern Idaho. *Ecological Modelling* **165**:23–47.
- Petit, J. R., J. Jouzel, D. Raynaud, et al. 1999. Climate and atmospheric history of the past 420,000 years from the Vostok ice core, Antarctica. *Nature* **399**:429–436.
- Price, C., and D. Rind. 1994. The impact of a 2 × CO₂ climate on lightning-caused fires. *Journal of Climate* **7**:1484–1494.
- Prichard, S. J. 2003. Spatial and temporal dynamics of fire and forest succession in a mountain watershed, North Cascades National Park. Ph.D. dissertation. University of Washington, Seattle.
- Reed, W. J. 2002. Statistical inference for historical fire frequency. Pages 419–435 in E. A. Johnson and K. Miyanishi, editors. *Forest fires: behavior and ecological effects*. Academic Press, San Diego.
- Reed, W. J., C. P. S. Larsen, E. A. Johnson, and G. M. MacDonald. 1998. Estimation of temporal variations in fire frequency from time-since-fire map data. *Forest Science* **44**:465–475.
- Reinhardt, E. D., R. E. Keane, and J. K. Brown. 1997. First order fire effects model: FOFEM 4.0 user's guide. General technical report INT-GTR-344. U.S. Department of Agriculture Forest Service Rocky Mountain Research Station, Fort Collins, Colorado.
- Romme, W. H., and D. Knight. 1981. Fire frequency and subalpine forest succession along a topographic gradient in Wyoming. *Ecology* **62**:319–326.
- Ruggiero, L. E., K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. R. Squires. 2000. Ecology and conservation of lynx in the United States. General technical report RMRS-GTR-30WWW. U.S. Department of Agriculture Forest Service Rocky Mountain Research Station, Fort Collins, Colorado.
- Schimmelmann, A., C. B. Lange, W. H. Berger, A. Simon, K. S. Burke, and R. B. Dunbar. 1992. Extreme climatic conditions recorded in Santa Barbara Basin laminate sediments: the 1835–1840 Macoma event. *Marine Geology* **106**:279–299.
- Schmoldt, D. L., D. L. Peterson, R. E. Keane, J. M. Lenihan, D. McKenzie, D. R. Weise, and D. V. Sandberg. 1999. Assessing the effects of fire disturbance on ecosystems: a scientific agenda for research and management. General technical report PNW-GTR-455. U.S. Department of Agriculture Forest Service Pacific Northwest Research Station, Portland, Oregon.
- Skinner, W. R., B. J. Stocks, D. L. Martell, B. Bonsal, and A. Shabbar. 1999. The association between circulation anomalies in the mid-troposphere and area burned by wildfire in Canada. *Theoretical and Applied Climatology* **63**:89–105.
- Swetnam, T. W. 1993. Fire history and climate change in Giant Sequoia groves. *Science* **262**:885–889.
- Swetnam, T. W., and J. L. Betancourt. 1990. Fire–Southern Oscillation relations in the southwestern United States. *Science* **249**:1017–1020.
- Taylor, A. H. 1993. Fire history and structure of red fir (*Abies magnifica*) forests, Swain Mountain Experimental Forest, Cascade

- Range, eastern California. *Canadian Journal of Forest Research* **23**: 1672-1678.
- Veblen, T. T., T. Kitzberger, and J. Donnegan. 2000. Climatic and human influences on fire regimes in ponderosa pine forests in the Colorado Front Range. *Ecological Applications* **10**:1178-1195.
- Washington, W. M., et al. 2000. Parallel climate model (PCM): control and transient simulations. *Climate Dynamics* **16**:755-774.
- Webb, T., III, and J. E. Kutzbach. 1998. An introduction to 'late quaternary climates: data synthesis and model experiments'. *Quaternary Science Reviews* **17**:465-471.
- Weir, J. M. H., E. A. Johnson, and K. Miyanishi. 2000. Fire frequency and the spatial age mosaic in the mixedwood boreal forest of western Canada. *Ecological Applications* **10**:1162-1177.
- Werth, P., and R. Ochoa. 1993. The evaluation of Idaho wildfire growth using the Haines Index. *Weather and Forecasting* **8**:223-234.
- Wotton, B. M., and M. D. Flannigan. 1993. Length of the fire season in a changing climate. *Forestry Chronicle* **69**:187-192.
- Wright, C., and J. K. Agee. 2004. Fire and vegetation history in the East Cascade Mountains, Washington. *Ecological Applications* **14**: 443-459.
- Zedler, P. H., C. R. Gautier, and G. S. McMaster. 1983. Vegetation change in response to extreme events: the effects of a short interval between fires in California chaparral and coastal scrub. *Ecology* **64**: 809-818.

