Forest Pattern, Fire, and Climatic Change in the Sierra Nevada

Carol Miller^{1*} and Dean L. Urban²

¹Graduate Degree Program in Ecology, Colorado State University, Fort Collins, Colorado 80523; and ²Nicholas School of the Environment, Duke University, Durham, North Carolina 27708, USA

ABSTRACT

In the Sierra Nevada, distributions of forest tree species are largely controlled by the soil-moisture balance. Changes in temperature or precipitation as a result of increased greenhouse gas concentrations could lead to changes in species distributions. In addition, climatic change could increase the frequency and severity of wildfires. We used a forest gap model developed for Sierra Nevada forests to investigate the potential sensitivity of these forests to climatic change, including a changing fire regime. Fuel moisture influences the fire regime and couples fire to climate. Fires are also affected by fuel loads, which accumulate according to forest structure and composition. These model features were used to investigate the complex interactions between climate, fire, and forest dynamics. Eight hypothetical climate-change scenarios were simulated, including two general circulation model (GCM) predictions of a $2 \times CO_2$ world. The response of forest structure,

INTRODUCTION

The scientific community generally agrees that substantial warming of the earth's surface $(1.5^{\circ}-4.5^{\circ}C)$ will accompany increasing concentrations of greenhouse gases in the atmosphere (IPCC 1996). Precipitation is likely to change as well, although the magnitude and direction of this change are still uncertain. How vegetation will respond to these species composition, and the fire regime to these changes in the climate were examined at four sites across an elevation gradient. Impacts on woody biomass and species composition as a result of climatic change were site specific and depended on the environmental constraints of a site and the environmental tolerances of the tree species simulated. Climatic change altered the fire regime both directly and indirectly. Fire frequency responded directly to climate's influence on fuel moisture, whereas fire extent was affected by changes that occurred in either woody biomass or species composition. The influence of species composition on fuel-bed bulk density was particularly important. Future fires in the Sierra Nevada could be both more frequent and of greater spatial extent if GCM predictions prove true.

Key words: climatic change; forest gap model; fire regime; spatial pattern; connectivity.

changes in climate is of great economic, social, and ecological interest.

Species have environmental tolerances that largely determine where they can occur. If current species distributions are the result of climatic differences along environmental gradients, then climate change will cause shifts in these distributions. For example, species distributions would move farther north or uphill in the event of a warming trend. Global vegetation models have been used to predict vegetation distributions that would occur in a new climate (Prentice and others 1992; Nielsen 1995; Haxeltine and others 1996). These are static models that make equilibrium predictions of potential vegetation. Ecosystems, however, are complex systems where feed-

Received 5 May 1998; accepted 4 November 1998.

^{*}Corresponding author's current address: US Forest Service Aldo Leopold Wilderness Research Institute, Missoula, Montana 59807, USA. e-mail: cmiller/rmrs_missoula@fs.fed.us

backs and sensitivity to initial conditions can result in unexpected transient dynamics.

Forest gap models have been used to examine the potential transient responses of many different ecosystems to climatic change (Davis and Botkin 1985; Pastor and Post 1988; Bonan and others 1990; Overpeck and others 1990; Solomon and Bartlein 1992; Prentice and others 1993; Urban and others 1993). Results from these models suggest that forest response may lag 100-200 years behind an abrupt climatic change (Davis and Botkin 1985). Such lagged responses reflect the inertia that results from the age structure and composition of the forest (Urban and others 1993). In forests of large trees, the canopy must first be opened for species replacement to occur. Therefore, species replacement occurs very slowly and only when the canopydominant trees die. Disturbances can increase the rate of forest response to climate change by providing new establishment opportunities for species better suited to the new climate (Overpeck and others 1990). With climate-mediated disturbances such as fire, the indirect effects of warming may result in very complex forest responses to climatic change (Bonan and others 1990).

In the Sierra Nevada, changes in temperature or precipitation could lead to changes in species distributions. In addition, climatic change potentially could result in the loss of biotic diversity, increased frequency or severity of wildfires, and increased tree mortality (Stephenson and Parsons 1993). There is a strong relationship between fire and climate in the Sierra Nevada (Swetnam 1993) and a tight control over tree species distribution by the soil-moisture balance (Stephenson 1988; Urban and others forthcoming). Therefore, even a slight temperature increase could greatly affect forest structure and composition.

We developed a version of a forest gap model for Sierra Nevada forests that integrates climate, fire, and forest dynamics (Miller and Urban 1999). In the model, fires occur as a function of fuel moisture, thus coupling fire to climate. Fires also occur as a function of fuel loads, which accumulate as a function of forest structure and composition. The climate-fire coupling and the way that fuels track forest condition make it an appropriate model to use to investigate system-level feedbacks that may accompany transient responses to a climatic change. Our goal was not to predict what will happen under a particular climatic change scenario, but rather to demonstrate the sensitivity of responses as a result of the complex linkages among forest pattern, fire, and climate.

Methods

The forest gap model ZELIG (Smith and Urban 1988; Urban and others 1991) has been applied to Sierra Nevada forests by adding a new soil-moisture model (Urban and others forthcoming), a new fire model (Miller and Urban 1999, forthcoming a), and parameterizing it for mixed-conifer tree species. We refer to this version of the model as FM 97.5 (FACET model version 97.5). An overview of the key model components is presented next. For additional details, the reader is referred to Miller and Urban (1999), Urban and colleagues (forthcoming), and Miller and Urban (forthcoming a).

Model Description

Forest dynamics model FM simulates a forest stand as a grid of 15×15 -m forest plots. In this report, we use a 20×20 grid of forest plots to simulate a 9-ha forest stand. The model grid is defined by elevation, slope, and aspect, thus representing a slope "facet." Elevation and topographic position are used internally by FM's weather model to adjust radiation (Nikolov and Zeller 1992), and to adjust temperature and precipitation according to lapse rates (Running and others 1987) that we derived from seven meteorological stations in Sequoia National Park (Urban and others forthcoming).

As in other forest gap models, FM simulates seedling establishment, annual diameter growth, and mortality for individual trees on each plot. Tree growth is specified as a maximum potential, which is then reduced to reflect suboptimal environmental conditions (for example, low light, low temperatures, or drought). A key characteristic of gap models is that they simulate system feedbacks: not only are trees affected by their environment, but each tree exerts an influence on its environment (through shading, for instance).

Soil moisture is indexed as the number of drought days and temperature is scaled as a growing-season degree-day sum. The tolerance of species to drought and temperature govern each tree's growth response to that climatic environment (Miller and Urban 1999; Urban and others forthcoming). The soil water balance is sensitive to the temperature and precipitation gradients that exist with elevation (Urban and others forthcoming) and, although the model does not simulate transpiration explicitly, it is quite responsive to canopy development through its influence on interception and surface evaporation. The number of growing degree-days available for a site constrains tree growth and sorts out species abundance along temperature gradients with latitude or elevation. The degree-day curves in FM

improve upon the degree-day parabolas used in previous gap models [for example, see Botkin and others (1972)]. We assume that there is a cold temperature at which species growth response is low for physiologic reasons, and this is indexed by minimum growing degree-days. At Sierran latitudes, however, low species response in warmer environments is due primarily to temperature's effect on the water balance (Urban and others forthcoming). Therefore, we use one-sided temperature-response curves; only minimum growing degree-days are used to restrict growth. Other factors, especially low soil moisture, restrict tree growth in warmer environments.

Fire model In this model, fire frequency and fire extent are internally generated as a function of fuel moisture and fuel loads, unlike other gap models or landscape models that use known distributions of fire frequency and/or fire size to simulate fire regimes (Kercher and Axelrod 1984; Baker and others 1991; Keane and others 1996). Where other models use descriptions of fire frequency and fire size as input parameters, this model generates these fire regime descriptors as output.

Climate is coupled to the fire regime directly through fuel moisture and indirectly through fuel loads. A proxy for fuel moisture is computed from the soil water balance in FM's soil moisture model (Urban and others forthcoming). Fuel moisture is dynamic, changing from year to year, through the fire season and in response to current canopy conditions. Climate controls tree growth, indirectly influencing fuel loads. Fuels accumulate according to tree-level allometries, and so are sensitive to temporal changes in forest structure and composition.

Fine herbaceous fuels can be an important factor in Sierra Nevada fire regimes, particularly at lower elevations where open ponderosa pine woodlands can occur. Grass production is simulated as a function of precipitation, temperature, shade from overstory trees, and forest floor depth (Miller and Urban forthcoming a). Grass is included in the fuel bed, which also contains the woody fuels and forest litter. A fuel bed with a large grass component may burn more easily than a fuel bed comprised only of forest fuels.

In this version of the model, bulk density of the fuel bed is simulated as a function of species composition and grass content. Fuel-bed bulk density increases with elevation as species composition shifts from pine to fir and as grass production declines (Miller and Urban forthcoming a). Bulk density of fuels can strongly influence fireline intensity. For example, the loosely packed litter of longneedled ponderosa pine forests will burn more readily than a more tightly packed short-needled fir forest floor.

Fire events are simulated as a function of three factors: probability of fire, fuel load, and fuel moisture. The mean ignition interval, in years, for the model grid is specified at run time. Uniform-random numbers are drawn to generate stochastic ignition events around this mean interval. A maximum of one ignition event may occur in any year. For fire to occur from an ignition, however, low fuel moistures and sufficient fuel loadings must also exist in addition to the stochastic ignition event. Because the soil water balance—and thus fuel moisture—varies with elevation, the model generates a decreasing fire frequency with elevation; the simulated pattern agrees well with independent data (Miller and Urban 1999).

When an ignition occurs, the fireline intensity for each of the forest plots is computed from the accumulated fuels and fuel moisture conditions following equations for surface fire behavior (Rothermel 1972; Albini 1976). Only plots with intensities greater than 45 kW m⁻¹ (13 BTU ft⁻¹ s⁻¹) are considered to be burnable. Under typical conditions simulated here, this fire intensity corresponds approximately to a scorch height of 0.5 m. Plots with intensities less than this are assumed to "burn out." Fires may spread to all cells within the model grid, but they are restricted to those plots that are burnable and that are also spatially contiguous to a randomly located ignition point on the grid. Thus, fires are restricted to a contagious cluster of burnable plots and, on average, fires tend to burn the largest cluster of burnable plots. Although this does not realistically simulate the complex nature of fire spread, the model successfully reproduces empirical relationships between area burned and fire frequency (Miller and Urban 1999).

Fire effects are calculated for each plot that burns. Fuels are reduced as a function of prefire fuel load (Brown and others 1985), scorch height is calculated as a function of mean daytime temperature and fireline intensity (Van Wagner 1973), and fire mortality is computed as a function of crown damage (Ryan and Reinhardt 1988; Stephens 1995; Mutch and Parsons 1998).

Climate Scenarios

To investigate the sensitivity of the fire regime and forest condition to changes in climate, we used eight hypothetical scenarios where each scenario was simulated as a departure from baseline (current)



Figure 1. Climate predictions of the Oregon State University (OSU) and United Kingdom Meteorological Office (UKMO) general circulation models compared with baseline climate conditions: mean monthly (a) temperature and (b) precipitation.

mean temperature and precipitation. Two temperature (\pm 2°C) and three precipitation levels (no change, \pm 20%) were simulated using a 2 × 3 factorial design, and two additional scenarios were based on 2 × CO₂ predictions for the Sierra Nevada region from general circulation models (GCMs). The GCMs used were the Oregon State University (OSU) GCM and the United Kingdom Meteorological Office (UKMO) GCM. These represent the most conservative and most extreme GCM predictions, respectively, that were available to us (UCAR 1997). Both GCMs predict warmer temperatures, and the UKMO GCM predicts more precipitation compared with baseline (current) climate (Figure 1).

To illustrate the effect of altered temperature and precipitation on the climatic environment, we used the weather model in FM to simulate sites from 500- to 3500-m elevation and plotted growing degree-days against drought-days (Figure 2). Results are shown for baseline (current) climate, the two most extreme climate scenarios from the factorial design ($+2^{\circ}C \times -20\%$ precipitation and $-2^{\circ}C \times$



Figure 2. The climatic environment simulated by the FACET weather model for baseline conditions and three climate scenarios. Simulations were run for 100 years. The scenarios were cool-wet $(-2^{\circ}C \times +20\%)$ precipitation), Oregon State University (OSU) and United Kingdom Meteorological Office (UKMO) general circulation models. Each point represents conditions at a single site. The uppermost right-hand point on each curve is a site at 500 m, and the lowest left-hand point is a site at 3500 m. Points in between are sites at 100-m intervals. Pointers indicate the same site at 2600-m elevation under the different climate scenarios. The warm-dry scenario $(+2^{\circ}C \times -20\%)$ precipitation) is close to the OSU conditions at 2600 m but is not shown to improve the figure's clarity.

+20% precipitation), and the two GCM scenarios (OSU and UKMO). The points on each curve in Figure 2 describe the climatic environment for individual sites; an entire curve describes the gradient with elevation. The lower left corner of the graph represents cool and wet conditions, and the upper right corner represents warm and dry environments. On each curve, the point in the uppermost right-hand position represents the climatic environment simulated for a site at 500-m elevation. The point in the lowest left-hand position represents the climatic environment at 3500 m. Each point in between these two extremes represents conditions at sites between 500 and 3500 m at 100-m intervals. The difference between the baseline climate and the four climate scenarios can be seen by comparing the climatic environments for the same elevation. For a site at 2600-m elevation, the warm-dry scenario $(+2^{\circ}C \times -20\%)$ precipitation) results in approximately 30 more drought days than does the baseline climate and 80 more drought days than does the cool-wet scenario ($-2^{\circ}C \times +20^{\circ}\%$ precipitation). The UKMO scenario results in approximately 100 more drought days than the baseline climate, and the OSU scenario has approximately 50 more drought days than the baseline climate.

Simulations

We simulated forest growth by using the aforementioned eight different climate-change scenarios for flat ground at 1800-m, 2200-m, 2600-m, and 3000-m elevation. The simulations were run from bare ground for 800 years. The first 200 years were run without fire to allow successional dynamics to stabilize. After 200 years, a natural fire regime was simulated (ignition interval = 1). Climate changes were applied gradually with the temperature and precipitation change occurring linearly over 100 years from simulation years 501-600. Ten replicates of each simulation were run; replicates were identical in all respects except each one used a different random number seed to generate the pseudorandom weather used by the model. All simulations were for Sequoia National Park (36.6°N, 118.6°W), and all simulations used a homogeneous soil with soil depth of 1 m for a 9-ha forest stand (20 imes 20 grid).

Analysis

We examined how forest structure and species composition varied during the simulations as the climate changed. To assess changes in forest structure, we plotted total woody biomass against time. To examine changes in species composition through time, we estimated percent similarity (Mueller-Dombois and Ellenberg 1974) between the stand in the current simulation year and the mean stand condition during the last 100 years of the baseline climate (simulation years 401–500). Percent similarity was calculated as

$$PS = \frac{2 \cdot M_w}{M_a + M_b} \times 100 \tag{1}$$

 M_a is the total basal area of the first stand, in this case the average basal area during simulation years 401–500. M_b is the total basal area of the second stand, in this case the total basal area in the current simulation year. M_w is the sum of the smaller of the two values of species basal area for species that are common to both stands. We computed percent similarity each year during the simulation.

We also examined how the fire regime responded in the simulations as the climate changed. To illustrate changes in the fire regime that result from climatic change, we averaged the mean fire interval and mean area burned for years 501–800 for the 10 replicates.

In the results that follow, we display only four of the eight scenarios simulated ($+2^{\circ}C \times -20\%$ precipitation, $-2^{\circ}C \times +20\%$ precipitation, OSU GCM and UKMO GCM) to illustrate the range of re-

sponses that occurred. Each simulation was run for 800 years, with the climate transient occurring during simulation years 501–600. Here, we display only years 400–800 to focus on the responses to the climate transient. We averaged results from 10 replicate simulations and looked at woody biomass, species composition, and elements of the fire regime.

RESULTS

Forest Structure and Composition

At the three lowest-elevation sites, woody biomass decreased in all of the scenarios except the cool-wet scenario (Figure 3). Biomass declined to zero in the warm-dry, OSU, and UKMO scenarios at 1800 m and declined to nearly zero in the UKMO scenario at 2200 m. Biomass increased in the cool-wet scenario at these sites; changes were again especially pronounced at the lowest elevation (1800 m). The response of forest biomass to the different climate scenarios was markedly different at the 3000-m site. Here, the cool–wet scenario ($-2^{\circ}C \times +20\%$ precipitation) produced the most dramatic decline in biomass. In the UKMO scenario, biomass declined temporarily but largely recovered by the end of the simulation. Biomass increased slightly in the warmdry and OSU scenarios at this elevation.

In all scenarios except the cool–wet scenario, percent similarity decreased dramatically at the three lowest elevations, indicating a dramatic change in composition at these sites (Figure 4). Little change in species composition occurred in the cool–wet scenario at these sites. At the highest elevation, 3000 m, dramatic changes did not occur in the warm–dry ($+2^{\circ}C \times -20\%$ precipitation) or OSU scenarios, but pronounced shifts in species composition occurred in the cool–wet and UKMO scenarios (Table 1).

Fire Regime

Overall, mean fire interval increased with elevation (Figure 5), a pattern that is characteristic of the Sierra Nevada (Caprio and Swetnam 1995). Fires tended to be more frequent in all climate-change scenarios except the cool-wet scenarios. The most significant differences occurred at the highestelevation sites. Differences in fire extent as a result of climatic change were also apparent in the simulations at some of the sites. At 2600 m, area burned increased in the warm-dry, OSU, and UKMO scenarios. At 1800 m, area burned increased in the cool-wet and UKMO scenarios.



Figure 3. Total woody biomass simulated at four elevations for four climatic change scenarios and baseline conditions. Results were averaged over 10 replicate simulations. The scenarios were warm-dry ($+2^{\circ}C \times -20\%$ precipitation), cool-wet ($-2^{\circ}C \times +20\%$ precipitation), Oregon State University (OSU), and United Kingdom Meteorological Office (UKMO) general circulation models. The climate transient from baseline conditions occurred during simulation years 501–600.

DISCUSSION

Forest Structure and Composition

Forest response to the simulated climatic changes is best understood in terms of the water balance. As mean temperature increases, more energy is available to evaporate and transpire water. If precipitation does not increase enough to offset the increased demand, a larger water deficit will result. For such a



Figure 4. Change in species composition measured as percent similarity at four elevations for four climatic change scenarios and baseline conditions. Results were averaged over 10 replicate simulations. The scenarios were warm-dry ($+2^{\circ}C \times -20\%$ precipitation), cool-wet ($-2^{\circ}C \times +20\%$ precipitation), Oregon State University (OSU) and United Kingdom Meteorological Office (UKMO) general circulation models. The climate transient from baseline conditions occurred during simulation years 501–600.

scenario, the number of drought days simulated by the model increases, eventually resulting in altered forest structure and composition. The greatest impacts on woody biomass were seen at the most water-limited sites. At 1800 m, for example, the scenarios that have a net drying effect (warm-dry, OSU, and UKMO) are severe enough that the forest cannot persist and there is a transition to savannah or grassland conditions. When climatic change re-

Elevation and Species Name	Base-	Warm– Dry	Cool-	OSU	UKMO
	line		Wet		
1800 m					
White fir	1	0	16	0	0
Red fir	0	0	0	0	0
Incense cedar	9	1	15	1	0
Lodgepole pine	0	0	0	0	0
Jeffrey pine	3	1	5	1	0
Sugar pine	0	0	2	0	0
Western white pine	0	0	0	0	0
Ponderosa pine	15	1	15	1	0
Black oak	1	1	0	1	0
2200 m					
White fir	45	2	46	6	0
Red fir	0	0	14	0	0
Incense cedar	2	11	0	13	3
Lodgepole pine	0	0	0	0	0
Jeffrey pine	1	3	1	2	1
Sugar pine	4	0	1	0	0
Western white pine	0	0	0	0	0
Ponderosa pine	0	9	0	11	3
Black oak	0	0	0	0	1
2600 m					
White fir	9	41	0	48	13
Red fir	51	0	63	0	0
Incense cedar	0	0	0	0	13
Lodgepole pine	0	0	0	0	0
Jeffrey pine	1	3	0	1	2
Sugar pine	0	2	0	4	0
Western white pine	0	0	0	0	0
Ponderosa pine	0	0	0	0	14
Black oak	0	0	0	0	0
3000 m					
White fir	0	0	0	2	49
Red fir	53	59	0	61	2
Incense cedar	0	0	0	0	2
Lodgepole pine	1	0	20	0	0
Jeffrey pine	0	0	0	0	0
Sugar pine	0	0	0	0	11
Western white pine	1	1	8	0	0
Ponderosa pine	0	0	0	0	0
Black oak	0	0	0	0	0

Table 1. Species Basal Areas (m² ha⁻¹) in the Final Simulation Year for the Baseline and Four Climate Change Scenarios

OSU, Oregon State University; UKMO, United Kingdom Meteorological Office.

sults in a net increase in available water (for instance, the cool-wet scenario), woody biomass increases at these water-limited sites. Not all sites in the Sierra Nevada are water limited, however. At sites that are instead limited by the length of the growing season (for example, 3000 m), the response



Figure 5. Summary of the fire regime at four elevations for four climatic change scenarios and baseline conditions. The scenarios were cool-wet $(-2^{\circ}C \times +20\%)$ precipitation) and warm-dry $(+2^{\circ}C \times -20\%)$ precipitation), Oregon State University (OSU), United Kingdom Meteorological Office (UKMO) general circulation models: (a) mean fire interval during simulation years 501–800 and (b) percent of the total area burned during simulation years 501–800; these values were averaged over 10 replicate simulations. Error bars are \pm 1 standard deviation. The mean fire interval for the cool-wet scenario at 3000 m is not shown but was 202 years.

to a warmer and drier climate can be an increase in woody biomass.

Changes in species composition will be greatest when the new climate exceeds the environmental tolerances of the dominant species (Urban and others 1993). Not surprisingly, the UKMO scenario, which represents the largest environmental change from baseline conditions (Figure 2), results in the largest compositional change. At 3000 m, for example, red fir is dominant under baseline conditions and the UKMO scenario shifts the climatic environment outside the limits for red fir; eventually, white fir assumes dominance. If the new climate exceeds the environmental tolerances of all tree species, the



Figure 6. Major direct and indirect interactions among climate, forest structure, species composition, and the fire regime.

forest is converted to a grassland or other nonforest type. This conversion occurs in the UKMO scenario at 2200 m (Figure 3). The other climate-change scenarios that we simulated are also severe enough to produce dramatic shifts in species composition as well as conversion to nonforest conditions.

Fire Regime

The altered water balance that results from climatic change affects the fire regime in direct and indirect ways. Climatic change can influence the fire regime directly via its effect on fuel moisture and indirectly via its effect on forest structure and composition. Figure 6 depicts the major direct and indirect effects on the fire regime. Feedbacks from the fire regime on forest structure and composition are not depicted in this figure and are not discussed here. In some cases, effects from some interactions counter others and confound the simulation results. There are, however, examples from the simulations that illustrate each of the major direct and indirect effects of climatic change on the fire regime; these examples are discussed here.

In these simulations, a warmer and drier climate tends to generate more frequent fires, whereas a cooler and wetter climate generates fewer fires. Although the UKMO GCM predicts higher precipitation, this scenario results in actually drier conditions than current climate and fire frequency increases at all sites. Climate's direct effect on fire frequency is most easily seen in the simulations at 2600 m. Under current conditions, 2600 m lies within the red fir forest zone. Here, fires are relatively infrequent: fire-free intervals for individual trees have been estimated at approximately 65 years (Pitcher 1987). Below the red fir forest lies the mixed conifer forest, where fires are much more frequent. Generally, the warm-dry and OSU scenarios simulated at this elevation represent a downslope translation of about 300–400 m, whereas the UKMO scenario represents a downslope translation of about 800 m (Figure 2). The climatic change predicted by the UKMO GCM has the greatest impact on fire frequency.

Climatic change can influence fire extent indirectly because altered forest structure and composition affect both the amount of fuel and the type of fuel that is available for combustion. The simulations at 2600 m illustrate the effect of species composition and fuel-bed bulk density on fire extent. We examined the trend in area burned during the warm-dry scenario. We averaged area burned by 20-year intervals for the 10 replicates. More area burns in the warm-dry scenario (Figure 5b) when fuel-bed bulk density decreases as the forest composition shifts from red fir to white fir (Figure 7). When fuel-bed bulk density is very high, as it is in red fir forests (Van Wagtendonk and others 1998), fuels are tightly packed and do not burn readily. It appears that a threshold exists at which burnability of the fuel-bed changes dramatically with bulk density [see also Miller and Urban (forthcoming b)].

The model simulates the most complex responses at the lowest elevation, 1800 m; to illustrate these, we analyzed the connectivity of burnable area. Fire size is a function of connectivity, which is a function of fuel loads, fuel-bed bulk density, and fuel moisture. To examine how connectivity varies as climate changes, we computed correlation length (Stauffer 1985) for each fire year and averaged these values by 20-year intervals for the 10 replicate simulations. To emphasize changes in the fuel loads and fuel-bed bulk density, we held fuel moisture constant at 1%. This mean correlation length is plotted through time in Figure 8a. Connectivity increases in the cool-wet and UKMO scenarios but decreases in the warmdry and OSU scenarios. Because fuel-bed bulk density varies throughout the simulations (Figure 8b), we wanted to isolate the effect of fuel-bed bulk density on connectivity. We repeated the calculations of correlation length but held fuel-bed bulk density at a constant value of 12.8 kg m⁻³ (0.8 lb ft^{-3}); these results are plotted in Figure 9. For an unchanging bulk density of 12.8 kg m⁻³, connectivity in the UKMO scenario decreases while connectivity in the cool-wet scenario remains high. Thus, increased connectivity and fire size in the UKMO scenario are due to the changes in vegetation



Figure 7. The effect of species composition on fire extent: (a) species composition, (b) fuel-bed bulk density, and (c) average area burned at 2600-m elevation for the warmdry ($+2^{\circ}C \times -20\%$ precipitation) climate-change scenario. Values were averaged over 10 replicate simulations. Area burned was averaged by 20-year intervals before averaging over 10 replicates. The climate transient occurred during simulation years 501–600.

composition (conversion from forest to grass) that alter fuel-bed bulk density. On the other hand, increased connectivity and fire size in the cool–wet scenario are due to increased fuel loads that result from increased forest productivity.

Lagged Responses

Forest response can lag behind changes in climate because of the inertia that results from the age structure and composition of the forest (Davis and Botkin 1985; Urban and others 1993). In these simulations, both changes in biomass and in species composition lag behind the climate-change transient by 25–100 years or more. When one species is completely replaced by another, as is the case in the



Figure 8. Transient response of connectivity of burnable area with variable fuel-bed bulk density: connectivity of burnable area, measured by (a) correlation length and (b) fuel-bed bulk density. Simulations were run at 1800-m elevation for four climate-change scenarios and baseline conditions. Fuel moisture was held constant at 1% in the calculation of correlation length; fuel-bed bulk density was allowed to vary as shown.

warm-dry scenario at 2600 m (Figure 7A), it takes 200 years after the onset of the climate transient for the basal area of the establishing white fir to equilibrate. It has been suggested that disturbances may accelerate forest response to climate change (Overpeck and others 1990). To determine the effect of fire on the rate of forest response in this model, we repeated a subset of the simulations but excluded fire. We did not find any difference in the rate of forest response in these simulations without fire. This result is not unexpected because although disturbances that remove the canopy may allow forests to adjust more quickly to changing climate (Urban and others 1993), surface fires, as simulated by this model, usually leave the canopy intact.

In these simulations, the response of the fire regime also lags behind the climatic change and depends on the magnitude of the climatic change.



Figure 9. Transient response of connectivity of burnable area with constant fuel-bed bulk density. Connectivity was measured by correlation length at 1800-m elevation for four climate-change scenarios and baseline conditions; fuel-bed bulk density was held constant at 12.82 kg m⁻³ (0.8 lb ft⁻³), and fuel moisture was held constant at 1% in the calculation of correlation length.

This lag is illustrated for the site at 2600 m in Figure 10. We averaged the area burned by 20-year intervals and then averaged over the 10 replicate simulations. We compared the temporal trends in area burned for scenarios of varying severity. The scenarios were, in order of increasing severity: warm-no change, warm-dry and OSU, and UKMO. Fire size increases earlier in the simulation during the more extreme climate scenarios.

Uncertainties

The scenarios simulated here are intended to demonstrate the sensitivity of these forests to climatic change. They are not intended to make predictions of forest response to a particular climate-change scenario. Although we used climate predictions from GCMs, these climate predictions carry with them substantial uncertainties, especially with respect to precipitation. The GCMs that we used do not predict decreases in precipitation for the Sierra Nevada. If precipitation does decrease under a climatic warming in the future, the result could be even greater impacts on forest structure and composition and the fire regime.

Other disturbances could interact with climatic change to affect the fire regime and forest condition in the Sierra Nevada. For example, the frequency and severity of insect and disease outbreaks may increase under altered climatic conditions (Ferrell 1996). The associated tree mortality would provide



Figure 10. Transient response of average area burned. Simulations were run for the site at 2600-m elevation for four climatic change scenarios and baseline conditions. The scenarios were warm-dry ($+2^{\circ}C \times -20\%$ precipitation), Oregon State University (OSU) and United Kingdom Meteorological Office (UKMO) general circulation models, and warm-no change ($+2^{\circ}C \times$ no change in precipitation). Area burned was averaged by 20-year intervals before averaging over 10 replicate simulations. The climate transient occurred during simulation years 501–600.

increased fuels and could increase fire frequency and area burned. Furthermore, fire-damaged trees may be more susceptible to bark beetle attack, potentially resulting in a positive-feedback cycle between fire and insect outbreaks.

An important, yet often ignored, consequence of global climatic change is the potential for climate to become more variable (Rind and others 1989). We did not examine potential responses to increased variability in climate, yet an increase in variability could have important effects on both the forest response and the fire regime. For example, the connectivity of burnable area is highly sensitive to even small changes in fuel moisture that could result from brief climate events (Miller and Urban forthcoming b).

This model may underestimate the effects of fires because live canopy fuels, which can serve as ladders and facilitate crowning fire behavior, are not simulated. Furthermore, because it does not simulate short-term weather fluctuations, the model may underestimate the extent and intensity of some fires. Enhanced fire severity could open up the canopy more than is currently simulated by the model. This gap formation would provide more establishment opportunities for species better suited to the new climate and increase the rate of forest response to the simulated climatic change.

The expected rate of climatic change from increasing greenhouse gas concentrations may exceed previous climatic changes (IPCC 1996). The ability of forests to respond to this rapid change depends on the ability of tree species to migrate, the mechanisms of which are still unclear (Pitelka 1997). Clearly, the implications for migration rates that cannot keep pace with climatic change are profound (Davis 1990; Solomon and Kirilenko 1997). A major criticism of forest gap models is that they assume that all species can disperse to all sites and thus these models overstate the rate of forest response to climatic change (Loehle and LeBlanc 1996). Limitations in seed dispersal could slow the rate of tree migration and forest response to climatic change, especially when the species better adapted to the new climate is far away. Because most of the Sierran tree species simulated here have overlapping distributions, the assumption of unlimited seed dispersal may be valid.

The fire regime may be particularly sensitive to fuel-bed bulk density. In this model, fuel-bed bulk density is a function of species composition and grass content of the fuel bed. Other factors, such as the depth and duration of snowpack, also could affect fuel-bed bulk density. Therefore, as the climate changes, fuel-bed bulk density could change as a result of changes in the physical environment as well as species composition.

CONCLUSION

The forest gap model simulates profound impacts on forest structure and composition as a result of small changes in temperature and precipitation. The magnitude and direction of these effects are site specific. At water-limited sites, forest structure is most sensitive to those climatic changes that reduce water availability. At temperature-limited sites, forest structure is most sensitive to changes that affect the length of the growing season. Species composition is most affected when the climatic change exceeds the environmental tolerances of the dominant species.

Climatic change can alter the fire regime in several ways, both directly and indirectly. Fire frequency responds directly to climate's influence on fuel moisture, whereas fire extent can be affected by changes in either forest structure or species composition. The influence of species composition on fuel-bed bulk density may have particularly important impacts on the fire regime. If GCM predictions of future climate prove true, fires could be both more frequent and of greater spatial extent at certain sites.

ACKNOWLEDGMENTS

Funding for this research was provided by the United States Geological Service/Biological Resources Division, Sierra Nevada Global Change Research Program, under contract CA8800–1-9004. Many thoughtful and provoking discussions with all collaborators in the Sierra Nevada Global Change Research Program ultimately contributed to this work. Comments from two anonymous reviewers improved the manuscript. This work was completed as part of Carol Miller's doctoral degree at Colorado State University.

REFERENCES

- Albini FA. 1976. Estimating wildfire behavior and effects. USDA Forest Service; Ogden, UT, General Technical Report INT-30.
- Baker WL, Egbert SL, Frazier GF. 1991. A spatial model for studying the effects of climatic change on the structure of landscapes subject to large disturbances. Ecol Modell 56: 109–25.
- Bonan GB, Shugart HH, Urban DL. 1990. The sensitivity of some high-latitude boreal forests to climatic parameters. Clim Change 16:9–29.
- Botkin DB, Janak JF, Wallis JR. 1972. Some ecological consequences of a computer model of forest growth. J Ecol 60: 849–72.
- Brown JK, Marsden MA, Ryan KC, Reinhardt ED. 1985. Predicting duff and woody fuel consumed by prescribed fire in the northern Rocky Mountains, Ogden, VT. United States Department of Agriculture Forest Service; Research Paper INT-337.
- Caprio AC, Swetnam TW. 1995. Historic fire regimes along an elevational gradient on the west slope of the Sierra Nevada, California. In: Brown JK, Mutch RW, Spoon CW, Wakimoto RW, technical coordinators. Proceedings: symposium on fire in wilderness and park management, Missoula, MT, March 30–April 1, 1993. p 173–179.
- Davis MB 1990. Climatic change and the survival of forest species. In: Woodwell GM, editor. The earth in transition: patterns and processes of biotic impoverishment. Cambridge: Cambridge University Press. p 99–111.
- Davis MB, Botkin DB. 1985. Sensitivity of cool-temperate forest and their fossil pollen record to rapid temperature change. Quat Res (NY) 23:327–40.
- Ferrell GT. 1996. The influence of insect pests and pathogens on Sierra forests. In: Sierra Nevada Ecosystem Project: final report to Congress. Volume 2, Assessments and scientific basis for management options. Davis: University of California, Centers for Water and Wildland Resources. p 1177–92.
- Haxeltine A, Prentice IC, Cresswell ID. 1996. A coupled carbon and water flux model to predict vegetation structure. J Vegetat Sci 7:651–66.
- [IPCC] Intergovernmental Panel on Climate Change. 1996. Climate change 1995: the science of climate change. Cambridge: Cambridge University Press.
- Keane RE, Ryan KC, Running SW. 1996. Simulating effects of fire on northern Rocky Mountain landscapes with the ecological process model FIRE-BGC. Tree Physiol 16:319–31.

- Kercher JR, Axelrod MC. 1984. A process model of fire ecology and succession in a mixed-conifer forest. Ecology 65:1725–42.
- Loehle C, LeBlanc D. 1996. Model-based assessments of climate change effects on forests: a critical review. Ecol Modell 90: 1–31.
- Miller C, Urban DL. 1999. A model of surface fire, climate and forest pattern in Sierra Nevada, California. Ecol Modell. 114: 113–35.coming.
- Miller C, Urban DL. Forest heterogeneity and surface fire regimes. Can J For Res. Forthcoming a.
- Miller C, Urban DL. Connectivity of forest fuels and surface fire regimes. Landscape Ecol. Forthcoming b.
- Mueller-Dombois D, Ellenberg H. 1974. Aims and methods of vegetation ecology. New York: John Wiley and Sons.
- Mutch LS, Parsons DJ. 1998. Mixed conifer forest mortality and establishment before and after prescribed fire in Sequoia National Park, California. For Sci 44:341–55.
- Nielsen RP. 1995. A model for predicting continental-scale vegetation distribution and water balance. Ecol Appl 5:362–85.
- Nikolov NT, Zeller KF. 1992. A solar radiation algorithm for ecosystem dynamic models. Ecol Modell 61:149–68.
- Overpeck JT, Rind D, Goldberg R. 1990. Climate-induced changes in forest disturbance and vegetation. Nature 343:51–3.
- Pastor J, Post WM. 1988. Response of northern forests to CO₂-induced climate change. Nature 334:55–8.
- Pitcher DC. 1987. Five history and age structure in red fir forests of Sequoia National Park, CA. Can J For Res 17:582–87.
- Pitelka LF. 1997. Plant migration and climate change. Am Sci 85:464-73.
- Prentice IC, Cramer W, Harrison SP, Leemans R, Monserud RA, Solomon AM. 1992. A global biome model based on plant physiology and dominance, soil properties and climate. J Biogeogr 19:117–34.
- Prentice IC, Sykes MT, Cramer W. 1993. A simulation model for the transient effects of climate change on forest landscapes. Ecol Modell 65:51–70.
- Rind D, R Goldberg, R Ruedy. 1989. Change in climate variability in the 21st century. Clim Change 14:5–37.
- Rothermel RC. 1972. A mathematical model for predicting fire spread in wildland fuels. United States Department of Agriculture Forest Service; Research Paper INT-115.
- Running SW, Nemani R, Hungerford RD. 1987. Extrapolation of meteorological data in mountain terrain, and its use for

simulating forest evapotranspiration and photosynthesis. Can J For Res 17:472–83.

- Ryan KC, Reinhardt ED. 1988. Predicting postfire mortality of seven western conifers. Can J For Res 18:1291–7.
- Solomon AM, Bartlein PJ. 1992. Past and future climate change: response by mixed deciduous–coniferous forest ecosystems in northern Michigan. Can J For Res 22:1727–38.
- Solomon AM, Kirilenko AP. 1997. Climate change and terrestrial biomass: what if trees do not migrate? Global Ecol Biogeogr Lett 6:139–48.
- Stauffer D. 1985. An introduction to percolation theory. London: Taylor and Francis.
- Stephens SL. 1995. Effects of prescribed and simulated fire and forest history of giant sequoia [Sequoiadendron giganteum (Lindley) Buccholz.]-mixed conifer ecosystems of the Sierra Nevada, California [PhD dissertation]. Berkeley: University of California.
- Stephenson NL. 1988. Climatic control of vegetation distribution: the role of the water balance with examples from North America and Sequoia National Park, California [PhD dissertation]. Ithaca: Cornell University.
- Stephenson NL, Parsons DJ. 1993. A research program for predicting the effects of climatic change on the Sierra Nevada. In: Veirs SD Jr, Stohlgren TJ, Schonewald-Cox C, editors. Proceedings of the fourth conference on research in California's national parks. p 93–109. (US Department of the Interior National Park Service transactions and proceedings series, 9.)
- Swetnam TW. 1993. Fire history and climate change in giant sequoia groves. Science 262:885–9.
- [UCAR] University Corporation for Atmospheric Research. 1997. http://neit.cgd.ucar.edu/vemap/scenario.html
- Urban DL, Harmon ME, Halpern CB. 1993. Potential response of Pacific northwestern forests to climatic change, effects of stand age and initial composition. Clim Change 23:247–66.
- Urban DL, Miller C, Halpin PN, Stephenson NL. Forest gradient response in Sierran landscapes: the physical template. Landscape Ecol. Forthcoming.
- Van Wagner CE. 1973. Height of crown scorch in forest fires. Can J For Res 3:373–8.
- Van Wagtendonk JW, Benedict JM, Sydoriak WM. 1998. Fuel bed characteristics of Sierra Nevada conifers. West J Appl For 13:73–84.