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CLIMATE CHANGE EFFECTS ON VEGETATION DISTRIBUTION, CARBON, AND FIRE IN CALIFORNIA

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Abstract. The objective of this study was to dynamically simulate the response of vegetation distribution, carbon, and fire to the historical climate and to two contrasting scenarios of climate change in California. The results of the simulations for the historical climate compared favorably to independent estimates and observations, but validation of the results was complicated by the lack of land use effects in the model. The response to increasing temperatures under both scenarios was characterized by a shift in dominance from needle-leaved to broad-leaved life-forms and by increases in vegetation productivity, especially in the relatively cool and mesic regions of the state. The simulated response to changes in precipitation were complex, involving not only the effect of changes in soil moisture on vegetation productivity, but also changes in tree–grass competition mediated by fire. Summer months were warmer and persistently dry under both scenarios, so the trends in simulated fire area under both scenarios were primarily a response to changes in vegetation biomass. Total ecosystem carbon increased under both climate scenarios, but the proportions allocated to the wood and grass carbon pools differed. The results of the simulations underscore the potentially large impact of climate change on California ecosystems, and the need for further use and development of dynamic vegetation models using various ensembles of climate change scenarios.

Key words: California, USA; carbon; climate change; dynamic vegetation model; fire; vegetation distribution.

INTRODUCTION

California, USA, is one of the most climatically and biologically diverse areas in the world. There is more diversity in the state's land forms, climate, ecosystems, and species than in any comparably sized region in the United States (Holland and Keil 1995). The diversity of landscapes and climates supports a broad range of natural ecosystems ranging from the cool and wet redwood forests of the northwestern bioregion to the hot and dry Mojave and Sonoran Deserts (Fig. 1; Hickman 1993). This diversity of habitats sustains a greater level of species diversity and endemism than is found in any other region of the nation. The California flora includes ~25% of the flora of the continental United States, and ~25% of the plant species are endemic to the state (Davis et al. 1998).

Much of California's biological wealth is threatened by the state's burgeoning population and the consequent impacts on the landscape. Throughout the state, natural habitats have been and continue to be altered and fragmented, endangering the state's biological diversity (Barbour et al. 1993). Most of the state's forests have been logged, native oak woodlands are in serious decline, native grasslands have almost completely disappeared, and nearly 90% of the state's wetlands and riparian areas have been severely degraded or destroyed. Even relatively unmanaged natural systems have been significantly altered by introduction of nonnative species and fire suppression (Field et al. 1999).

In the future, global climate change will increasingly interact with and intensify the pressures of a growing population on the natural ecosystems of California. Recent studies show that even gradual and apparently small changes in climate can lead to catastrophic shifts in ecosystems when ecosystem resilience has been compromised by human exploitation (Scheffer et al. 2001). Regional climate studies indicate that on average California may experience substantially warmer and wetter winters, somewhat warmer summers, and an enhanced El Niño Southern Oscillation (ENSO) during the next century (Field et al. 1999, Gutowski et al. 2000). All natural ecosystems, whether managed or unmanaged, will be impacted by these changes in climate. It is not possible to accurately predict the response of the natural systems to global climate change through direct experimentation. The physical extent, complexity, and expense of even a single factor experiment for an entire ecosystem is usually prohibitive (Aber et al. 2001). However, analyses of the sensitivity of natural ecosystems to climate change can be made using ecosystem models that integrate information from direct experimentation.

In this study we used MAPSS-CENTURY 1 (MC1; Daly et al. 2000, Bachelet et al. 2001*a*), a state-of-the-

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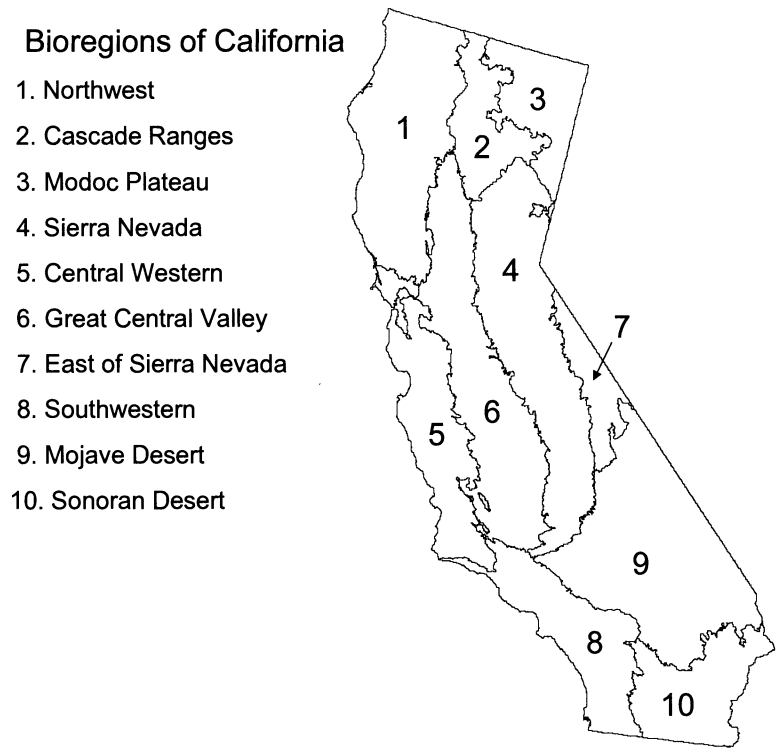

FIG. 1. Bioregions of California, USA (Hickman 1993).

art dynamic vegetation model, to investigate the sensitivity of natural ecosystems in California under two different future climate scenarios. MC1 simulates vegetation succession at large spatial extents through time while estimating variability in the carbon budget and responses to episodic events such as drought and fire. While MC1 does not as yet simulate interactions with land use effects or constraints on ecosystem change imposed by dispersal of propagules, the model has been used to examine the sensitivity of natural ecosystems to global climate change for several national-scale studies, most recently for the United States Global Change Research Program's National Assessment of Climate Change Impacts on the United States (Aber et al. 2001, National Assessment Synthesis Team 2001).

METHODS

The model

MC1 is a dynamic vegetation model (DVM) that simulates life-form mixtures and vegetation types; ecosystem fluxes of carbon, nitrogen, and water; and fire disturbance. MC1 is routinely implemented (Bachelet et al. 2000, 2001*b*, Daly et al. 2000, Aber et al. 2001) on spatial data grids of varying resolution (i.e., grid cell sizes ranging from 900 m^2 to ~2500 km^2) where the model is run separately for each grid cell (i.e., there is no exchange of information across cells). The model reads climate data at a monthly time step and calls interacting modules that simulate biogeography, biogeochemistry, and fire disturbance.

Biogeography module.—The biogeography module simulates the potential life-form mixture of evergreen needleleaf, evergreen broadleaf, and deciduous broadleaf trees, and C_3 and C_4 grasses. The tree life-form mixture is determined at each annual time step by locating the grid cell on a two-dimensional gradient of annual minimum temperature and growing season precipitation. Life-form dominance is arrayed along the minimum temperature gradient from more evergreen needleleaf dominance at relatively low temperatures to more deciduous broadleaf dominance at intermediate temperatures to more broadleaf evergreen dominance at relatively high temperatures. The precipitation dimension is used to modulate the relative dominance of deciduous broadleaved trees, which is gradually reduced to zero towards low values of growing season precipitation. Mixtures of C_3 vs. C_4 grasses are determined by reference to their relative potential productivity during the three warmest consecutive months. Potential grass production by life-form is simulated as a function of soil temperature using equations from the CENTURY model (Parton et al. 1994). The tree and grass life-form mixtures together with wood and grass biomass simulated by the biogeochemistry module are used in a rule base to determine which of 22 possible potential vegetation types occurs at the grid cell each year.

Biogeochemistry module.—The biogeochemistry module is a modified version of the CENTURY model (Parton et al. 1994), which simulates plant productivity,

organic matter decomposition, and water and nutrient cycling. Plant productivity is constrained by temperature, effective moisture (i.e., a function of soil moisture and potential evapotranspiration), and nutrient availability. In this study, simulated vegetation productivity was assumed to be unconstrained by nutrient availability. The simulated effect of increasing atmospheric CO_2 is to increase maximum potential production and to decrease transpiration (thus reducing the constraint of effective moisture on productivity). Trees compete with grasses for soil moisture, light, and nutrients. Competition for water is structured by rooting depth. Trees and grasses compete for soil moisture in the upper soil layers where both life-forms are rooted, while the deeper-rooted trees have sole access to moisture in deeper layers. Grass productivity is constrained by light availability in the understory, which is reduced as a function of tree leaf carbon. Parameterization of the tree and grass growth processes in the model is based on the current life-form mixture, which is updated annually by the biogeography module. For example, an increase in annual minimum temperature that shifted the dominance of evergreen needle-leaved trees to codominance with evergreen broadleaved trees would trigger an adjustment of tree growth parameters (e.g., the optimum growth temperature) that would, in turn, produce a modified tree growth rate.

Fire disturbance module.—The MC1 fire module (Lenihan et al. 1998) simulates the occurrence, behavior, and effects of fire. The module consists of several mechanistic fire behavior and effect functions (Rothermel 1972, Peterson and Ryan 1986, van Wagner 1993, Keane et al. 1997) embedded in a structure that provides two-way interactions with the biogeography and biogeochemistry modules. Live crown structure and fuel loading in several size classes of both dead and live fuels are estimated using life-form-specific allometric functions of the different carbon pools. The moisture content of each dead fuel size class is estimated as a function of antecedent weather conditions averaged over a period of days dependent on size class. The moisture content of each live fuel class is a function of the soil moisture content to a specific depth in the profile. Fuel moisture and distribution of the total fuel load among different size classes determine potential fire behavior estimated using the Rothermel (1972) fire spread equations.

The rate of fire spread and fire line intensity are the model estimates of fire behavior used to simulate fire occurrence and effects. The occurrence of a fire event is triggered by thresholds of fire spread, fine fuel flammability, and coarse woody fuel moisture (given a constraint of just one fire event per year). The thresholds were calibrated to limit the occurrence of simulated fires to only the most extreme events. Large and severe fires account for a very large fraction of the annual area burned historically (Strauss et al. 1989). These events are also likely to be least constrained by heterogeneities in topography and fuel moisture and loading that are poorly represented by relatively coarse-scale input data grids (Turner and Romme 1994).

The direct effect of fire in the model is the consumption and mortality of dead and live vegetation carbon that is removed from (or transferred to) the appropriate carbon pools in the biogeochemistry module. This direct effect is a function of the simulated fraction of the cell burned, fire line intensity, and tree canopy structure. The fraction of the cell burned depends on the simulated rate of fire spread and the time since the last fire event relative to the current fire return interval simulated for the cell. Higher rates of spread and longer intervals between fires generally produce more extensive fire events in the model. Live carbon mortality and consumption within the area burnt are functions of fire line intensity and the tree canopy structure (i.e., crown height, crown length, and bark thickness). Dead biomass consumption is simulated using functions of fire intensity and fuel moisture that are fuel-class specific.

Fire effects extend beyond the direct impact on carbon and nutrient pools to more indirect and complex effects on tree vs. grass competition. Fire tends to tip the competitive balance towards grasses in the model because much, or all, of the grass biomass consumed regrows in the year following a fire event. Woody biomass consumed or killed is more gradually replaced. A greater competitive advantage over trees promotes greater grass biomass which, in turn, produces higher fine-fuel loadings and changes in the fuel bed structure that promote greater rates of spread and thus more extensive fire.

Climatic data

The climate data used as input to the model in this study consisted of monthly time series for all the necessary variables (i.e., precipitation, minimum and maximum temperature, and vapor pressure) distributed on a 100-km^2 resolution data grid for the state of California. Spatially distributed monthly time series data for historical (1895–1993) precipitation, temperature, and vapor pressure already existed at a 100-km^2 resolution. This data set was developed from a subset of climate data generated by VEMAP (Kittel et al. 1997) and from observed California station data interpolated to the data grid by the PRISM model (Daly et al. 1994).

Spatially distributed climatic time series data for the two potential future climatic periods (1994–2100) were constructed using coarse-scale monthly output generated by two general circulation models (GCMs): the Hadley Climate Center HADCM2 model (HAD) and the National Center for Atmospheric Research (NCAR) Parallel Climate Model (PCM). Both are state-of-the-art GCMs that include the influence of dynamic oceans and aerosol forcing on the atmosphere. Most GCM experiments predict a warmer and wetter future for California. That prediction is represented in this study by

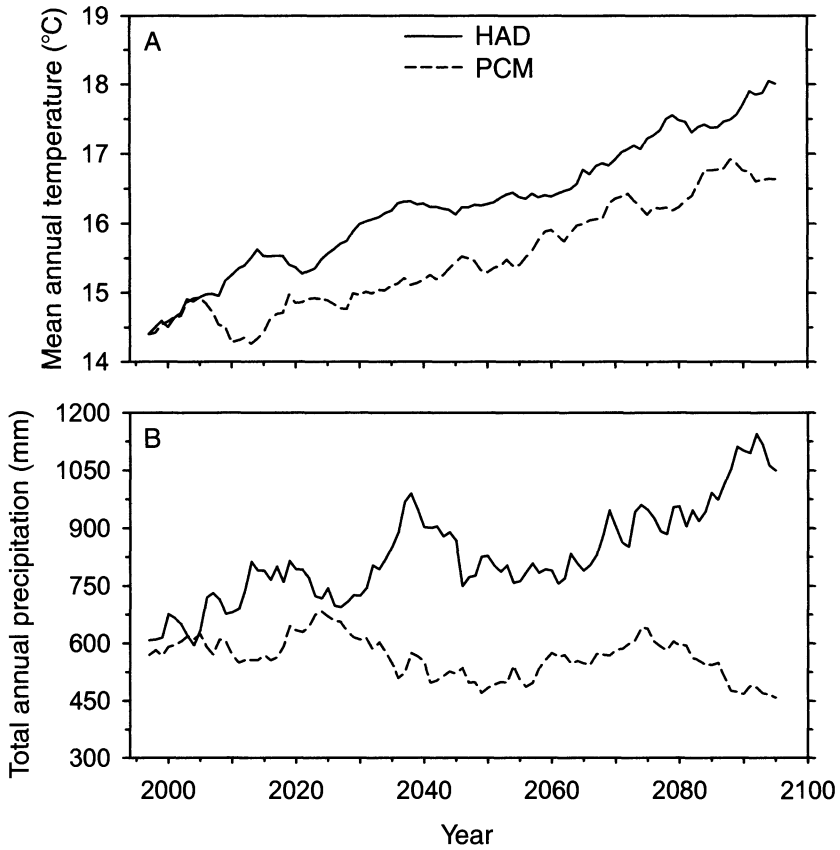

FIG. 2. Future trends in (A) mean annual temperature and (B) total annual precipitation under the the Hadley Climate Center HADCM2 model (HAD) and the National Center for Atmospheric Research's Parallel Climate Model (PCM) future climate scenarios. Annual values are means across all grid cells. Trends were smoothed for display using a 10-yr running average.

the HAD scenario developed from results of the HADCM2SUL integration (Mitchell and Johns 1997). The second climate scenario generated from results of the PCM B06.06 simulation (Dai et al. 2001) predicts a generally warmer and drier California. The PCM scenario thus provided a useful contrast to the HAD scenario for testing the model's sensitivity to climatic change. Both GCMs were run from the 1800s to 1995 using observed increases in greenhouse gas concentrations and into the future using Intergovernmental Panel on Climate Change (IPCC) projections of a 1% increase per year (Kattenberg et al. 1996).

There are distinctly different trends of mean annual temperature and total annual precipitation under the two future climate scenarios. Both scenarios show an increase in annual temperature relative to the mean for the historical base period (Fig. 2A), but the increase is significantly greater for the HAD scenario. The two scenarios are even more distinct in terms of projected trends in precipitation (Fig 2B). The HAD scenario is wetter and the PCM scenario is drier than the historical mean for most years, but the contrast between the two is especially pronounced in the last few decades of the future period.

A change in the seasonal trend of temperature and precipitation may have as much impact on ecosystem properties as changes in annual trends. Mean monthly values for temperature and precipitation over the 30-yr historical base period (Fig. 3) show the characteristic trends for a Mediterranean climate with cool wet winters and hot dry summers. For both scenarios, monthly temperature and precipitation averaged over the future 30-yr period retain these seasonal trends. Changes in monthly temperature and precipitation under the two scenarios interact to produce shifts in the amount of precipitation that falls while vegetation growth is dormant or active. Given an approximate threshold of 13°C to define the beginning and end of the growing season, dormant season precipitation increases by ~46% relative to historical levels under the HAD scenario and declines by ~19% under the PCM scenario. This is an important feature of the scenarios in determining the response of the model because dormant season precipitation is most effective at recharging the deep soil moisture exclusively available to the woody life-forms. Thus an increase in dormant season precipitation, such as that under the HAD scenario, will be more advantageous to the growth and competitiveness of the

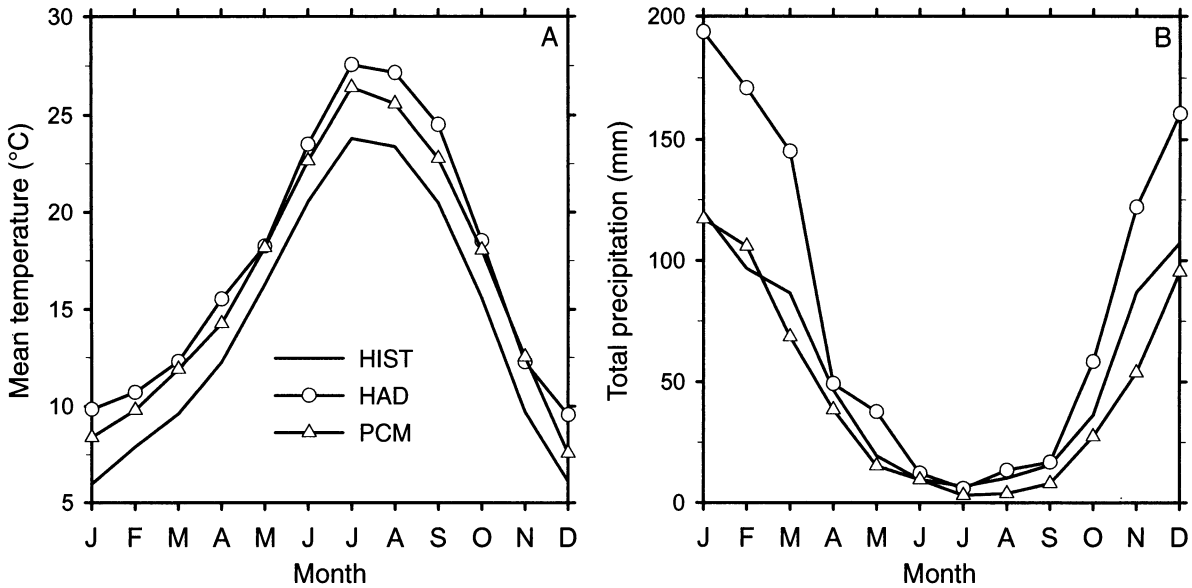

FIG. 3. Seasonal trends in (A) mean monthly temperature and (B) total monthly precipitation trends for the historical period (1961–1990) and the future period (2070–2099) of the Hadley Climate Center HADCM2 model (HAD) and the National Center for Atmospheric Research's Parallel Climate Model (PCM) future climate scenarios. Monthly values are means for the time period and across all grid cells.

woody life-forms in the model. A decline in precipitation during the dormant season, such as that under the PCM scenario, will produce a decline in the growth and competitiveness of the woody life-forms to the benefit of the grass life-forms in the model.

RESULTS AND DISCUSSION

Vegetation distribution

Response to the historical climate.—Of the 22 possible vegetation types predicted by the biogeography module, 12 occurred in the simulations for California. These types were aggregated into seven vegetation classes to simplify the visualization of results. The aggregation scheme and lists of typical regional examples in each vegetation class (Table 1) indicate the range of each class in terms of physiognomy and species dominance.

The results of the vegetation class simulation for the historical period are shown (Fig. 4A) as the distribution of the most frequent vegetation type simulated for the 1961–1990 climate period. The simulated vegetation class distribution is difficult to validate against different maps of vegetation available for California. The MC1 biogeography module simulates the life-form mixture and vegetation type that could potentially occur given climatic conditions and the simulated fire regime. Many of the available vegetation maps show the distribution of vegetation types highly modified by urbanization, agriculture, and forestry practices including fire suppression. Others show the distribution

TABLE 1. MC1 vegetation type aggregation scheme and regional examples of the vegetation classes.

MC1 vegetation class	MC1 vegetation type	Regional examples
Alpine/subalpine forest	tundra, boreal forest	alpine meadows, lodgepole pine forest, white-bark pine forest
Evergreen conifer forest	maritime temperate conifer forest, continental temperate coniferous forest	coastal redwood forest, coastal closed-cone pine forest, mixed conifer forest, ponderosa pine forest
Mixed evergreen forest	warm temperate/subtropical mixed forest	Douglas-fir–tan oak forest, tan oak–madrone–oak forest, ponderosa pine–black oak forest
Mixed evergreen woodland	temperate mixed Xeromorphic woodland, temperate conifer xeromorphic woodland	blue oak woodland, canyon live oak woodland, northern juniper woodland
Grassland	C_3 grassland C_4 grassland	valley grassland, southern coastal grassland, desert grassland
Shrubland	mediterranean shrubland, temperate arid shrubland	chamise chaparral, southern coastal scrub, sagebrush steppe
Desert	subtropical arid shrubland	creosote brush scrub, saltbrush scrub, Joshua tree woodland

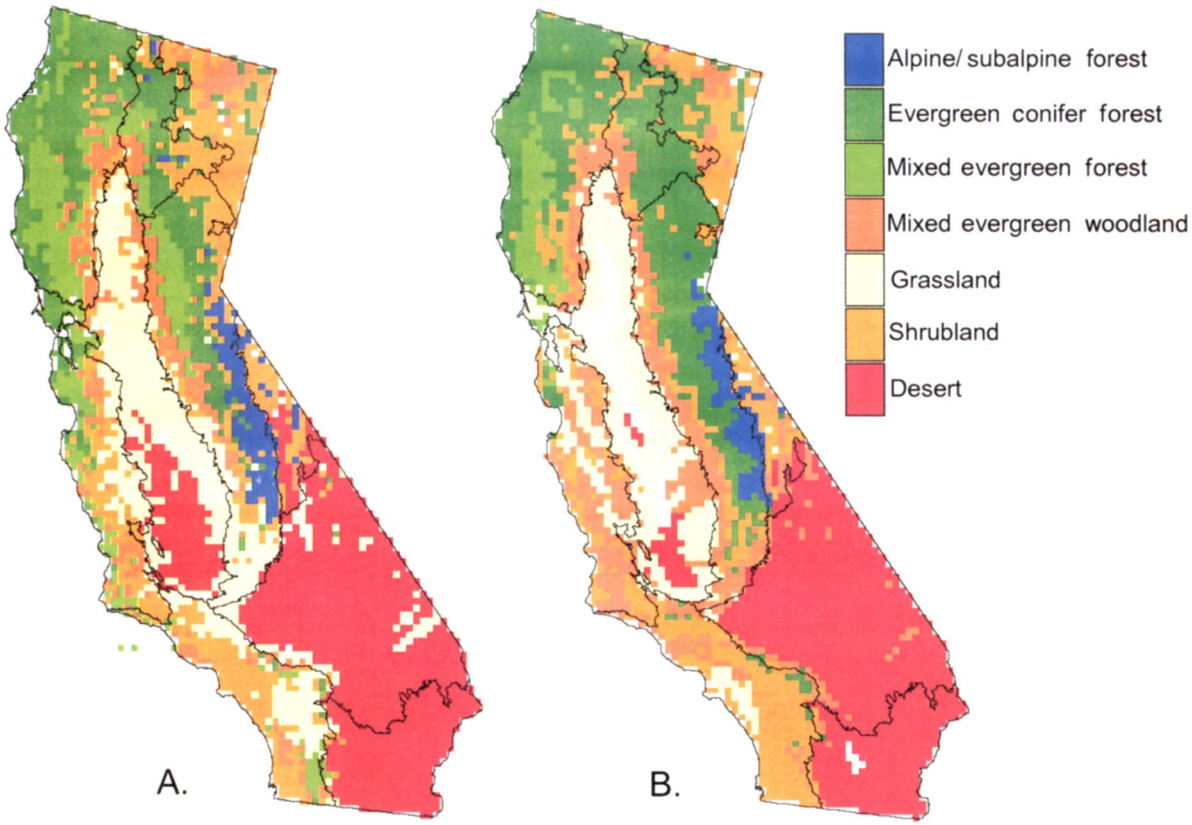

FIG. 4. (A) Map of the distribution of the simulated vegetation classes for the historical period (1961–1990) and (B) baseline vegetation map. The vegetation class mapped at each grid cell in (A) is the most frequent class simulated during the historical period.

of potential vegetation types, but comparisons to these involve difficulties associated with different criteria for classification and potential errors associated with cross-walking different classification schemes. The Küchler (1975) potential vegetation map of the United States was selected as a baseline for comparison against the vegetation class simulation for the historical period. A baseline vegetation map (Fig. 4B) was created for California by aggregating the 28 vegetation types mapped by Küchler in California into the seven vegetation classes simulated by MC1.

The overall distribution of the vegetation classes simulated for the historical period was very similar to the distribution on the baseline vegetation map. The percentage of coverage of the vegetation classes for the MC1 simulation also compared favorably to the baseline map (Fig. 5). However, there were a few notable differences in terms of both distribution and coverage in the different regions of the state. For example, MC1 predicted greater coverage of mixed evergreen forest, especially along the western slope of the Sierra Nevada where the baseline map shows evergreen conifer forest. In the Central Western Region, MC1 predicts a mixture of evergreen conifer forest and mixed evergreen forest where the baseline map shows evergreen woodland and

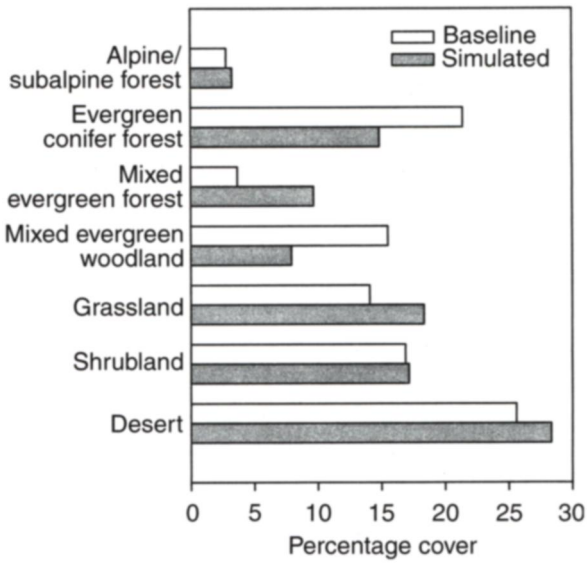

FIG. 5. Percentage of land cover of vegetation classes for the historical period (1961–1990) simulation compared to the baseline vegetation map.

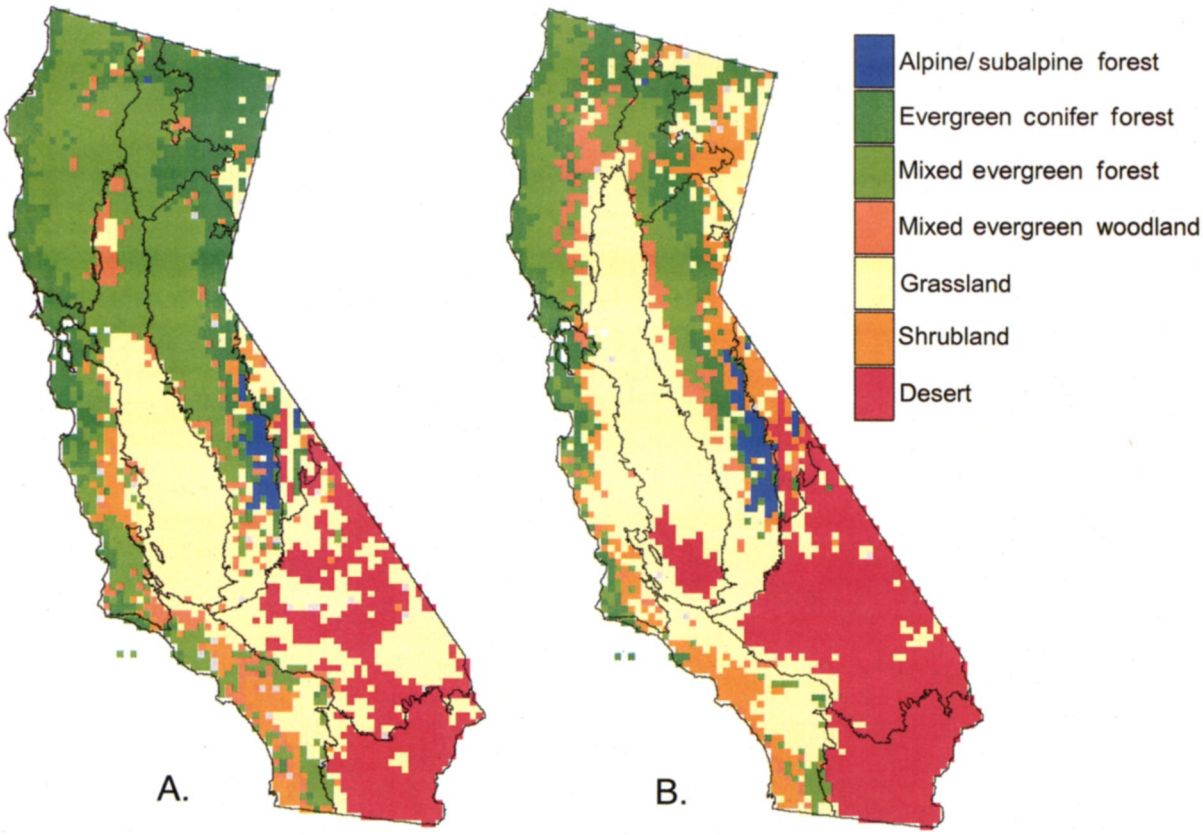

FIG. 6. Distribution of the vegetation classes simulated for the future period 2070–2099 by (A) the Hadley Climate Center HADCM2 model (HAD) and (B) the National Center for Atmospheric Research's Parallel Climate Model (PCM) climate scenarios. The vegetation class mapped at each grid cell is the most frequent class simulated during the time period.

shrubland. Other discrepancies occur in the Southwestern Region and at the southern end of the Sierra Nevada where the MC1 simulation shows more grassland than the baseline map and in the eastern half of the Cascade Range region where MC1 predicted more shrubland.

Not all the instances in which the simulated vegetation class distribution differs with the baseline distribution are necessarily errors in the simulation. For example, on the baseline map there is no mixed evergreen forest in the region between mixed evergreen woodland and evergreen conifer forest along the western slope of the Sierra Nevada. However, a Sierran mixed hardwood forest with a strong resemblance to the mixed evergreen forests of the coastal mountains has been described for this region (Holland and Keil 1995). The simulated occurrence and distribution of evergreen conifer and mixed evergreen forest along the coastal sector of the Central Western Region is also supported by descriptions of closed-cone coniferous forest and mixed hardwood forest (Holland and Keil 1995, Sawyer et al. 1995, Vogel et al. 1995) for this region of California.

Response to the future climate scenarios.—The response of vegetation class distribution under the two future climate scenarios was determined by comparing the distribution of the most frequent vegetation type simulated for the 30-year historical period (Fig. 4A) against the same for the last 30 years (2071–2100) of the future scenarios (Fig. 6A, B). The simulated response of the vegetation classes in terms of changes in percentage of coverage (Fig. 7) was surprisingly similar under the two future climates. There was agreement on the direction of change (i.e., decrease or increase in coverage) for all but the evergreen conifer forest class, and the amounts of change were comparable for a few of the vegetation classes. However, these similarities in the response of class coverage were often the net result of very different responses to each scenario in terms of the spatial distribution of vegetation classes as discussed below.

A prominent feature of the response of the vegetation class distribution under the HAD scenario (Fig. 6A) was the advancement of forest classes into the Modoc Plateau, into the northern end of the Great Central Valley, towards higher elevations in the Sierra Nevada, and inland along the coast. Increases in both temperature and dormant season precipitation under this scenario favored expansion of forest, and they were especially favorable for mixed evergreen forest. The rel-

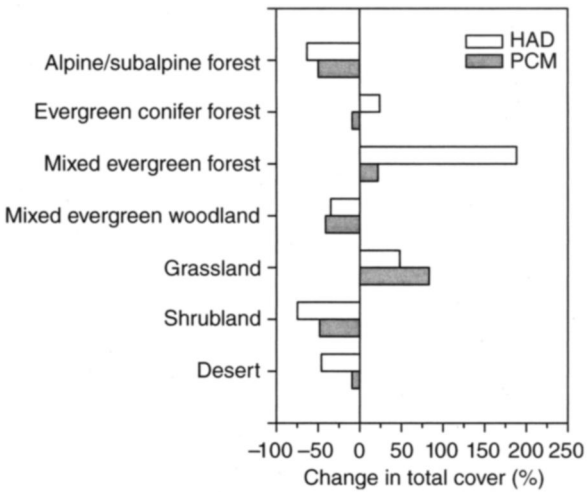

FIG. 7. Percentage changes in the total cover of the vegetation classes under the Hadley Climate Center HADCM2 model (HAD) and the National Center for Atmospheric Research's Parallel Climate Model (PCM) scenarios.

atively high degree of warming under the HAD scenario promoted a widespread change in the simulated life-form composition from needleleaf dominance to mixed needleleaf–broadleaf in the northern half of the state. Consequently, mixed evergreen forest replaced evergreen conifer forest throughout much of the latter's simulated historical range. Two examples of this transition in terms of species dominance within the different bioregions might include the replacement of Douglas-fir–white fir forest by Douglas-fir–tan oak forest in the Northwest Region, and the replacement of white fir–ponderosa pine forest by ponderosa pine–black oak forest in the Sierra Nevada. Greater moisture availability under the HAD scenario also promoted the advancement of mixed evergreen forest into mixed evergreen woodland, shrubland, and grassland. Movement into the northern end of the Great Central Valley could represent the replacement of blue oak woodlands, chaparral, and perennial grassland by tan oak–madrone–canyon live oak forest with scattered Douglas-fir and ponderosa pine. In the Central Western and Southwestern bioregions, mixed evergreen forests of coast live oak–madrone or canyon live oak–Coulter pine might replace chaparral and live oak woodlands.

Evergreen conifer forest showed a net increase in percentage of coverage under the HAD scenario despite the loss of much of its simulated historical range to mixed evergreen forest. The main region of evergreen conifer advancement was in the cold desert region of the Modoc Plateau and east of the Sierra Nevada Range. Here higher moisture availability promoted the advancement of evergreen conifer forest into mixed evergreen woodland and shrubland. On the Modoc Plateau, this transition would likely be characterized by replacement of northern juniper woodland and Great Basin sagebrush scrub by ponderosa pine–Jeffrey pine forest. Another region of evergreen conifer forest expansion under the warmer and wetter HAD scenario was along the coast, especially in the Central Western Region. Here the simulated advancement of this class into mixed evergreen forest and shrubland would likely represent the expansion of redwood and closed-cone pines from remnant, fragmented groves into surrounding canyon live oak–madrone forests and chaparral. Evergreen conifer forest also advanced into the high-elevation subalpine/alpine forest in the Cascade Range and Sierra Nevada regions under the HAD scenario. Here the model responded to an increase in the length of the growing season past a threshold in the biogeographic rule base. Advancement of red fir or lodgepole pine forest into subalpine parks and meadow would be a likely example of this transition.

In addition to widespread advancement of forest, another prominent feature of the response of vegetation distribution under the HAD scenario was the advancement of grassland, particularly in the southern end of the Great Central Valley and in the uplands of the Mojave Desert where grassland replaces desert. Here the response to increased precipitation was an increase in both tree and grass biomass. The increase in grass biomass translated to more fine flammable fuels in the fire disturbance module, promoting more fire that in turn reduced the competitiveness of the woody life-forms. In the Mojave Desert, this transition could represent an increase in the extent of desert grassland interspersed with Joshua tree desert woodland and creosote bush scrub.

The most prominent feature of the vegetation class response to the drier PCM scenario (Fig. 6B) was the advancement of grassland into the simulated historical range of mixed evergreen woodland and shrubland. This transition was prompted by a decline in the competitiveness of woody life-forms as a response to the decline in dormant season precipitation, and an increase in fire, which further constrained the woody life-forms. The advancement of grassland occurred primarily on the Modoc Plateau, in the foothills surrounding the Great Central Valley, and in the interior of the Central Western Region. On the Modoc Plateau, a likely example of this transition would be an increase in the extent of the grassland interspersed within the northern juniper woodland and sagebrush scrub communities. A similar transition is already occurring under present-day conditions in the sagebrush scrub communities of the intermountain west. Here drought, increasing cheatgrass abundance, and fire are interacting to significantly reduce the woody scrub component (D'Antonio and Vitousek 1992). In the foothills of the Great Central Valley and Central Western Region, the model simulation could indicate the loss of various oak woodland and chaparral communities to nonnative grassland communities.

Mixed evergreen woodland and shrubland show too little advancement to compensate for the loss to grass-

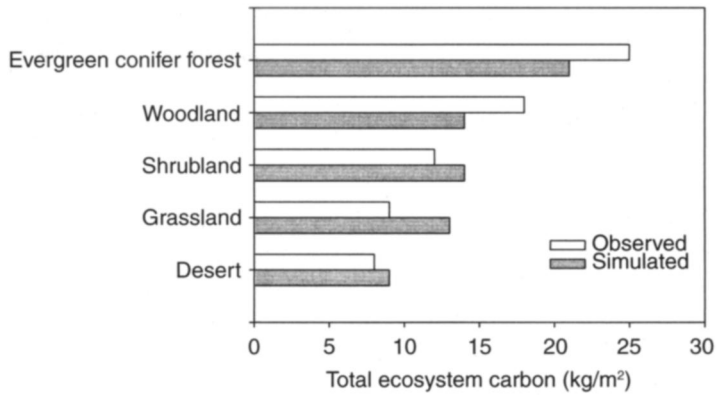

FIG. 8. Observed vs. simulated values for total ecosystem carbon density by vegetation class. Simulated values are mean annual values for the historical period (1961–1990) averaged across the state. Observed values are estimates for the United States reported by Houghton and Hackler (2000) and Atay et al. (1979).

land under the PCM scenario. Consequently, there is a net decline in the coverage of mixed evergreen woodland and shrubland and a narrowing of the simulated ecotones between forest and grassland. One local exception to this trend is in the eastern half of the Northwest Region, where there was some mixed evergreen woodland advancement into forest. In this bioregion, northern oak woodland advancing into Douglas-fir–tan oak and Douglas-fir–white fir forests would be a likely example of this transition. An exception to the general decline in shrubland was in the Sierra Nevada region, where shrubland advanced into alpine/subalpine forest. Here a regional example of the model's response to a lengthened growing season could be an increase in whitebark pine krummholtz within alpine meadow communities.

In contrast to the simulation for the HAD scenario, the distribution of mixed evergreen forest and evergreen conifer forest remained relatively static under the PCM scenario. Mixed evergreen forest showed a relatively small gain in coverage with limited advancement into evergreen conifer forest in the Northwest and Sierra Nevada regions. This transition was prompted by a temperature-driven shift in life-form composition like that under the HAD scenario, but the response was more constrained under the cooler PCM scenario. There was a net loss in the statewide coverage of evergreen conifer forest, but the class showed some advancement at high elevations in the Sierra Nevada and on the Modoc Plateau, and along the coast in the Central Western Region. In these relatively cool regions of the state, tree productivity increased as a response to increases in temperature and relatively small declines in precipitation.

Carbon

Response to the historical climate.—The successful simulation of the vegetation class distribution for the historical climate was, in part, a result of accurately simulating the relative distribution of wood and grass carbon across the state. The model also accurately predicted the absolute density of carbon within the different vegetation classes. Carbon density values within each of the simulated classes were averaged over the last 30 yr of the historical simulation and compared to observed values for equivalent vegetation classes (Fig. 8). The observed values (Atjay et al. 1979, Houghton and Hackler 2000) are for the United States across the entire range of each vegetation type, so there was likely some error associated with their use in representing observed values for California alone. Nevertheless, the results of the comparison showed a strong similarity between simulated and observed values.

Response to the future climate scenarios.—The trend in simulated annual net primary production (NPP) for the entire state of California (Fig. 9A) was a response to the continuous increase in temperature and fluctuations in precipitation under each scenario. The increase in temperature under both scenarios (Fig. 2A) increased the maximum productivity of life-forms in the model. Under the HAD scenario, the temperature-driven increase in NPP was relatively unconstrained by precipitation, which also increased throughout the future period (Fig. 2B). Nevertheless, fluctuations in the trend of NPP under the HAD scenario were clearly related to fluctuations in the trend of precipitation. In contrast to the HAD scenario, the temperature-driven increase in NPP was more constrained under the drier PCM scenario. Periods of decline in NPP corresponded to declines in precipitation below mean historical precipitation. Not until the end of the future period, where mean annual temperature was highest, did NPP under the PCM scenario remain above the historical mean despite declining precipitation.

When heterotrophic respiration was subtracted from NPP to derive net ecosystem productivity (NEP), there was a narrowing of the gap between trends in productivity under the two scenarios (Fig. 9B). This was also a response to the contrasting trends in temperature and precipitation. There was a greater annual percentage loss of soil carbon to heterotrophic respiration under the warmer and wetter HAD scenario compared to the cooler and drier PCM scenario.

When simulated losses of carbon to biomass consumption by fire are subtracted from NEP to derive net ecosystem exchange (NEE, Fig. 9C), the trends in pro-

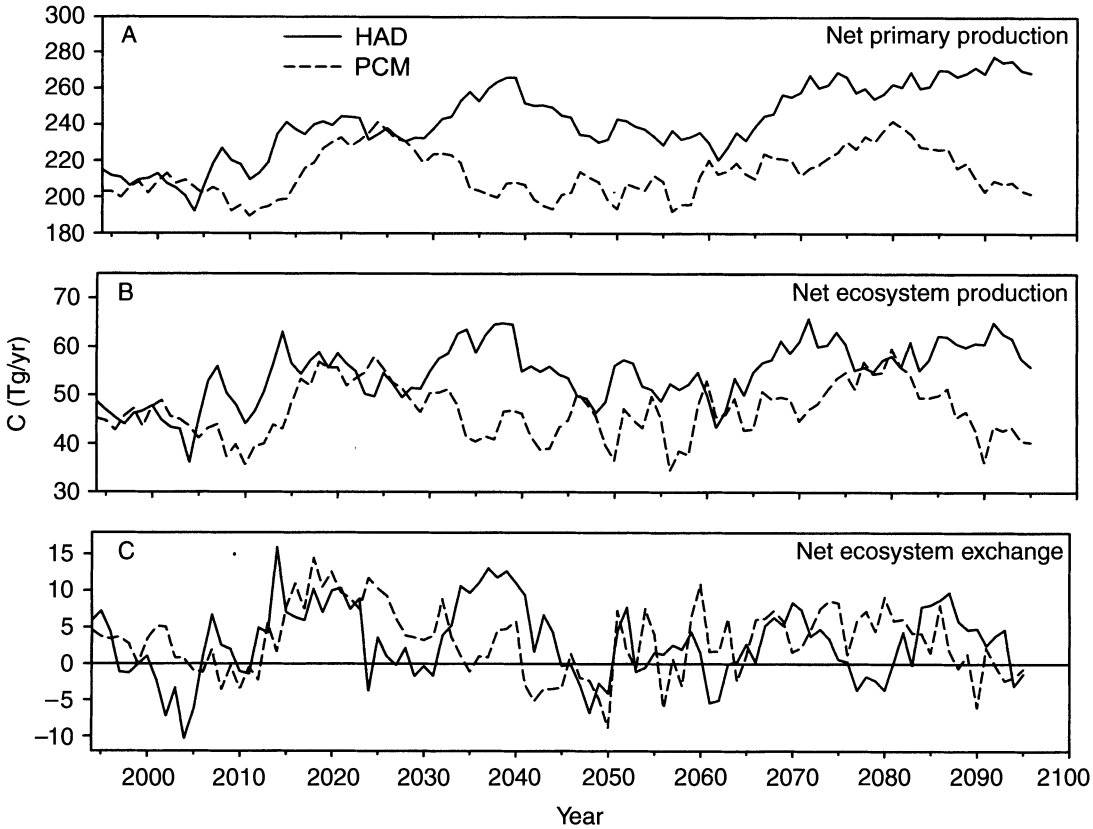

FIG. 9. Simulated trends in (A) total net primary production, (B) total net ecosystem production, and (C) total net ecosystem exchange for the entire state of California under the Hadley Climate Center HADCM2 model (HAD) and the National Center for Atmospheric Research's Parallel Climate Model (PCM) scenarios.

ductivity under the two scenarios became even less disparate. NEE under the PCM scenario actually exceeded that under the HAD scenario for certain periods. This somewhat counterintuitive result stemmed from the response of the model to changes in dormant season precipitation. Under the HAD scenario, where there was a significant increase in dormant season precipitation relative to the historical level, the model allocated relatively more annual production to woody biomass. Under the PCM scenario, where dormant season precipitation declined, more production was allocated to grass biomass. Consumption by fire had less effect over time on grass biomass because a greater proportion of grass biomass is stored underground where it is protected from fire. Moreover, any grass biomass consumed by fire was quickly reestablished the following year, in contrast to woody biomass, which was more gradually replaced. After periods of fire, NEE was relatively lower for longer periods of time under the HAD scenario because a greater proportion of the predominately woody biomass was consumed and was slower to reestablish.

TABLE 2. Size of the historical carbon pools simulated for the state of California, USA, and future changes in size simulated under the Hadley Climate Center HADCM2 model (HAD) and the National Center for Atmospheric Research's Parallel Climate Model (PCM) climate scenarios.

Carbon pool	Historical Mass (Tg)	HAD		PCM	
		Mass (Tg)	Change (%)	Mass (Tg)	Change (%)
Total ecosystem	5765	6077	5.4	6090	5.6
Soil and litter	5305	5508	3.8	5551	4.6
Live vegetation	461	568	23.2	539	16.9
Live wood	300	399	33.0	338	12.7
Live grass	161	170	5.6	202	25.5

Notes: Historical values in teragrams are the mean masses for the 30-yr (1961–1990) base period. HAD and PCM change values in teragrams are the mean masses for the 30-yr (2070–2099) future period subtracted from the mean masses for the historical period.

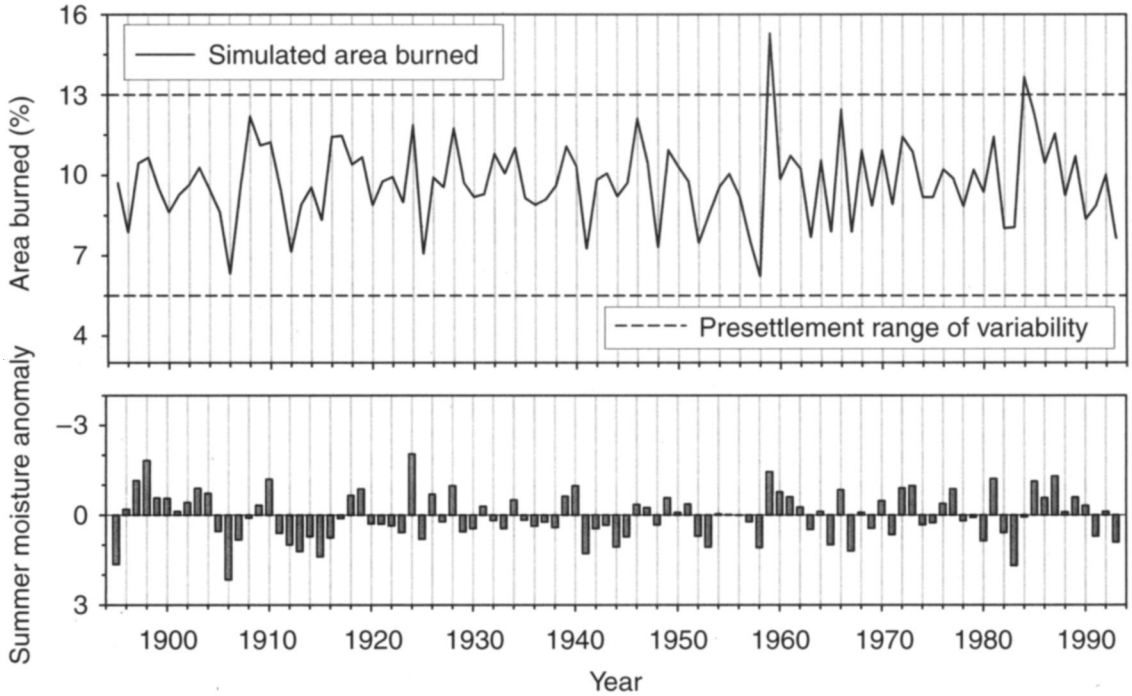

FIG. 10. Trend in the simulated annual percentage of area of California burned for the historical period (1895–1993) compared to the mean annual summer moisture anomaly. Statewide values of the summer moisture anomaly were calculated by averaging observed values (National Climatic Data Center 1994) for three summer months (June–August) for all five climatic divisions in California.

Mean simulated NEE over the last 30 yr of the future period was 2.5 and 3.1 Tg/yr under the HAD and PCM scenarios, respectively. Mean total ecosystem carbon storage over the same period was also similiar under the two scenarios (Table 2). The increase in total carbon storage was just less than 6% over the historical mean under both scenarios. This was the net result of a greater increase in soil carbon under the PCM scenario and a greater increase in live vegetation carbon under the HAD scenario. A greater percentage of the total increase in live vegetation carbon was allocated to the live grass biomass pool under the PCM scenario as a result of the decline in dormant season precipitation, which was especially steep during the last three decades of the future period (Fig. 2B). The decline in precipitation and the proportional increase in grass carbon relative to woody carbon were both factors in the increase in soil and litter carbon under the PCM scenario. Soil decomposition was slower under the drier conditions, and grass carbon is an especially effective contributor to soil carbon in the model because of the fast turnover rate and the large proportion of biomass belowground.

Fire

Response to the historical climate.—The MC1 fire module simulates fire severity under conditions of potential natural vegetation and no fire suppression, so validating the historical simulation of fire involves some of the same difficulties listed for the vegetation class simulation. Martin and Sapsis (1995) estimated that fire burned 5.5–13% of California annually under presettlement conditions. The range of percentage of total area burned simulated by MC1 during the 100 yr of the historical simulation (6.3–15.5%, Fig. 10) was remarkably similar to this independent estimate. The simulated trend of percentage of area burned showed a significant and fairly strong relationship (Spearman rank correlation = -0.70, $P < 0.001$) with the historical trend of a drought index (Fig. 10) calculated from the monthly moisture anomaly (i.e., a product of the moisture departure of the most recent 4 wk and a climate weighting factor; Palmer 1965). A state-wide annual value of the index was calculated by averaging published values of the moisture anomaly (National Climatic Data Center 1994) over three summer months (June–August) and over all five climatic divisions in California. Several severe fire years simulated by the model were coincident with some of the driest years (e.g., 1910, 1924, 1928, 1959, 1966), and several of the least severe fire years were coincident with some of the wettest years (e.g., 1906, 1912, 1941, 1958, 1983). Three of the most severe fire years (e.g., 1908, 1959, 1984) were preceded by one or more relatively wet years in which a build-up of fuels was simulated by the model. A similar pattern of large fire years promoted by sequences of wet seasons followed by average or drier than average seasons has been identified

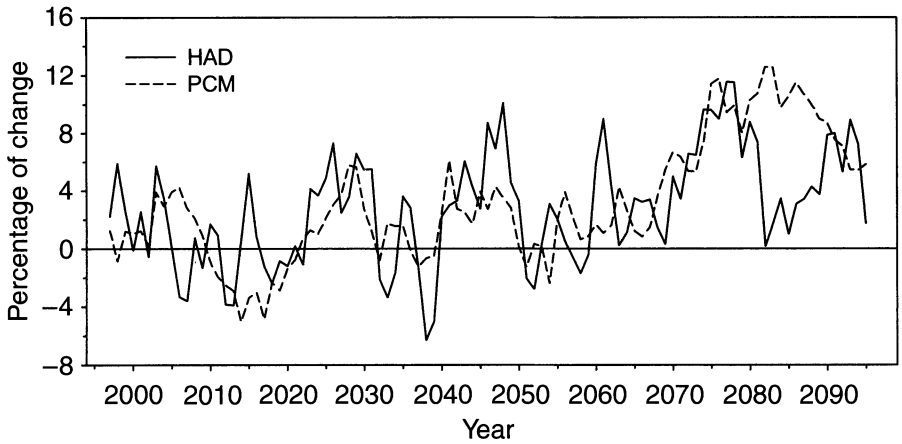

FIG. 11. Simulated trend in percentage change of total annual area burned relative to the historical (1895–1993) mean under the Hadley Climate Center HADCM2 model (HAD) and the National Center for Atmospheric Research's Parallel Climate Model (PCM) climate scenarios.

in the southwestern United States (Swetnam and Betancourt 1998).

Response to the future climate scenarios.—The simulated trends in percentage of area burned under both scenarios (Fig. 11) show periods of both increase and decline relative to the mean for the historical period. Only in the last few decades of the future period did area burned stay consistently above the historical mean. However, linear regression analysis showed that only in the case of the PCM scenario was the slope of the overall trend for area burned significantly different than zero.

The simulated fluctuations in area burned under both scenarios was a complex response to temperature and precipitation as they affected fuel moisture and to the buildup of fuel biomass prior to dry years that triggered fire events The influence of biomass buildup was particularly evident under the HAD scenario where the coefficient of variation for the overall trend in area burned (21%) was higher than for either the PCM scenario or the historical period (10% and 15%, respectively). The increase in precipitation under the HAD scenario served to increase the variability of the fire regime by reducing area burned to lower levels and contributing to greater biomass buildup during relatively wet years, thus setting the stage for higher levels of area burned promoted by higher fuel loads during relatively dry years. This interaction between fuels and the interannual variability in precipitation produced the somewhat counterintuitive result of more severe fire years simulated under the wetter HAD scenario than under the drier PCM scenario. Three years under the HAD scenario were also more severe in terms of total area burned than any year in the simulation for the historical period. Under the PCM scenario, less interannual variation in precipitation together with a higher proportion of fine fuels with a relatively rapid drying rate (i.e., grass biomass) produced a less variable simulated fire regime.

CONCLUSIONS

The MC1 simulation for the historical climate of California appeared to have achieved a reliable level of prediction, although validation of a broad-scale model of potential vegetation presents numerous difficulties. The simulation of the coverage and distribution of vegetation classes was largely in agreement with the baseline vegetation map, and some of the discrepancies between the two were likely attributable to lack of detail in the baseline map. The success of the vegetation class simulation was, in part, a result of successfully simulating the relative distribution of tree and grass carbon. And the absolute values of simulated total vegetation carbon per vegetation class were largely in agreement with published values for equivalent classes. Simulated values of total area burned over the length of the historical simulation were within a range of values expected for California under the assumptions of the model (i.e., a natural fire regime unconstrained by fire suppression). Also, the simulated peak fire years during the historical period were coincident with observed drier-than-normal years, in conformance to the well-established relationship between drought and severe fire episodes.

More rigorous validation of the simulation results for the historical climate was difficult given the nature of the simulations. The model simulates dynamic ecosystem properties only as a function of climate and soils and does not include the effects of land use practices that modify life-form mixtures, carbon stocks, and fire regimes. Also, the model does not include lags in vegetation change due to migration and dispersal over a landscape fragmented by land use practices. Ongoing efforts to incorporate land use effects in MC1 and to increase the spatial resolution of the model simulations should increase the realism of the model results and facilitate their validation against observed data from the extant landscape.

Compounding the uncertainty arising from the limitations of the model are the existence of a large number of GCM-generated global climate change scenarios that could be used to construct regional-scale scenarios for California. In a recent analysis, the California portions of over 20 GCM simulations were examined to ascertain any consistent projections of climate change (T. Wrigley, *personal communication*). All the models estimated warmer temperatures for the state, but there was much less consistency regarding precipitation. The models ranged from estimating a 56% increase to a 10% decrease in winter precipitation, with about two-thirds of the models estimating an increase in winter precipitation. The mean change in summer precipitation was near zero. The conclusion was that California is likely to be warmer and probably wetter during the winter months. This scenario is well-represented by the HAD scenario. However, none of the available scenarios should be interpreted as predictions of climate change in California. Their proper use is in the investigation of the sensitivities of natural and managed systems to potential changes in climate.

The results of the MC1 simulations for California demonstrate certain ecosystem sensitivities and interactions that are likely to be features of the response of both natural and seminatural (e.g., managed forests and rangelands) systems to the relatively certain rise in temperature and the less certain changes in precipitation. An increase in temperature could increase vegetation productivity given adequate moisture availability, especially in cooler regions of the state (e.g., along the north-central coast or at high elevations). For example, currently the highest monthly mean temperatures along the north-central coast (14.6°–16.8°C; Major 1995) are below the mean summer temperature for optimal coast redwood forest productivity (17.8°C; Kuser 1976) and for optimal redwood seedling growth (18.9°C; Hellmers and Sundahl 1959). An increase in temperature could also alter forest composition by increasing the competitiveness of evergreen hardwood species that are less tolerant of low winter temperatures than conifers (Woodward 1987).

The relative dominance of woody life-forms could be sensitive to the changes in dormant season precipitation forecast for California, especially given the predicted persistence of a Mediterranean climate where woody plants must compete with more drought-tolerant grasses during the dry growing season. With the increase in winter precipitation forecast by the majority of GCMs for California, the model results suggest a widespread expansion of forest, overtaking both woodland and shrubland, and constrained only where climate is still arid enough to support sufficient grass biomass to fuel frequent fire.

The model results indicate fire will play a critical role in the adjustment of vegetation to any of the altered precipitation regimes forecast for California, be it slowing the encroachment of woody vegetation in grasslands under wetter conditions or hastening the transition from woody communities to grassland under drier conditions. With a persistence of the summer dry climate, changes in the fire regime are likely to be less a product of altered fire weather than changes in the amount and character of fuels. The model results suggest that an increase in dormant season precipitation, especially when accompanied by greater interannual variability in rainfall, could lead to greater accumulation of relatively coarse woody fuels during sequences of wet seasons, fuels that retain relatively high moisture content during all but relatively infrequent years of fire-promoting drought. The result could be an altered fire regime characterized by more year-to-year variability in area burned and more extreme events.

The model results also suggest that changes in fire and shifts in the relative dominance of woody and grass life-forms could buffer the effect of different climatic perturbations on total ecosystem carbon storage. Under a wetter climate, an increase in carbon storage with the increase in vegetation productivity could be limited by greater losses to combustion during more extreme fire events. Under a drier climate, a decrease in carbon storage with the decrease in vegetation productivity could be limited by a shift towards greater dominance of grass life-forms that are better adapted to more frequent fire and more effective contributors to soil carbon stocks.

While neither of the model simulations for the two climate scenarios should be taken as predictions of the future, it is evident from the results that all the natural ecosystems of California, whether managed or unmanaged, are likely to be affected by changes in climate. Changes in temperature and precipitation will alter the structure, composition, and productivity of vegetation communities, and wildfire may become more frequent and intense. The incidence of pest outbreaks in forests stressed by a changing climate could act as a positive feedback on the frequency and intensity of fire. Nonnative species preadapted to disturbance could colonize altered sites in advance of native species, preventing the already problematical redistribution of natives across a landscape highly fragmented by land use practices. Both plants and animals already stressed by human development will be further stressed by climate change. Some may not be able to adapt, and there could be a significant rise in the number of threatened and endangered species. Tree species better adapted to a changed climate could be planted in forests managed for wood production, but better-adapted species may not have the same market value (e.g., conifer species vs. hardwood species). The expansion of grasslands under a drier climate might profit grazing livestock, but any gains might be offset by decreased water availability.

Considerable uncertainty exists with respect to regional-scale impacts of global warming. Much of this uncertainty resides in the differences among the dif-

ferent GCM climate scenarios as illustrated in this study. In addition, models that translate climatic scenarios into projections of ecosystem impacts can always be improved through reexamination and improvement of model processes. Nevertheless, the results of this study underscore the potentially large impact of climate change on California ecosystems and the need for further use and development of dynamic vegetation models using various ensembles of climate change scenarios.

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