



Contents lists available at ScienceDirect

Global and Planetary Change

journal homepage: www.elsevier.com/locate/gloplachaSimulated response of conterminous United States ecosystems to climate change at different levels of fire suppression, CO₂ emission rate, and growth response to CO₂James M. Lenihan^{a,*}, Dominique Bachelet^b, Ronald P. Neilson^a, Raymond Drapek^a^a USDA Forest Service Pacific Northwest Research Station, Corvallis, OR 97731, USA^b Oregon State University, Corvallis, OR 97331, USA

ARTICLE INFO

Article history:

Accepted 13 January 2008

Available online xxxx

Keywords:

climate change

biogeography

carbon

CO₂ effect

fire suppression

MC1 DGVM

ABSTRACT

A modeling experiment was designed to investigate the impact of fire management, CO₂ emission rate, and the growth response to CO₂ on the response of ecosystems in the conterminous United States to climate scenarios produced by three different General Circulation Models (GCMs) as simulated by the MC1 Dynamic General Vegetation Model (DGVM). Distinct regional trends in response to projected climatic change were evident across all combinations of the experimental factors. In the eastern half of the U.S., the average response to relatively large increases in temperature and decreases in precipitation was an 11% loss of total ecosystem carbon. In the West, the response to increases in precipitation and relatively small increases in temperature was a 5% increase in total carbon stocks. Simulated fire suppression reduced average carbon losses in the East to about 6%, and preserved forests which were largely converted to woodland and savanna in the absence of fire suppression. Across the west, unsuppressed fire maintained near constant carbon stocks despite increases in vegetation productivity. With fire suppression, western carbon stocks increased by 10% and most shrublands were converted to woodland or even forest. With a relatively high level of growth in response to CO₂, total ecosystem carbon pools at the end of the century were on average about 9–10% larger in both regions of the U.S. compared to a low CO₂ response. The western U.S. gained enough carbon to counter losses from unsuppressed fire only with the high CO₂ response, especially in conjunction with the higher CO₂ emission rate. In the eastern U.S., fire suppression was sufficient to produce a simulated carbon sink only with both the high CO₂ response and emission rate. Considerable uncertainty exists with respect to the impacts of global warming on the ecosystems of the conterminous U.S., some of which resides in the future trajectory of greenhouse gas emissions, in the direct response of vegetation to increasing CO₂, and in future tradeoffs among different fire management options, as illustrated in this study.

© 2008 Elsevier B.V. All rights reserved.

1. Introduction

Several modeling studies have been conducted with the MC1 DGVM (Daly et al., 2000; Bachelet et al., 2001b) to investigate the sensitivity of natural ecosystems to potential climate change in the United States, both at regional and national scales (Daly et al., 2000; Bachelet et al., 2000, 2003, 2004, 2005; Hayhoe et al., 2005; Lenihan et al., 2003, 2006, in press). The results show equally plausible GCM climate scenarios can generate significant differences in the simulated future response of ecosystems. Different trends in projected precipitation have produced much of the regional variation in ecosystem response simulated by MC1 within the conterminous U.S. (e.g., Bachelet et al., 2003; Lenihan et al., 2003). Continual improvements in GCM technology and computing resources will presumably result in greater convergence among GCM-simulated climate scenarios over

time, thereby reducing uncertainty related to model inputs in simulating the ecosystem response to climate change.

There are additional sources of uncertainty in simulating the ecosystem response apart from differences among climate scenarios, including those which stem from an uncertain understanding of key ecosystem processes. For example, the direct response of vegetation productivity to increasing concentrations of atmospheric CO₂ could play a key role in the future response of ecosystems, but results of various free-air CO₂ enrichment (FACE) experiments have yet to provide definitive guidance for ecosystem modelers (Boisvenue and Running, 2006). Experiments in young forest stands have shown an average 23% increase in net primary production (NPP) for CO₂ concentrations of 550 ppm as compared to ambient concentrations (Norby et al., 2005). However, experiments in older forest stands have shown little or no increase in carbon storage with increases in NPP (e.g., DeLucia et al., 2005; Körner et al., 2005; Ashoff et al., 2006). Uncertainty regarding the direct CO₂ effect and its role in the ecosystem response to climatic change is compounded by the uncertain future trend in atmospheric CO₂. In a study comparing the response of MC1 and LPJ (Stich et al., 2003) to climate change scenarios for the U.S.

* Corresponding author. USFS Pacific Northwest Research Laboratory, 3200 SW Jefferson Way, Corvallis, OR, USA. Tel.: +1 541 750 7432; fax: +1 541 750 7329.
E-mail address: lenihan@fs.fors.gov (J.M. Lenihan).

(Bachelet et al., 2003), different sensitivities to CO₂ interacting with different assumed trajectories in atmospheric CO₂ concentrations were prominent factors explaining significant differences in the responses simulated by the two models.

Additional uncertainty resides in the assumed future capacity of human intervention to alter climate-driven trends in ecosystem properties. For example, future wildland fire management could be a significant factor in the response of U.S. ecosystems to a changing climate. Past and present fire regimes in the U.S. are strongly controlled by climate at multiple time scales (Swetnam and Betancourt, 1998; Whitlock et al., 2003; Westerling and Swetnam, 2003; Schoennagel et al., 2004), and there is growing evidence that rising temperatures throughout the western U.S. are driving recently observed increases in wildfire frequency and area (Westerling et al., 2006). Fire is a global control on vegetation structure (Bond 2005, Bond et al., 2005), and fire disturbance has triggered abrupt changes in vegetation structure and composition in response to past changes in climate (Green, 1982; Overpeck et al., 1990; Clark 1990; Keely and Rundel, 2005). Decades of fire suppression have significantly altered vegetation structure and fire regimes in the U.S., especially in the semi-arid forests of the West (Covington and Moore, 1994; Allen et al., 2002; Schoennagel et al., 2004), and wildland fire management will continue to shape vegetation and its adjustment to climatic change into the future.

Here we describe the results of a modeling experiment designed to investigate the effect of different levels of fire suppression, CO₂ emission rate, and the direct CO₂ effect on the ecosystem response to climatic change simulated by MC1. Results were calculated as averages across simulations for different GCM climate scenarios to reduce variation associated with different climatic projections and to focus the investigation on the response to the CO₂ and fire treatment factors.

2. Methods

2.1. MC1 model description

MC1 is a dynamic vegetation model (DGVM) that simulates plant type mixtures and vegetation types; the movement of carbon, nitrogen, and water through ecosystems; and fire disturbance. MC1 routinely generates century-long, regional-scale simulations on relatively coarse-scale data grids (Daly et al., 2000; Bachelet et al., 2000, 2001a, 2003, 2004, 2005; Hayhoe et al., 2005; Lenihan et al., 2003, 2006, in press). The model reads soil and monthly climate data, and calls interacting modules that simulate biogeography, biogeochemistry, and fire disturbance (Bachelet et al., 2001a).

The biogeography module simulates mixtures of evergreen needleleaf, evergreen broadleaf, and deciduous broadleaf trees, and C3 and C4 grasses. The tree lifeform mixture is determined at each annual time-step as a function of annual minimum temperature and growing season precipitation. The C3/C4 grass mixture is determined by reference to their relative potential productivity during the three warmest consecutive months. The tree and grass lifeform mixtures together with growing degree-day sums and biomass simulated by the biogeochemistry module are used to determine which of twenty-two possible potential vegetation types occur at the grid cell each year. For this study, the twenty-two types were aggregated into twelve vegetation classes to simplify the presentation of results.

The biogeochemistry module is a modified version of the CENTURY model (Parton et al., 1994) which simulates plant growth, organic matter decomposition, and the movement of water and nutrients through the ecosystem. Plant growth is determined by empirical functions of temperature, moisture, and nutrient availability which decrement set values of maximum potential productivity. In this study, plant growth was assumed not to be limited by nutrient availability. The direct effect of an increase in atmospheric carbon dioxide (CO₂) is simulated using a beta factor (Friedlingstein et al., 1995) that increases maximum potential productivity and reduces the moisture constraint

on productivity. Grasses compete with woody plants for soil moisture and nutrients in the upper soil layers where both are rooted, while the deeper-rooted woody plants have sole access to resources in deeper layers. The growth of grass may be limited by reduced light levels in the shade cast by woody plants. The values of model parameters that control woody plant and grass growth are adjusted with shifts in the lifeform mixture determined annually by the biogeography module.

The MC1 fire module simulates the occurrence, behavior, and effects of fire. The module simulates the behavior of a simulated fire event in terms of the potential rate of fire spread, fireline intensity, and the transition from surface to crown fire (Rothermel, 1972; van Wagner, 1993; Cohen and Deeming, 1985). Several measurements of the fuel bed are required for simulating fire behavior, and they are estimated by the fire module using information provided by the other two MC1 modules. The current lifeform mixture is used by the fire module to select factors that allocate live and dead biomass into different classes of live and dead fuels. The moisture content of the two live fuel classes (grasses and leaves/twigs of woody plants) is estimated from moisture at different depths in the soil provided by the biogeochemical module. Dead fuel moisture content is estimated from climatic inputs to MC1 using different functions for each of four dead fuel size-classes (Cohen and Deeming, 1985).

Fire events are triggered in the model when the Palmer Drought Severity Index (PDSI), the moisture content of coarse woody fuels, and the flammability of fine fuels all meet set thresholds. Sources of ignition (e.g., lightning or anthropogenic) are assumed to be always available. Area burned is not simulated explicitly as fire spread within a given cell. Instead, the fraction of a cell burned by a fire event is estimated as a function of set minimum and maximum fire return intervals for the dynamically-simulated vegetation type, the current monthly value of PDSI, and the number of years since a simulated fire event.

Because the fire module was designed to simulate the natural fire regime, total area burned in the conterminous United States over the historical period is overpredicted in comparison to observed data, especially over the last half century when fire suppression was most effective. Unpublished comparisons to observed total annual area burned showed simulated area burned was, on average, about eight times greater than observed. Accordingly, to roughly estimate the effect of fire suppression in MC1 simulations, there is a provision within the module to dynamically limit annual area burned in each grid cell to 12.5% of the unconstrained value.

The fire effects simulated by the model include the consumption and mortality of dead and live vegetation carbon, which is removed from (or transferred to) the appropriate carbon pools in the biogeochemistry module. Live carbon mortality and consumption are simulated as a function of fireline intensity and the tree canopy structure (Peterson and Ryan, 1986), and dead biomass consumption is simulated using functions of fuel moisture that are fuel-class specific (Anderson et al., 2005).

2.2. Model inputs

The climate data used to generate the MC1 simulations for this study were monthly values for the input variables (i.e., precipitation, minimum and maximum temperature, and vapor pressure) distributed on a 0.5° resolution data grid for the conterminous United States. Climate data for the historical (1895–2003) and future period (2004–2100) were generated by the VINCERA (Vulnerability and Impacts of North American Forests to Climate Change: Ecosystem Response and Adaptation) project (Price, this issue). Two sets of three monthly future climate scenarios were generated at the 0.5° resolution from the output of three General Circulation Models (Canadian CGCM2, UK HADCM3, and Australian CSIRO Mk2) forced by two different greenhouse gas (GHG) emission scenarios (IPCC SRES A2 and B2).

2.3. Experimental design and analysis

The modeling experiment was designed to investigate the effect of fire suppression, the direct CO₂ response, and the CO₂ emission rate on the simulated response to a set of three GCM climate scenarios. Model simulations were generated for two levels of fire suppression (i.e., no fire suppression and fire suppression after 1950 at the historical level), relatively high and low levels of CO₂ response, and relatively high and low levels of CO₂ emission (i.e., A2 and B2 emission scenarios, respectively). The high level CO₂ response treatment was applied by adjusting a beta factor in MC1 to generate an average response near the 23% NPP increase observed in young FACE stands. The lower level CO₂ response was produced using default beta value for MC1 which generated about an 8% average increase in NPP at 550 ppm CO₂.

Three factors with two treatment levels each yielded eight (i.e., 3²) different treatment combinations (e.g., no fire suppression combined with a high response to CO₂ combined with a high level of emissions). The model was run for each treatment combination and for each of three GCM climate scenarios forced by the high or low emission rate to yield twenty-four different simulations. To focus on the response to the three factors, and to reduce the dimensionality of the analysis, the model runs for the three different GCM scenarios were treated as ensemble members, and the results for each treatment combination were calculated as the ensemble mean or mode. Total ecosystem carbon and vegetation type distribution were the simulated response variables examined for this study.

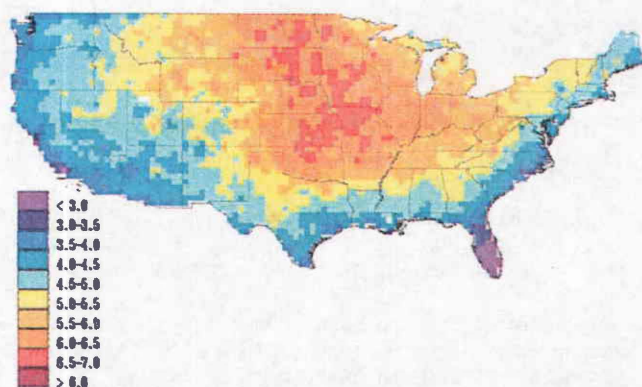
3. Results

3.1. Climate

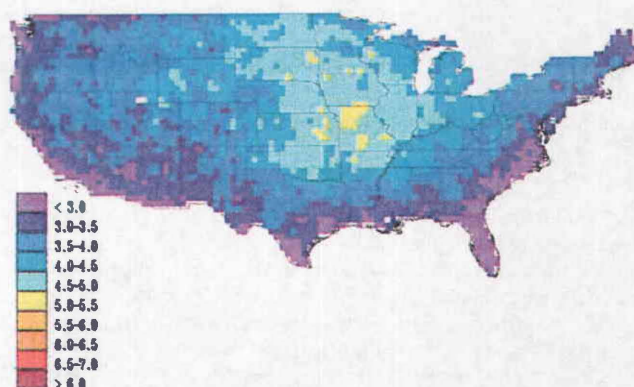
Projected increases in the mean monthly minimum and maximum temperature under the different future climate scenarios were calculated as differences in degrees between the mean for the historical period (1971–2000) and the future period (2070–2099). Changes in annual total precipitation and mean monthly relative humidity were calculated as percentage differences for the future period relative to the historical period. These differences were then averaged across the three GCM scenarios by emission scenario to produce the map pairs for each variable shown in Figs. 1–2. The electronic supplement to this paper includes all twenty-four maps showing changes in the four climatic variables by three GCMS by two emission scenarios.

Projected increases in mean monthly maximum and minimum temperatures across the U.S. (Fig. 1) were substantially higher with the stronger forcing of the A2 emission scenario. Increases in maximum temperature under the A2 scenario (Fig. 1A) ranged from about 4 to 7 °C, with the largest increases in the Central Plains and inland portions of the East and Southeast. Increases in minimum temperature under the A2 scenario (Fig. 1C) were generally lower than those for maximum temperature, ranging from about 3.5 to 6.5 °C, with the largest increases more confined to the northern half of the Central Plains, but with greater extent in the Southwest and Northeast. Under the weaker forcing of the B2 emission scenario, increases in maximum

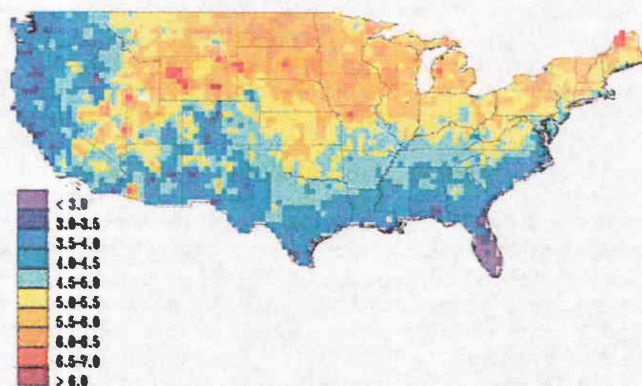
A. TMAX-A



B. TMAX-B



C. TMIN-A



D. TMIN-B

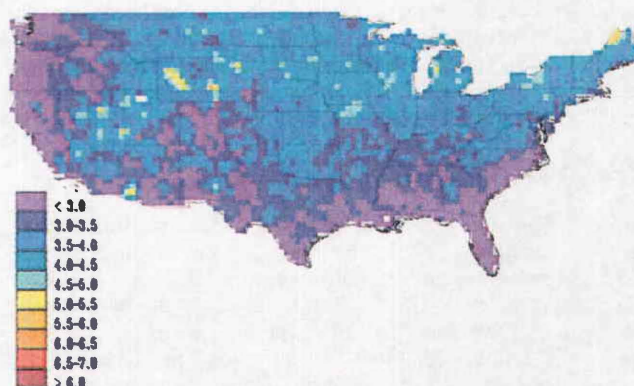
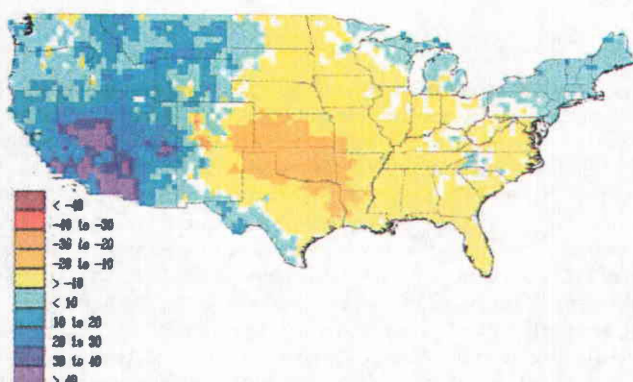
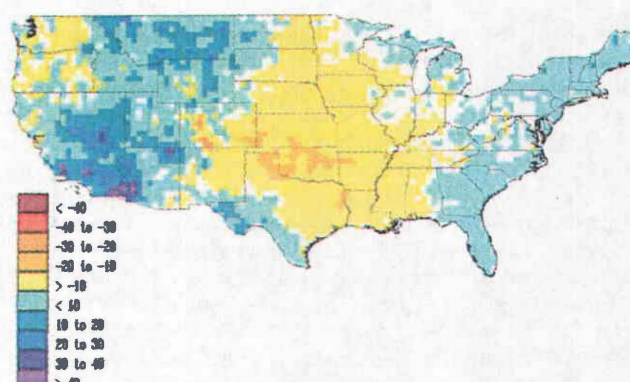


Fig. 1. Delta (°C) for 2070–2099 period (relative to 1971–2000 period) averaged across three GCMs. TMAX: Average monthly maximum temperature. TMIN: Average monthly minimum temperature. A: SRES-A2, B: SRES-B2.

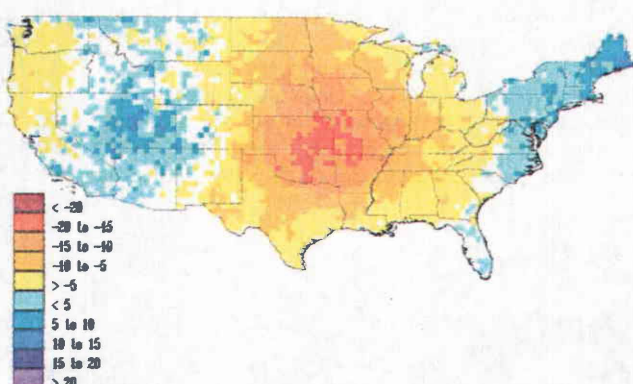
A. PPT-A



B. PPT-B



C. RH-A



D. RH-B

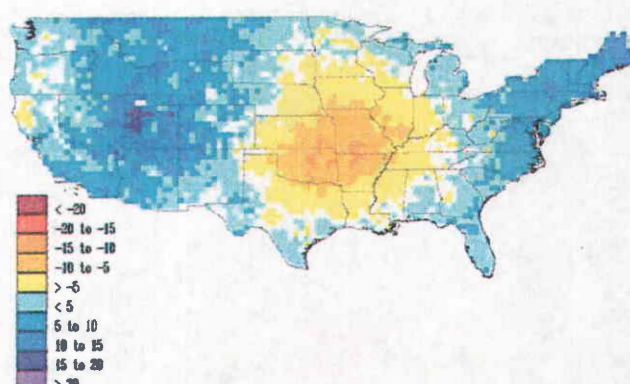


Fig. 2. Delta (%) for 2070–2099 period (relative to 1971–2000 period) averaged across three GCMs. PPT: Total annual precipitation. RH: Average monthly minimum relative humidity. A: SRES-A2, B: SRES-B2.

and minimum temperature were generally about 0.5 to 1.0 °C less than under the A2 scenario (Fig. 1B,D).

There was a widespread increase in mean annual total precipitation west of the Rocky Mountains, in sharp contrast to the general decrease throughout much of the East, especially under the A2 scenario (Fig. 2A). Under the B2 scenario, drying was less extensive east of the Rockies, but more extensive in the Pacific Northwest (Fig. 2B). Mean monthly minimum relative humidity declined throughout much of the U.S. under the A2 scenario (Fig. 2C), especially in the Central Plains where the decrease was partly a function of increased maximum temperatures (Fig. 1A). Regions that showed relatively slight increases in relative humidity under the A2 scenario (i.e., the Southwest and the Eastern seaboard), showed larger and more extensive increases under the B2 scenario (Fig. 2D). Decreases in relative humidity persisted in the Central Plains under the B2 scenario, but were smaller and less extensive than under the A2 scenario.

3.2. Vegetation class distribution

The response of vegetation class distribution to the different treatment combinations was determined by comparing the distribution of the most frequent vegetation type simulated for the 30-year historical period (1961–1990) against the same for the last 30 years (2071–2100) of the future scenarios. The most frequent vegetation type at each cell was determined from the combined results for all three members of the climate scenario ensemble. There were only very slight differences in vegetation class distribution due to CO₂ response level, so only the results for the high CO₂ response are presented

(Figs. 3–4). The electronic supplement to this paper includes all twelve maps showing the distribution of vegetation classes under each of the three GCM scenarios by two fire suppression levels and by two emission scenarios.

The simulated vegetation type distribution for the historical period under the no fire suppression treatment (Fig. 3A) was generally accurate when compared to canonical maps of potential natural vegetation distribution for the conterminous U.S. (e.g., Küchler, 1975; Bailey et al. 1994). Exceptions included portions of the Midwest generally portrayed as grassland or woodland/savanna, but simulated as forest by MC1, and in the Southwest where forest was under represented in the simulation for the historical period.

The most prominent change in vegetation distribution under the future climate with unsuppressed fire (Figs. 3B,C and 5) was the widespread expansion of woodland/savanna both in the Southeast, where it replaced forest, and in the interior West, where it replaced shrubland. Other notable features were a near complete loss of alpine and subalpine forest vegetation to temperate forest types, a northward shift of forest-type boundaries in the East, and a consequent reduction in the extent of cool mixed forest in the Northeast. There were only subtle differences in the simulated future vegetation type distributions due to the CO₂ emission level (Fig. 3B vs. C, Fig. 5).

The role of unsuppressed fire in shaping the simulated historical and future vegetation type distributions was evident in contrast to the results for suppressed fire (Fig. 3 vs. Fig. 4). The results for the historical period (Fig. 4A) showed more woodland and forest in the West, and more shrubland and woodland in the Central grasslands with suppressed fire. Differences due to fire treatment were even more evident

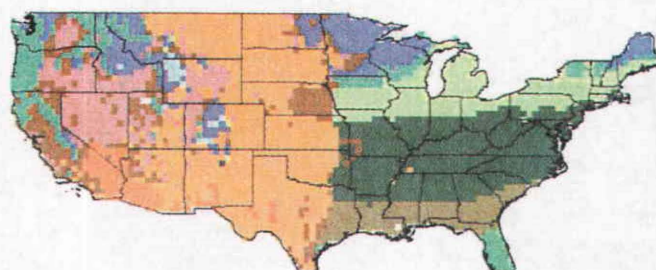
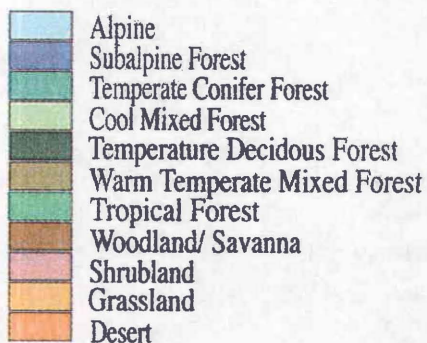
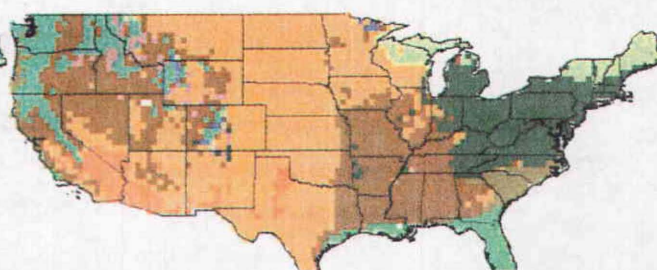
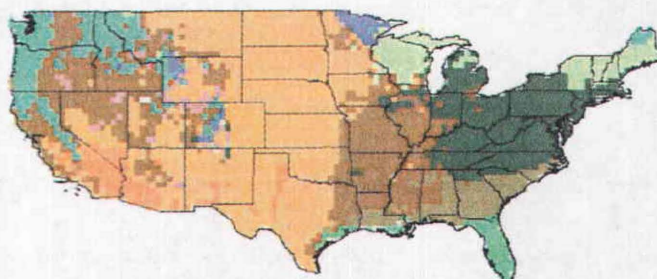
A. USF-HIST**B. USF-A****C. USF-B**

Fig. 3. Model simulated vegetation type with unsuppressed fire (USF) for 1971–2000 historical period and 2070–2099 future period. A: SRES-A2, B: SRES-B2.

in the results for the future climate period (Fig. 4B,C). The Southeast remained forest with suppressed fire, in striking contrast to the extensive conversion of forest to woodland without suppression. In

the West, there was widespread conversion of shrubland to woodland and woodland to forest with suppressed fire. The woody encroachment also extended into the Central Plains where grassland and

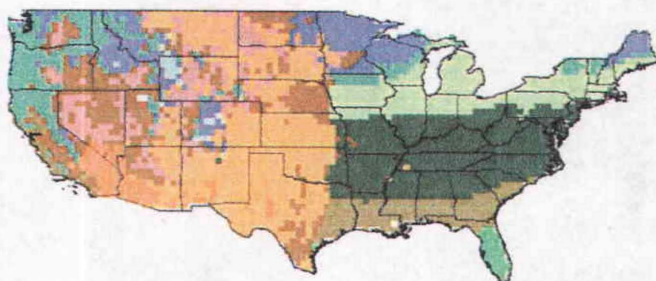
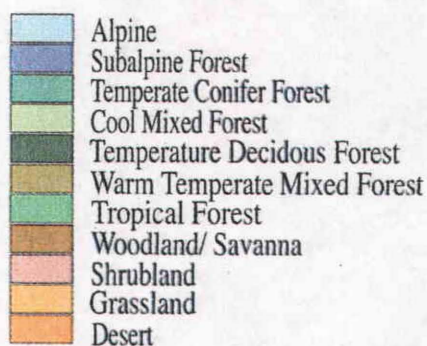
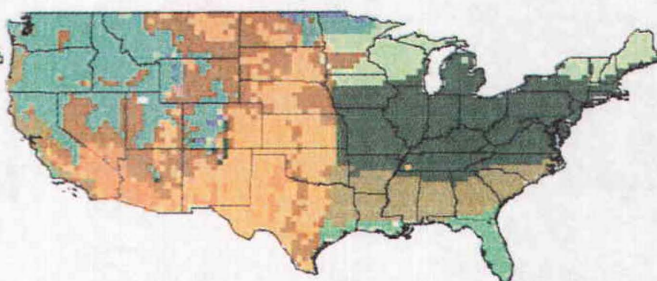
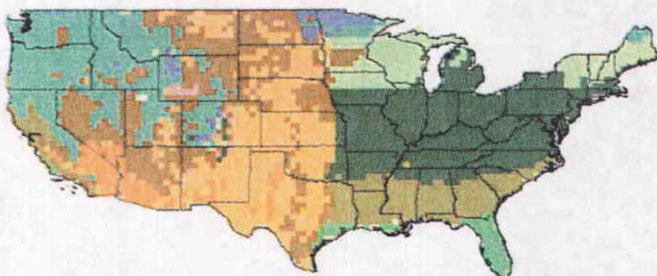
A. SF-HIST**B. SF-A****C. SF-B**

Fig. 4. Model simulated vegetation type with suppressed fire (SF) for 1971–2000 historical period and 2070–2099 future period. A: SRES-A2, B: SRES-B2.

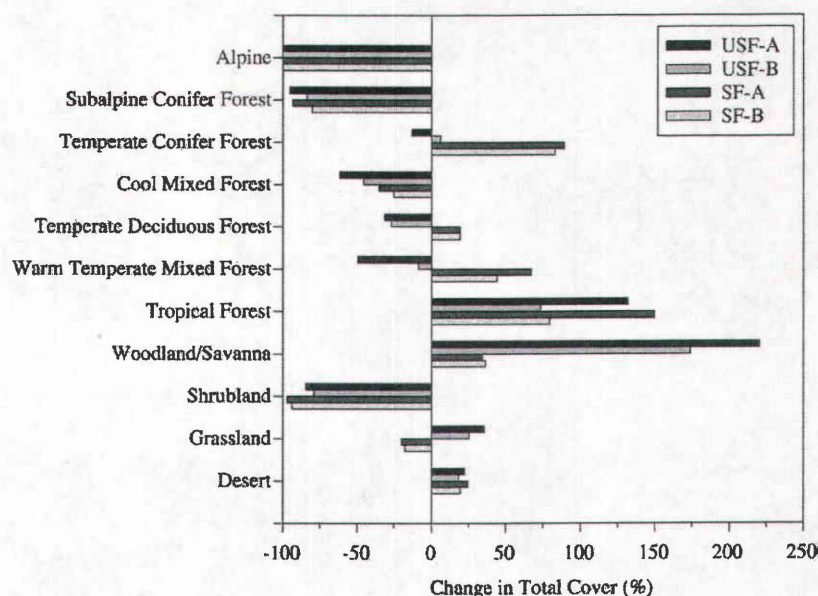


Fig. 5. Change in vegetation type cover (%) for 2070–2099 period (relative to 1971–2000 period). USF: Unsuppressed fire. SF: Suppressed fire. A: SRES-A2, B: SRES-B2.

shrubland converted to woodland. As in the results for unsuppressed fire, there were only subtle differences in the simulated future vegetation type distributions due to the CO₂ emission level (Fig. 4B vs. C, Fig. 5).

3.3. Total ecosystem carbon

The future response of total ecosystem carbon to each treatment combination was first determined by calculating the percent

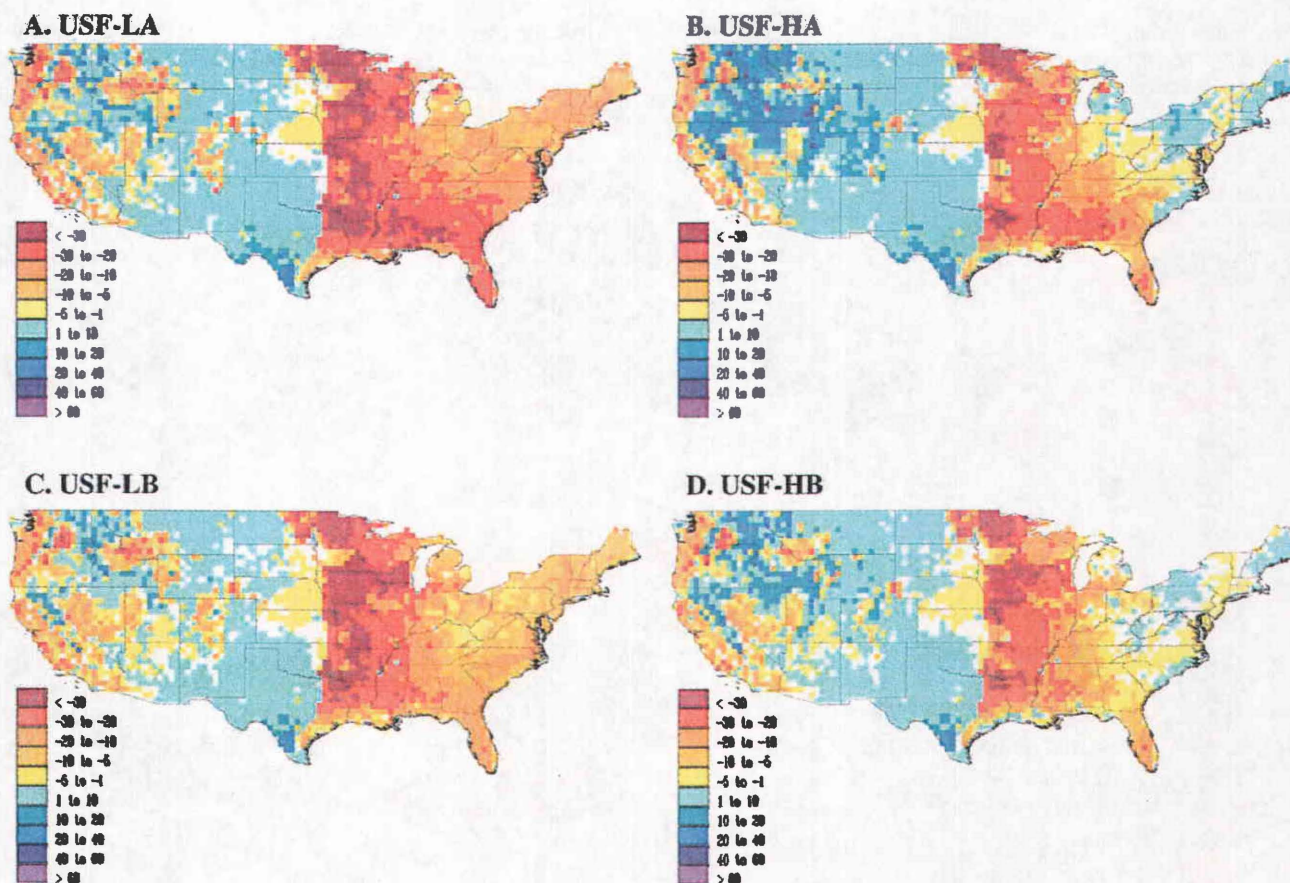
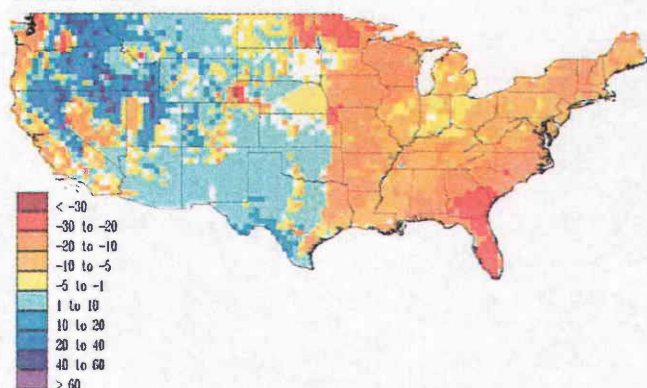
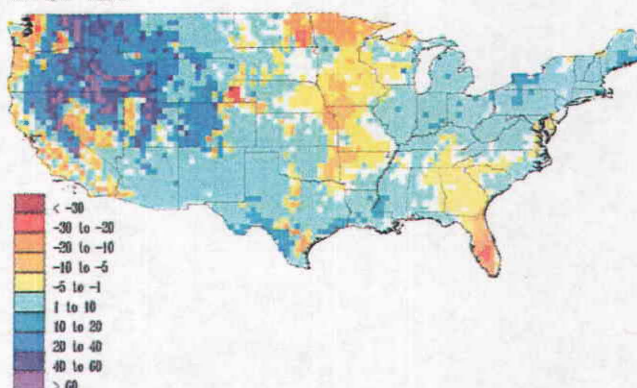


Fig. 6. Delta total ecosystem carbon (kg/m²) for 2070–2099 period (relative to 1971–2000 period) for unsuppressed fire (USF). L: Low CO₂ response, H: high CO₂ response. A: SRES-A2, B: SRES-B2.

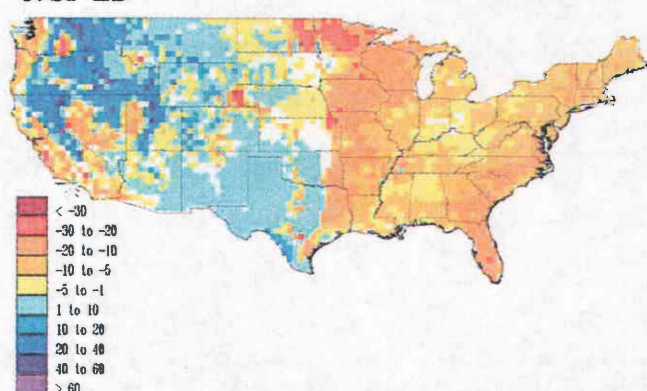
A. SF-LA



B. SF-HA



C. SF-LB



D. SF-HB

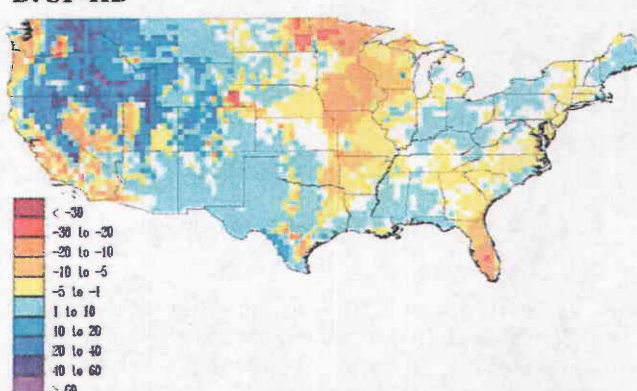


Fig. 7. Delta total ecosystem carbon (kg/m^2) for 2070–2099 period (relative to 1971–2000 period) for suppressed fire (SF). L: Low CO_2 response, H: high CO_2 response. A: SRES-A2, B: SRES-B2.

difference for the mean of the annual values simulated for the 2070–2099 period of each GCM future climate scenario relative to the mean for the historical period (1971–2000). The results were then averaged across the three members of the scenario ensemble for each treatment combination. The electronic supplement to this paper includes all twenty-four maps showing changes in total ecosystem carbon under each of the three GCM scenarios and by each of the eight treatment combinations.

As in the results for vegetation type, the unsuppressed vs. suppressed fire treatment had a significant effect on the response of total carbon to future climate (Fig. 6 vs. Fig. 7). But unlike vegetation type, total carbon was also responsive to the CO_2 effect and emission treatments, and to their interactions. Carbon loss underlying the simulated conversion of forest to woodland in the Southeast was most pronounced in response to unsuppressed fire, especially in combination with the low CO_2 effect and the high A2 CO_2 emission rate (Fig. 6A). There was considerably less carbon loss in the Southeast with suppressed fire, but significant and widespread losses were still evident in conjunction with the low CO_2 response (Fig. 7A,C). Increases

in carbon underlying the simulated conversion of shrubland to woodland in the West were most pronounced with suppressed fire, especially in combination with the high CO_2 response and high A2 emission rate (Fig. 7B).

The simulated trends in total ecosystem carbon were analyzed separately for the western and eastern halves of the U.S. (dividing line along the eastern border of Colorado) to further emphasize the contrasting response of the two regions to the future climate and treatment combinations (Tables 1–2, Figs. 8–9). In the western region, there was a 5.3% increase in the total carbon pool averaged across all treatments (Table 1). With unsuppressed fire, carbon gain in the West was negligible (0.4%) when averaged across a 3.5% loss and 4.3% gain under the low and high CO_2 responses, respectively. Carbon gain with unsuppressed fire and the high CO_2 response was significantly greater in conjunction with the high A2 CO_2 emission rate (Fig. 8A). With suppressed fire, carbon gains under all treatments averaged 10.3% (Table 1), with the greatest gains simulated in response to the high CO_2 effect, especially in combination with the high A2 emission rate (Fig. 8B).

Table 1

Simulated percentage change in historical total ecosystem carbon at the end of the future period by fire suppression and CO_2 response level for the western United States

Western United States		Fire suppression		Mean
		Yes	No	
CO_2 response	High	15.1	4.3	9.7
	Low	5.4	−3.5	1.0
Mean		10.3	0.4	5.3

Table 2

Simulated percentage change in historical total ecosystem carbon at the end of the future period by fire suppression and CO_2 response level for the eastern United States

Eastern United States		Fire suppression		Mean
		Yes	No	
CO_2 response	High	−0.9	−10.1	−5.5
	Low	−12.6	−18.7	−15.7
Mean		−6.8	−14.4	−10.6

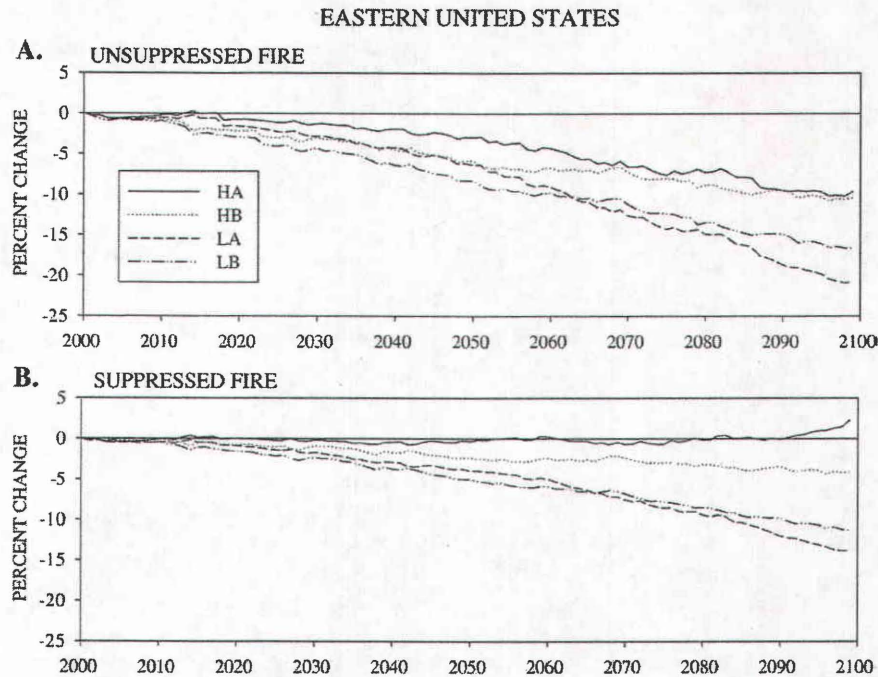


Fig. 8. Trend in future total ecosystem carbon (Pg) for the eastern United States for A and B. L: Low CO₂ response, H: high CO₂ response. A: SRES-A2, B: SRES-B2.

In the eastern United States, there was a 10.6% loss of total carbon averaged across all treatments (Table 2). Average losses were greatest with unsuppressed fire and the low CO₂ response, which together produced an average 18.7% decrease in the total carbon pool. Suppressed fire and the high CO₂ response reduced average carbon losses in the East to near zero (−0.9%), and even produced a slight carbon sink by the end of the century in conjunction with the high A2 emission rate (Fig. 8B).

4. Discussion

There were distinct regional trends in ecosystem response to projected climatic change that were evident across all treatment combinations. While there was some variation in the projected changes in temperature and precipitation among the three GCM scenarios, relatively large increases in temperature and decreases in precipitation were the general climatic trends in the eastern half of the

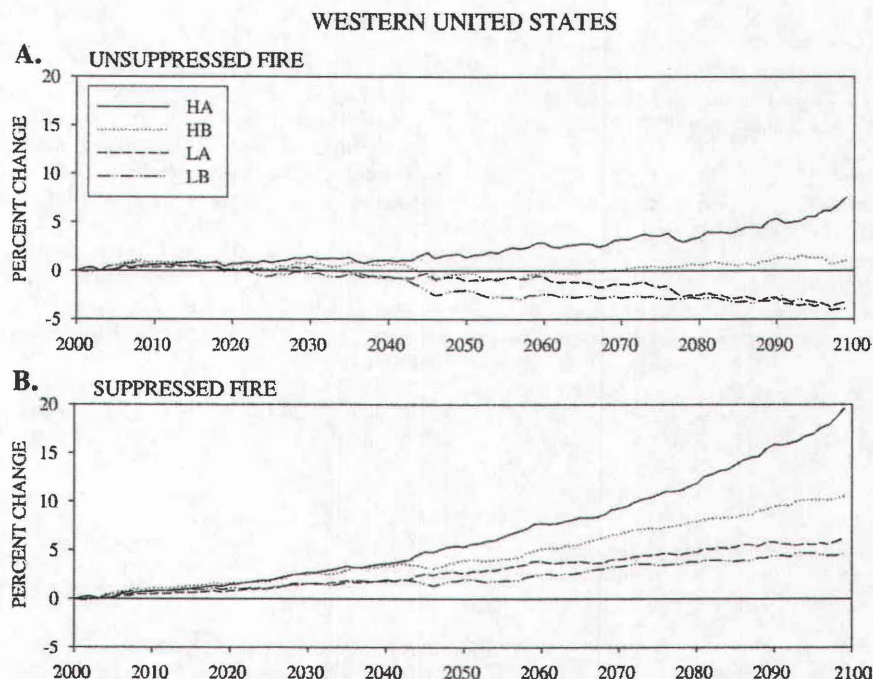


Fig. 9. Trend in future total ecosystem carbon (Pg) for the western United States for A and B. L: Low CO₂ response, H: high CO₂ response. A: SRES-A2, B: SRES-B2.

U.S. The simulated ecosystem response to this increase in water demand relative to supply was an 11% loss of total ecosystem carbon averaged across all treatments. In contrast to the East, increases in precipitation accompanied by relatively small increases in temperature were the general projections for the West, and here the ecosystem respond to increases in effective moisture with a 5% average increase in total carbon storage.

The model treatments had significant effects on the simulated future trends in total ecosystem carbon in both the eastern and western U.S., especially fire suppression. Average carbon losses in the East were reduced by half (from 14% to 7%) and average carbon gains in the West went from nearly zero to 10% with simulated fire suppression. Spatial variation in suppression level was not represented in the simulations, and the historical level of suppression imposed everywhere on the model was assumed to be constant for the length of the future period. More realistically, future levels of fire suppression in the U.S. will be responsive in both space and time to not only to shifts in fire weather and fuels, but also perhaps even more importantly, to trade-offs among different land management goals. Assuming “healthy” ecosystems are comprised of vegetation adjusted to its climatic environment and natural disturbance regime, then the results suggest woodland and savannas will comprise the future healthy ecosystems in the eastern U.S. However, results also indicate the transition from forest to woodland and savanna would be accompanied by increases in fire disturbance. Resisting this changing fire regime with an enhanced level of fire suppression might be more consistent with future goals of fire protection and carbon management.

Across the west, unsuppressed fire maintained a near net zero change in total carbon stocks despite climate-driven increases in vegetation productivity, but there were regions where both increases and decreases in carbon were sufficient to trigger simulated changes in vegetation type, especially in the Great Basin Region where shrubland was lost to both woodland in the north and grassland in the south. These regional-scale adjustments of vegetation to changes in climate and fire disturbance were overwhelmed by a sustained historical level of fire suppression, such that the woody densification observed in recent decades over much of the interior west continued into the future, and existing shrublands were converted to woodland or even forest. The results indicate that projected climate change in conjunction with historical levels of fire suppression could offer significant opportunity for carbon sequestration in western forests and rangelands, but perhaps only at the expense of a “healthier” adjustment of vegetation to the changed climate and disturbance regime. Levels of fire suppression sufficient to protect sequestered carbon in the west would also be increasing difficult to maintain if accumulating biomass fueled increasingly intense fire events.

The CO₂-related treatments and their interaction also had a significant impact on the simulated ecosystem response, especially the direct CO₂ response. With the high CO₂ response, simulated total ecosystem carbon pools at the end of the century were on average about 9–10% larger in the conterminous United States compared to results for the low response. The western U.S. gained enough carbon to counter losses from unsuppressed fire only with the high CO₂ response, especially in conjunction with the higher A2 emission rate. In the eastern U.S., fire suppression was sufficient to produce a simulated carbon sink only with the interacting high CO₂ response and emission rate.

The results show that an increase in ecosystem productivity and carbon storage in direct response to increased atmospheric CO₂ could mitigate climate-driven losses of carbon in the eastern U.S., while also promoting carbon sequestration in the West. However, the capacity of vegetation to respond at the level of increased productivity and carbon gain simulated in this study is uncertain. Results from four FACE experiments in young forest stands have shown an average 23% increase in forest NPP for CO₂ concentrations of 550 ppm as compared to ambient concentrations (Norby et al., 2005). The high CO₂ response

in our modeling experiment produced a similar increase in MC1-simulated NPP, and is the response level normally simulated by several other DGVMs (Ian Woodward, personal communication). Data from a larger set of FACE experiments (Nowak et al., 2004) show a less than 20% increase in NPP on average, and indicate using a single beta factor for global predictive purposes is unrealistic given observed differences in the growth response among species, during stand development, and at different levels of moisture and nutrient availability.

NPP controls the amount of carbon entering an ecosystem, but the fate of that carbon is more germane to the potential for carbon sequestration or loss. There is some evidence for the allocation of CO₂-enhanced NPP to woody tissues in certain species of young trees (e.g., DeLucia et al., 2005), thus promoting carbon storage and more rapid maturation of individuals and stand structure. But in other species of young trees (DeLucia et al., 2005; Norby et al., 2005) and in mature forest stands (Ashoff et al., 2006; Körner et al., 2005), the CO₂-induced increase in NPP is allocated to fine roots which decompose rapidly, adding carbon to the soil which is rapidly respired by microbes. Körner et al. (2005) described this response as a carbon “pump” producing little or no carbon storage. The allocation of NPP to different plant tissues simulated by MC1 varied by tree lifeform and stand age, but not in response to atmospheric CO₂ concentration. Thus increases in carbon storage with CO₂-enhanced NPP may be overestimated in this study, even for the low CO₂ response treatment.

Considerable uncertainty exists with respect to the impacts of global warming on the ecosystems of the conterminous U.S. Some of this uncertainty resides in the future trajectory of greenhouse gas emissions, in the direct response of vegetation to increasing CO₂, and in future tradeoffs among different fire and land management options, as illustrated in this study. In addition, ecosystem models and their response to projected climate change can always be improved through testing and enhancement of model processes. Dynamic General Vegetation Models are an especially new technology still undergoing rapid development to improve existing algorithms and introduce new ones. Currently, DGVMs fail to account for lags in species migration, pests and pathogens, non-native invasive plant species, spatio-temporal variation in fire ignition and fire suppression, activities such as logging, grazing, agriculture, and urbanization, and other potentially important factors. It is unclear how climate change will impact these factors and their interaction with natural ecosystems, but in some cases, the effects could result in vegetation responses not predicted by extant DGVMs. Unrepresented or poorly understood processes and the uncertain fate of policy-driven factors preclude the use of these simulations as unflinching predictions of the future. Nevertheless, the results of this and previous studies underscore the potentially large impacts of climate change on U.S. ecosystems.

5. Conclusions

Averages across three different GCM climate scenarios showed contrasting projections for temperature and especially precipitation in the western and eastern United States. The averaged results of the MC1 simulations showed eastern U.S. ecosystems as a carbon source and western ecosystems as a carbon sink in response to projected changes in effective moisture. Trends in carbon storage and vegetation distribution were sensitive to the different levels of fire suppression and CO₂ response in both regions of the United States. Carbon and forest losses were much reduced by fire suppression in the East, and fire suppression in conjunction with high levels of CO₂ response and emission were even sufficient to produce a slight carbon sink despite declines in effective moisture. Gains in carbon with increases in effective moisture were largely consumed by unsuppressed fire in the West, and the region was even a slight carbon source with unsuppressed fire and the low level CO₂ treatments. With fire suppression, recently observed woody encroachment in semi-arid regions of the West continues into

the future, especially under the high level CO₂ treatments. The results of the modeling experiment demonstrate there are significant uncertainties regarding the future response of U.S. ecosystems to climatic change apart from those posed by a growing number of plausible GCM climatic scenarios.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.gloplacha.2008.01.006.

References

- Allen, C.D., Savage, M., Falk, D.A., Suckling, K.F., Swetnam, T.W., Schulke, T., Stacey, P.B., Morgan, P., Hoffman, M., Klingel, J.T., 2002. Ecological restoration of southwestern ponderosa pine ecosystems: a broad perspective. *Ecol. Appl.* 12, 1418–1433.
- Anderson, G.K., Ottmar, R.D., Prichard, S.J., 2005. CONSUME 3.0 User's Guide. Pacific Wildland Fire Sciences Laboratory. USDA Forest Service Pacific Northwest Research Station, Seattle, WA. 183 pp.
- Ashoff, R., Zotz, G., Körner, C., 2006. Growth and phenology of mature temperate forest trees in elevated CO₂. *Glob. Chang. Biol.* 12, 848–861.
- Bachelet, D., Lenihan, J.M., Daly, C., Neilson, R.P., 2000. Simulated fire, grazing and climate change impacts at Wind Cave National Park, SD. *Ecol. Model.* 134 (2–3), 229–244.
- Bachelet, D., Lenihan, J.M., Daly, C., Neilson, R.P., Ojima, D.S., and Parton, W.J., 2001a. MC, a Dynamic Vegetation Model for estimating the distribution of vegetation and associated carbon and nutrient fluxes, Technical Documentation Version 1.0, USDA Forest Service Pacific Northwest Station, General Technical Report PNW-GTR-508. 95 pp.
- Bachelet, D., Neilson, R.P., Lenihan, J.M., Drapek, R.J., 2001b. Climate change effects on vegetation distribution and carbon budget in the U.S. *Ecosystems* 4, 164–185.
- Bachelet, D., Neilson, R.P., Hickler, T., Drapek, R.J., Lenihan, J.M., Sykes, M.T., Smith, B., Sitch, S., Thonicke, K., 2003. Simulating past and future dynamics of natural ecosystems in the United States. *Glob. Biogeochem. Cycles* 17 (2), 1045–1054.
- Bachelet, D., Neilson, R.P., Lenihan, J.M., Drapek, R.J., 2004. Regional differences in the carbon source-sink potential of natural vegetation in the U.S. *Environ. Manag.* 33 (Supp.#1), S23–S43.
- Bachelet, D., Lenihan, J.M., Neilson, R.P., Drapek, R.J., Kittel, T., 2005. Simulating the response of natural ecosystems and their fire regimes to climatic variability in Alaska. *Can. J. For. Res.* 35, 2244–2257.
- Bailey, R.G., Avers, P.E., King, T., McNab, W.H., eds. 1994. Ecoregions and Subregions of the United States (Map). Washington, DC: USDA Forest Service. 1:7,500,000. With Supplementary Table of Map Unit Descriptions, Compiled and Edited by W. H. McNab and R. G. Bailey.
- Boisvenue, C., Running, S.W., 2006. Impacts of climate change on natural forest productivity – evidence since the middle of the 20th century. *Glob. Biogeochem. Cycles* 12, 862–882.
- Bond, W.J., 2005. Large parts of the world are black or brown: a different view on the "Green World" hypothesis. *J. Veg. Sci.* 16, 261–266.
- Bond, W.J., Woodward, F.I., Midgley, G.F., 2005. The global distribution of ecosystems in a world without fire. *New Phytol.* 165, 525–538.
- Clark, J.S., 1990. Fire and climate change during the last 750 years in northwestern Minnesota. *Ecol. Monogr.* 60, 135–159.
- Cohen, J.D., Deeming, J.E., 1985. The National Fire Danger Rating System: Basic Equations. USDA Forest Service Pacific Southwest Forest and Range Experimental Station General Technical Report PSW-82. 16 pp.
- Covington, W.W., Moore, M.M., 1994. Southwestern ponderosa forest structure: changes since Euro-American settlement. *J. For.* 92, 39–47.
- Daly, C., Bachelet, D., Lenihan, J., Neilson, R., Parton, W., Ojima, D., 2000. Dynamic simulation of tree-grass interactions for global change studies. *Ecol. Appl.* 10, 449–469.
- DeLucia, E.H., Moore, D.J., Norby, R.J., 2005. Contrasting responses of forest ecosystems to rising atmospheric CO₂: implications for the global C cycle. *Glob. Biogeochem. Cycles* 19, GB3006.
- Friedlingstein, P., Fung, I., Holland, E., John, J., Brasseur, G., Erickson, D., Schimel, D., 1995. On the contribution of CO₂ fertilization to the missing biospheric sink. *Glob. Biogeochem. Cycles* 9, 541–556.
- Green, D.G., 1982. Fire and stability in the postglacial forests of Nova Scotia. *Journal of Biogeography* 9, 29–40.
- Hayhoe, K., Cayan, D., Field, C., Frumhoff, P., Maurer, E., Miller, N., Moser, S., Schneider, S., Cahill, K., Cleland, E., Dale, L., Drapek, R., Hanemann, R., Kalkstein, L., Lenihan, J., Lunch, C., Neilson, R., Sheridan, S., Verville, J., 2005. Emission pathways, climate change, and impacts on California. *Proc. Natl. Acad. Sci.* 101, 12422–12427.
- Keely, J.E., Rundel, P.W., 2005. Fire and the Miocene expansion of C₄ grasslands. *Ecol. Lett.* 8, 683–690.
- Körner, C., Ashoff, R., Bignucolo, O., Hättenschwiler, S., Keel, S.G., Peláez-Riedl, S., Pepin, S., Siegwolf, R.T.W., Zotz, G., 2005. Carbon flux and growth in mature deciduous forest trees exposed to elevated CO₂. *Science* 309, 1360–1362.
- Küchler, A., 1975. Potential natural vegetation of the United States. 2nd ed. Map 1:3,168,000. American Geographic Society, New York.
- Lenihan, J.M., Drapek, R.J., Bachelet, D., Neilson, R.P., 2003. Climate changes effects on vegetation distribution, carbon, and fire in California. *Ecol. Appl.* 13 (6), 1667–1681.
- Lenihan, J.M., Bachelet, D., Drapek, R., Neilson, R.P., 2006. The response of vegetation distribution, ecosystem productivity, and fire in California to future climate scenarios simulated by the MC1 Dynamic Vegetation Model. California Climate Change Center Report CEC-500-2005-191-SF. 19 pp.
- Lenihan, J., Drapek, R., and Neilson R., in press. Impacts on vegetation distribution, fire, and carbon. Chapter in: J. Smith and R. Mendelson (eds.), Making Regional Assessments of Climate Change: A Comprehensive Analysis of California. Edward Elgar Publications. Northampton, MA.
- Norby, R.J., DeLucia, E.H., Gielen, B., Calfapietra, C., Giardina, C.P., King, J.S., Ledford, J., McCarthy, H.R., Moore, D.J.P., Ceulemans, R., De Angelis, P., Finzi, A.C., Karnosky, D.F., Kubske, M.E., Lukac, M., Pregitzer, K.S., Scarascia-Mugnozza, G.E., Schlesinger, W.H., Oren, R., 2005. Forest response to elevated CO₂ is conserved across a broad range of productivity. *Proc. Natl. Acad. Sci.* 102, 18052–18056.
- Nowak, R.S., Ellsworth, D.S., Smith, S.D., 2004. Functional responses of plants to elevated atmospheric CO₂ – do photosynthetic and productivity data from FACE experiments support early predictions? *New Phytol.* 162, 253–280.
- Overpeck, J.T., Rind, D., Goldberg, R., 1990. Climate-induced changes in forest disturbance and vegetation. *Nature* 343, 51–53.
- Parton, W., Schimel, D., Ojima, D., Cole, C., 1994. A general study model for soil organic carbon dynamics, sensitivity to litter chemistry, texture, and management. *Soil Sci. Soc. Am. Special Publication* 39, 147–167.
- Peterson, D., Ryan, K., 1986. Modeling postfire conifer mortality for long-range planning. *Environ. Manage.* 10, 797–808.
- Rothermel, R., 1972. A Mathematical Model for Fire Spread Predictions in Wildland Fuels. USDA Forest Service Research Paper INT-115. 40 pp.
- Schoennagel, T., Veblen, T.T., Romme, W.H., 2004. The interaction of fire, fuels, and climate across Rocky Mountain forests. *Bioscience* 54, 661–676.
- Sitch, S., Smith, B., Prentice, I.C., Arneth, A., Bondeau, A., Cramer, W., Kaplan, J., Levis, S., Lucht, W., Sykes, M., Thonicke, K., Venevski, S., 2003. Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ Dynamic Vegetation Model. *Glob. Chang. Biol.* 9, 161–185.
- Swetnam, T.W., Betancourt, J.L., 1998. Mesoscale disturbance and ecological response to decadal climatic variability in the American Southwest. *J. Climate* 11, 3128–3147.
- van Wagner, C.E., 1993. Prediction of crown fire behavior in two stands of jack pine. *Can. J. For. Res.* 23, 442–449.
- Whitlock, C., Shafer, S., Marlon, J., 2003. The role of climate and vegetation change in shaping past and future fire regimes in the northwestern US and the implications for ecosystem management. *For. Ecol. Manag.* 178, 5–21.
- Westerling, A.L., Swetnam, T.W., 2003. Interannual to decadal drought and wildfire in the western United States. *EOS* 84, 545–560.
- Westerling, A.L., Hidalgo, H.G., Cayan, D.R., Swetnam, T.W., 2006. Warming and earlier spring increases western U.S. forest wildfire activity. *Science* 0: 1128834.