Forest Processes and Global Environmental Change: Predicting the Effects of Individual and Multiple Stressors

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WE REVIEW THE EFFECTS OF SEVERAL RAPIDLY CHANGING ENVIRONMENTAL DRIVERS ON ECOSYSTEM FUNCTION, DISCUSS INTERACTIONS AMONG THEM, AND SUMMARIZE PREDICTED CHANGES IN PRODUCTIVITY, CARBON STORAGE, AND WATER BALANCE

Global change involves the simultaneous and rapid alteration of several key environmental parameters that control the dynamics of forests. We cannot predict with certainty, through direct experimentation, what the responses of forests to global change will be, because we cannot carry out the multisite, multifactorial experiments required for doing so. The physical extent, complexity, and expense of even single-factor experiments at the scale of the whole ecosystem challenge our abilities, although several such experiments have been successfully undertaken (e.g., DeLucia et al. 1999, Wright and Rasmussen 1998). To inform policy decisions, however, the scientific community can offer an interdisciplinary synthesis of existing information. When this synthesis takes the form of a computer model, quantitative predictions can be made that integrate what has been learned from single-factor experiments. The success of such an approach depends on the quality and completeness of the information base and on the rigor of the modeling effort.

The direct and secondary physiological effects of changes in the physical and chemical climate on plants and soils are relatively well known. We also know which primary environmental drivers—precipitation, temperature, and atmospheric concentrations of carbon dioxide (CO_2), ozone (O_3), and nitrogen (N), for example—are being altered by human activities, and we can directly measure temporal change in these parameters. Despite this relatively rich information base, predictions of future responses of forests to environmental change show significant variation. This is due in part to differences between the models of ecosystem function derived from the existing database and in part to differences in climate scenarios generated by the general circulation models (GCMs) used to predict future climates. Understanding both the trend in predicted futures and the uncertainties surrounding those trends is critical to policy formation. At this time, the major mechanism for determining the degree of uncertainty in predictions is through comparison of results from runs of different models using identical input parameters.

The purpose of this article is to review the state of prediction of forest ecosystem response to envisioned changes in the physical and chemical climate. These results are offered as one part of the forest sector analysis of the National Assessment

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of the Potential Consequences of Climate Variability and Change; other contributions to this assessment appear in this edition of *BioScience*. This article has three sections. The first offers a very brief review of the literature on the effects of environmental factors on forest ecosystem function (some references are also made to changes in species composition, but Hansen et al. [2001] provide a more complete discussion). The second and largest part of the article is a summary of results from the Vegetation/Ecosystem Modeling and Analysis Project (VEMAP), an integrated effort to predict ecosystem response to climate change. The third is a brief review of other regional modeling efforts that have addressed climate change or have looked at the possible effects of other components of global change, using tropospheric ozone and nitrogen deposition as examples, or both.

Field and laboratory evidence for direct physiological effects

All of the direct effects discussed in this article interact by affecting the cycling of carbon, water, and nitrogen between plants and soils (Figure 1). These interactions are discussed briefly at the end of this section.

Carbon dioxide. Experimental tree exposure studies have shown significant changes in physiological processes, phenology, and growth under elevated CO_2. The most consistent effect is an increase in the rate of carboxylation by the photosynthetic enzyme system and a reduction in photorespiration (Long et al. 1996), leading to increased rates of net photosynthesis and tree growth, at least in the short term (Eamus and Jarvis 1989, Bazzaz 1990, Long et al. 1996, Mohren et al. 1996, Kozlowski and Pallardy 1997). There is, however, only limited evidence for direct tree growth responses to increased CO_2 (Jacoby and Darrigo 1997), the most recent being a 25% increase under conditions of continuously elevated CO_2 (560 ppm) for loblolly pine in the Duke free-air CO_2 enrichment (FACE) experiments in North Carolina (DeLucia et al. 1999).

Two major questions arise from tree CO_2 exposure studies. The first is sustainability of increases in photosynthesis and growth. Some longer-term exposure studies suggest that down-regulation of photosynthetic rates (reduction in carbon gain due to nutrient limitations or end-product inhibition) occur over time (Long et al. 1996, Lambers et al. 1998, Rey and Jarvis 1998), attributable perhaps to an accumulation of photosynthetic reserves (Bazzaz 1990). Morphological changes in exposed trees could also account for a reduced response to elevated CO_2 over time (Norby et al. 1992, Pritchard et al. 1998, Tjoelker et al. 1998b). Declining photosynthetic rates attributed to acclimation factors can also be a simple matter of water or nutrient stress imposed on pot-grown seedlings where root growth is limited (Will and Teskey 1997a, Curtis and Wang 1998), and at least one major review (Saxe et al. 1998) found no convincing evidence for down-regulation.

The second question concerns the influence of other limiting factors such as nutrients, water, and light on tree responses. Johnson et al. (1998) demonstrated the importance of nutrient availability, showing that growth responses of ponderosa and loblolly pine ranged from zero to more than

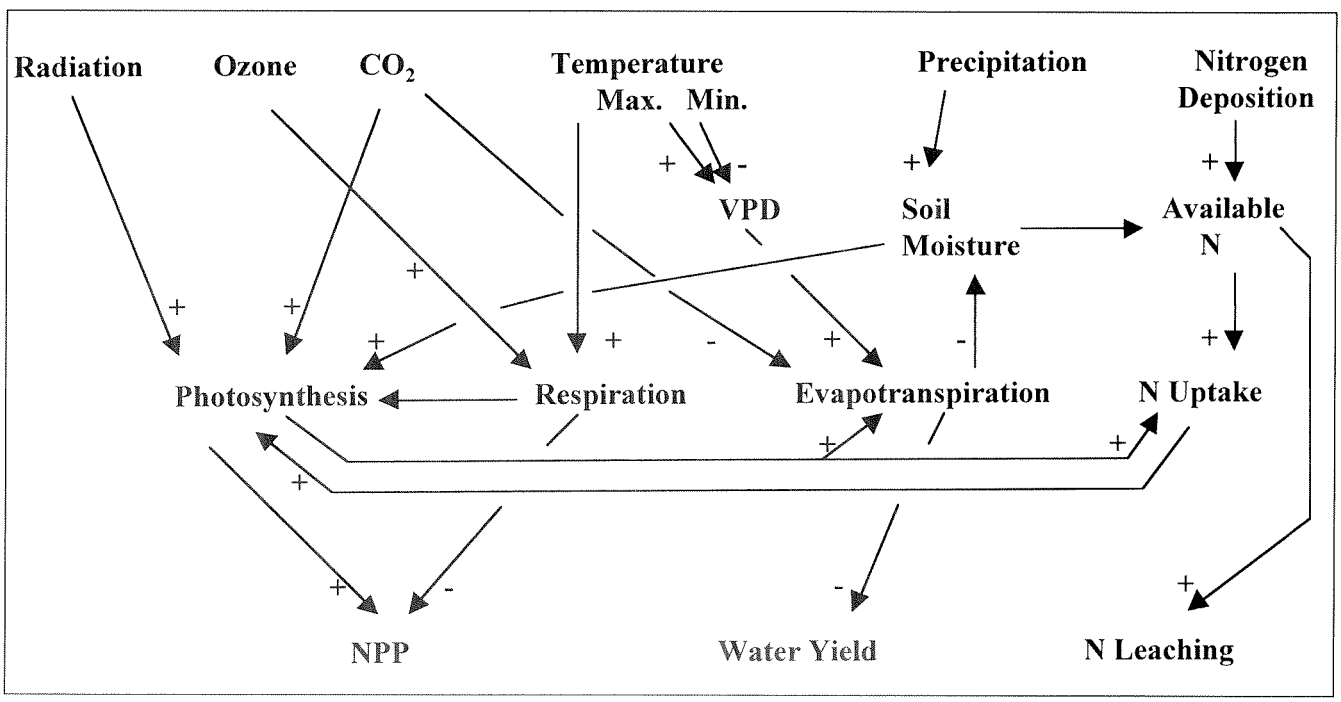

Figure 1. Interactions among environmental factors that are subject to change through human activities, and major processes affecting carbon, water, and nitrogen dynamics in forest ecosystems. (+) Indicates an enhancement, and (–) a suppression, of the receptor process.

1000%, depending on soil N status. Curtis and Wang (1998) in a metanalysis of 500 tree exposure studies found that carbon gain increased an average of 31% under optimal conditions and only 16% with nutrient limitations.

Water use efficiency (WUE) is increased in CO_2-enriched atmospheres, and reductions in water stress may be a significant response. While there is still uncertainty whether stomatal conductance is decreased under elevated CO_2 (Long et al. 1996, Will and Teskey 1997b, Curtis and Wang 1998, Saxe et al. 1998), WUE will increase either with or without changes in stomatal conductance. With constant conductance, the higher atmospheric CO_2 concentration increases carbon (C) uptake with constant water loss. If conductance is reduced, a trade-off is established between increased C gain (which is partially reduced by decreased conductance) and decreased water loss (also reduced by decreased conductance).

For light availability, a review by Curtis and Wang (1998) suggested that low light conditions increased the response to elevated CO_2 from +31% to +52%, whereas a review by Kerstiens (1998) concluded that shade-tolerant trees show greater growth responses to CO_2 than do shade-intolerant species because of more efficient use of light, water, and nutrients.

Indirect effects of elevated CO_2 on trees and forests are likely to be as or more important than their direct effects on photosynthesis. For example, elevated CO_2 can decrease N concentrations and increase nonstructural carbohydrates and secondary metabolites, all of which can alter tree resistance to pests and herbivores and influence rates of litter decomposition and nutrient cycling (Landolt and Pfenninger 1997, Roth et al. 1997, Cotrufo et al. 1998, Scherzer et al. 1998, Williams et al. 1998). Elevated CO_2 may also increase the ability of some species to recover from herbivore-induced defoliation (Kruger et al. 1998) and alter mycorrhizal root colonization and morphotype in others (Godbold et al. 1997). Many authors suggest that there is insufficient information to develop generalized predictions of ecosystem response to elevated CO_2; they suggest also that many responses are species- and site-specific (Egli and Korner 1997, Berntson and Bazzaz 1998, Crookshanks et al. 1998, Kerstiens 1998, Tjoelker et al. 1998a).

Temperature and precipitation. Temperature and precipitation jointly determine the large-scale patterns of distribution and growth of woody plants (Hansen et al. 2001). Responses to change in either of these variables can be positive or negative, because response functions for most physiological processes are not linear but asymptotic or hyperbolic. For example, low temperatures affect trees and other vegetation directly by limiting energy for biochemical processes, decreasing membrane permeability, and increasing the viscosity of protoplasm, whereas excessive temperatures can denature or inactivate enzymes and decrease carbohydrate pools through high respiration rates (Graumlich and Brubaker 1995, Kozlowski and Pallardy 1997, Lambers et al. 1998). Similarly, decomposition and mineralization rates and plant root function are optimal when soil water content is near field capacity; they decline as soils become either dry or saturated (Linn and Doran 1984, Skoop et al. 1990, Castro et al. 1995, Riley and Vitousek 1995).

While the temperature tolerance of a particular species is often inferred from the northern and southern limits of its geographic range (e.g., Brooks et al. 1998), other factors such as water stress and interactions with competing species also play a significant role in determining species distributions (Loehle and LeBlanc 1996, Loehle 1998). Exposure to extreme events also has the potential to influence the survival and growth of some species (Bassow et al. 1994).

There is evidence that both photosynthesis and respiration in many plants adapt to changing temperatures (Lambers et al. 1998), although the extent to which this happens under field conditions remains a significant unknown in global change research. Changes in air temperature in the autumn and spring can also affect frost tolerance of tree needles (Guak et al. 1998), and temperature also affects fruit and seed yields and quality by influencing factors such as flowering, bud dormancy, and ripening of fruits and cones (Kozlowski and Pallardy 1997).

The interaction of air temperature, soil water content, and CO_2 concentration also produces effects. For example, growth responses of boreal species to elevated CO_2 have been found to increase with temperature (Tjoelker et al. 1998b). Elevated CO_2-induced reductions in whole-shoot dark respiration and transpiration have been shown to ameliorate high-temperature stress on tree seedlings and to reduce the susceptibility of dormant winter buds to freezing stress (Wayne et al. 1998). The response of trees to intermittent drought, and even the frequency of drought events, can be affected by the interactions among CO_2, transpiration, and soil water content, as described in the previous section.

Increases in temperature also lengthen the growing season in temperate or cold-deciduous systems. In regions where drought stress is not important because of high levels of precipitation, or if increases in CO_2 concentration increase water use efficiency and thus reduce water stress, longer growing seasons could result in increased growth. Where drought stress is important, a longer growing season may mean only that plant respiration exceeds photosynthesis for a longer time, which would result in reduced growth.This effect could be augmented by the effect of temperature on vapor pressure deficit. Increased temperature and changes in the range between minimum and maximum temperature can alter vapor pressure deficit and thus alter water use efficiency and water stress.

Differences in water content at different soil depths during dry periods can affect the relative impact of drought on the net carbon balance. Goulden et al. (1996) reported that a period of prolonged drought in midsummer in a mixed forest in central Massachusetts caused, through surface drying, a larger reduction in microbial and root respiration from soils than in photosynthesis, and hence an increase in net carbon storage relative to other years.

The impacts of temperature and water stress on photosynthesis, respiration, and carbon storage are incorporated at the process level in most of the global change models (see section on models below). Effects of long-term climatology are also included in those models that predict shifts in biome distribution (Hansen et al. 2001). Major research challenges remain on the question of acclimation of plant processes to altered temperature regimes.

Nitrogen deposition and ozone. Increased atmospheric CO_2 is one important consequence of human activity, and the direct physiological effects and indirect climatic effects of this increase are the focus of current assessment activities. However, human activity is also altering the biogeochemistry of other elements and compounds, which may significantly modify ecosystem response. Two of the most widespread and important examples of this modification concern nitrogen and tropospheric (near-ground) ozone. The distribution and effect of N and O_3 are closely linked through the role that oxides of N (NO_x) play in the formation of ozone near the Earth's surface. We include these two change factors here to indicate the potential for factors that lie outside the current review process to affect forests.

Total N deposition in some parts of the United States has increased as much as 10-fold over global background levels as a result of human activity (Galloway 1995). The short residence time of reactive forms of N in the atmosphere relative to CO2 results in a pronounced regional distribution of deposition. In the United States, deposition is highest in the northeast and midwest, although deposition can be high in and around larger cities in western states as well.

Low availability of N often limits forest production in the United States, and increases in forest growth in response to N deposition have been reported in Scandinavia and the United States. Negative effects are linked to soil acidification and cation depletion under conditions of excessive nitrate leaching. These are expressed as imbalances in the N:magnesium and calcium:aluminum ratios in foliage and decreases in net photosynthesis and tree growth (Schulze 1989, Aber et al. 1995). These negative effects of excess anion leaching are inhibited by processes that suppress the production of nitrate or retain nitrate ions in soils. Retention can be attributable to a combination of biotic and abiotic processes that remain difficult to predict or may be related to long-term patterns of forest management and human land use (Aber et al. 1998).

Ozone is a secondary pollutant in the lower atmosphere resulting mainly from the combustion of fossil fuels. Its formation requires the presence of nitrogen oxides, simple hydrocarbons, and sunlight. Ozone is a highly reactive gas with a short half-life in the atmosphere. Important ozone events are linked to periods when warm, stagnant air masses remain over densely populated and highly industrialized regions for extended periods of time. Thus the distribution of ozone concentrations is very irregular in space and time. Severe events tend to occur throughout the eastern United States and in isolated western cities (e.g., Los Angeles) where conditions are most favorable for ozone formation.

Unlike N deposition, the effects of ozone on ecosystems are direct and immediate, because the primary mechanism for damage is through direct uptake from the atmosphere into plant leaves through the stomates. Ozone is a strong oxidant that damages cell membranes and requires the plant to increase its energy expenditures to repair these sensitive tissues. The net effect is a decline in net photosynthetic rate.

Indices developed to predict the effects of ozone on plant growth generally use a threshold value (such as 40 parts per billion [ppb]) below which no damage is expected to occur. Several studies have shown that reduced photosynthesis and growth can be related to the accumulated dose of ozone above this threshold (Reich and Amundson 1984, Reich 1987, Tjoelker et al. 1995). Greater precision can be obtained by converting dose (dose equals the sum of hours times concentration) to actual uptake rates (Ollinger et al. 1997). It has been shown that the degree to which photosynthesis is reduced is a function of dose and species conductance rates (the rate at which gases are exchanged with the atmosphere by leaves). Faster-growing species have higher rates of gas exchange, take up more ozone, and thus experience a greater reduction in net photosynthesis (Reich 1987).

Interactions. The components of physical and chemical climate change described above can interact in either reinforcing or offsetting ways (Figure 1). It is crucial to begin to understand not only the direct effects of CO_2, ozone, temperature, precipitation, and N and sulfur (S) deposition on forests but also the interactive effects of these stressors.

For example, if canopy conductance in forests is reduced in response to CO_2 enrichment, then ozone uptake will be reduced and the effects of this pollutant mitigated. Drought stress has a similar effect by reducing stomatal conductance. On the other hand, if N deposition increases N concentrations in foliage and so increases photosynthesis and stomatal conductance, then the positive effects of increased photosynthesis will be partially offset by increased ozone uptake. Reductions in production caused by ozone could speed the onset of N saturation and the attendant development of acidified soils and streams. These interactions, and others that could be listed, underscore the need to develop integrated models that can predict the effects of these pollutant interactions.

Models of forest response to environmental change

The complexity of climate–forest interactions requires the use of models to forecast ecosystem responses to environmental change. Several such models exist. In this section we concentrate mainly on the models used in the VEMAP program and summarize their results. We then follow this with a brief review of additional models dealing with different combinations of environmental stressors.

The VEMAP program

The Vegetation/Ecosystem Modeling and Analysis Project (VEMAP) was established to serve as a repository for information related to climate change issues and as a vehicle for comparing several different model predictions of ecosystem response to climate change. Sponsored by the Electric Power Research Institute, National Aeronautics and Space Administration, and the US Department of Agriculture's Forest Service–Southern Global Change Program, VEMAP has developed a set of spatially and temporally consistent data sets for use in global change analyses. Spatial data are rendered on a $0.5° \times 0.5°$ grid covering the coterminous 48 states at roughly a 50-km resolution. Climate scenarios are of two types. In the first phase of the program (VEMAP 1), equilibrium climates were derived for current conditions ($1 \times CO_2$) and for a $2 \times CO_2$ environment. In the second phase (VEMAP 2), transient predictions were made which involve important time lags and feedbacks in the atmosphere–ocean system.

VEMAP has also sponsored sensitivity analyses and intermodel comparisons involving several models of ecosystem distribution and function. In VEMAP 1, three biogeochemistry models and three biogeography models were used separately to predict changes in both ecosystem distribution and function. The biogeography models used included MAPSS (Neilson 1995), BIOME2 (Haxeltine and Prentice 1996), and DOLY (Woodward and Smith 1994, Woodward et al. 1995); the three biogeochemistry models were TEM (Raich et al. 1991, McGuire et al. 1992, Melillo et al. 1993), CENTURY (Parton et al. 1987, 1988, 1993), and BIOME-BGC (Hunt and Running 1992, Running and Hunt 1993).

The biogeography models predict forest distribution, but they do not calculate or only partially calculate the cycling of carbon and nutrients within ecosystems. The biogeochemistry models simulate the carbon and nutrient cycles within ecosystems, but they lack the ability to determine what kind of vegetation could live at a given location (but see Haxeltine and Prentice 1996). The two classes of global models were compared and loosely coupled for an assessment of both model capabilities and the potential impacts of global warming on US ecosystems (VEMAP members 1995). In VEMAP 2, efforts have been made to combine the functional features of the two types of models into single models, such that feedbacks between changes in species and changes in processes can be predicted.

VEMAP 1

Biogeography models. Climate is the primary force shaping the major physiognomic features of the world's vegetation (Whittaker 1975, Daubenmire 1978). Simple biome distribution models based only on mean annual precipitation and temperature provide reasonable predictions of existing global vegetation maps (Woodward 1987, Prentice 1990). However, the process-based biogeography models used in VEMAP 1 are thought to rely less on conditions-specific correlations that might not hold under future climate regimes, and so they may provide more accurate predictions outside of current climate conditions. One notable feature of the newer models is incorporation of the physiological effects of CO_2 which produce profound differences in biogeographic responses to potential future climates (VEMAP members 1995). These models also couple vegetation processes with hydrologic processes so that climate-induced alterations in both vegetation and water resources are addressed in a more integrated fashion.

The VEMAP 1 biogeography models assume that ecosystem development is limited by either energy (light, temperature) or water (nutrients in some situations) and that biomass and vegetation carbon content will increase until one of these limitations is expressed. Thus, gradients in light and water will produce gradients in vegetation density and structure, and the models require a process-based coupling of a full-site water balance with the simulation of leaf area index (LAI). Energy-limited LAI is either directly simulated via a photosynthesis calculation or through a relationship to the thermal regime.

In each model, rules that determine the boundary between vegetation types and the characteristics of dominant species are applied (e.g., broad-leaved or needle-leaved, evergreen or deciduous). The large diversity of species are aggregated into these broad functional types. Despite these improvements, the VEMAP 1 biogeography models are still equilibrium based in nature, in that they simulate potential natural vegetation, given a long-term average climate. Therefore, they do not capture the effects of interannual patterns of climate variation. Some of the models (e.g., MAPSS; Neilson 1995) do incorporate disturbance by fire but do not include land-use conversion from natural to managed (e.g., agriculture and plantation forestry) ecosystems, grazing, and pestilence, which can further modify the aerial extent of biomes. Extreme climate events (e.g., occasional drought), which can also play an important role in vegetation distribution, also are not incorporated (Allen and Hoefstra 1990, Kingsolver et al. 1993).

Biogeochemistry models. Biogeochemistry models simulate the gain, loss, and internal cycling of carbon, nutrients, and water using algorithms describing physical, chemical, and physiological processes in plants and soils; they are parameterized according to life-form type. Common outputs include net primary production (NPP) and its distribution among tissue types; net mineralization and uptake of nutrients; and the partitioning of precipitation between evaporation, transpiration, drainage, and storage.

The three VEMAP 1 biogeochemistry models simulate the effects of precipitation and increased CO_2 in different ways, while all three realize the effects of temperature in similar ways. BIOME-BGC and TEM calculate the ratio of CO_2 outside and inside the leaf (C_a/C_i) and use it to alter rates of photosynthesis. CENTURY uses an empirical constant in defining the effect of CO_2 on photosynthesis. Both BIOME-BGC and CENTURY prescribe a 20% reduction in conductance at $2 \times CO_2$, simulating a reduction in transpiration; transpiration is un-

affected by CO_2 in TEM. BIOME-BGC and CENTURY also prescribe a 20% reduction in leaf nitrogen concentration, whereas this value is determined by internal C:N balances in TEM. In both BIOME-BGC and CENTURY, net primary production is a specified fraction of gross photosynthesis; TEM calculates respiration directly. Other important differences in structure, requirements, and predictions of the three biogeochemistry models used in VEMAP 1 have been presented elsewhere and are only summarized briefly here (VEMAP members 1995, Pan et al. 1998).

Climate scenarios. The VEMAP 1 models were run for three contrasting climate-change scenarios generated by three different general circulation models (Table 1). All three scenarios represent equilibrium runs with mixed-layer oceans that include vertical exchange of heat but no horizontal transport. The three scenarios were selected to represent the range of climate change predictions available at the time of the VEMAP 1 analysis. Spatial patterns in the predicted changes in Table 1 vary between models, and details are provided by VEMAP members (1995). It should be noted that although predicted changes in temperature and precipitation are outputs from climate models, radiation changes are simulated based on the difference between maximum and minimum temperatures. This has been shown to be an inaccurate approximation under some conditions (Aber and Freuder 2000).

Table 1. Changes in mean annual precipitation and temperature with a doubling of CO_2 generated by three different general circulation models used for the VEMAP 1 analysis: OSU, Oregon State University (Schlesinger and Zhao 1989); GFDL, Geophysical Fluids Dynamics Laboratory (Manabe et al. 1990, Wetherald et al. 1990); UKMO, United Kingdom Meteorological Laboratory (Wilson and Mitchell 1987).

Name	delta T (°C)	Delta P (%)
OSU	+3.0	+4
GFDL	+4.3	+21
UKMO	+6.7	+12

Predictions on forest biome redistribution. With a doubling of atmospheric CO_2 and the equilibrium climate conditions predicted to result, significant changes in total area of forest coverage are predicted under certain scenario and model combinations (Table 2). Coniferous forests are predicted to more than double using the MAPSS model and GFDL scenario, and to decline by more than 50% in the BIOME2–UKMO combination. Broad-leaved forest areas are larger and percentage changes are generally smaller, ranging from an increase of more than 20% for the DOLY–GFDL combination to a decrease of more than 15% for MAPSS–UKMO. Even though changes between these two forest types are included in the predictions, the predicted overall changes in forest area cover nearly the same range as for broad-leaved forests alone (Table 2), ranging from an increase of 23% in the MAPSS–OSU combination to a decrease of 14% in the BIOME2–OSU and BIOME2–UKMO combinations. These nationwide average values mask much larger changes in predicted distributions of forests and forest types (VEMAP members 1995, Hansen et al. 2001). These predictions cover distributions of native vegetation types only and in equilibrium with altered climate. Both transient changes and the effects of land use are described below.

Predicted changes in forest productivity and carbon storage. Under VEMAP 1, all three of the biogeochemistry models were run assuming either that biome distribution did not change or that biomes were redistributed according to the predictions cited above. The latter are summarized here and include changes in both climate and CO_2. Results for the coterminous 48 states were not partitioned among vegetation types (Table 3). Among the Phase 1 biogeochemistry models, BIOME-BGC is the most sensitive to water stress and predicts the largest net loss of carbon (nearly 40% with the BIOME2–UKMO combination). The TEM model estimates the greatest enhancement in productivity and total carbon storage among the three biogeochemistry models (as much as a 39% increase in NPP and a 32% increase in carbon storage with the MAPSS–OSU combination). CENTURY predicts intermediate NPP and C storage gains.

Summary. The VEMAP 1 analysis offers a unique 3 ×3 × 3 cross-model comparison (climate × biogeography × biogeochemistry) that suggests the direction of the response to be expected from terrestrial ecosystems and the degree of uncertainty, given the current understanding of climate, vegetation distribution, and nutrient cycling captured in the various models. Overall predictions, expressed as the average of all separate climate–model combinations (+/– 1 standard error), would suggest that total forest area (2.0% +/– 3.48%) and total carbon storage (2.05% +/– 3.85%) would remain relatively constant while NPP would increase significantly (20.8%, +/– 2.37%). As with the biogeography models, these gross continental means mask significant local to regional variation in response (see VEMAP members 1995 for a detailed discussion).

VEMAP 2

VEMAP 2 adds two goals to the original project. The first is to combine biogeography and biogeochemical models in order to integrate responses in vegetation dynamics and ecosystem processes. The second is to develop and use transient rather than static climate-change scenarios.

Combined biogeography–biogeochemistry models. The new generation of dynamic general vegetation models (DGVMs) now emerging as part of the International Geosphere-Biosphere Program (IGBP) and VEMAP 2 processes couple vegetation structure and biogeochemical

Table 2. Results of VEMAP 1 biogeography model simulations for changes in land area covered by forest (coniferous, broad-leaved, and all forests) in the coterminous 48 US states, under control climate and three climate change scenarios.

Model	Climate scenario for coniferous forests[a]				Climate scenario for broad-leaved forests[a]				Climate scenario for all forests[b]		
	Control	OSU	GFDL	UKMO	Control	OSU	GFDL	UKMO	OSU	GFDL	UKMO
MAPSSS	0.8	1.3	1.7	0.7	2.5	2.8	2.2	2.1	+23	+20	–13
DOLY	0.8	0.6	0.6	0.5	2.3	2.3	2.8	2.6	–7	+11	+2
BIOME2	0.9	0.7	0.8	0.4	2.6	2.6	3.0	2.5	–14	+10	–14

Source: Adapted from VEMAP members (1995).
a. Values in 10^6 km^2.
b. Values in percentage change in conifer and broad-leaved forests.

fluxes and simulate dynamic changes in response to changes in climate and disturbance regimes (Neilson and Running 1996, Foley et al. 1996, Friend et al. 1997, Daly et al. 2000). Although more complete and integrated than the VEMAP 1 models, the new DGVMs still lack important constraints on ecosystem change, such as soil development and seed dispersal. Of these new models, MC1 (a combination of the MAPSS and CENTURY models with a process-based fire model [Lenihan et al. 1998, Daly et al. forthcoming]) and LPJ (an extension of BIOME3) have been applied to the emerging transient climate change predictions. However, quantitative data from only MC1 were available for this paper.

Transient climate scenarios. Two transient global climate models were used as input to the forest biogeography and process models. The Canadian Global Coupled Model (CGCM1) has a surface grid resolution of 3.7° × 3.7°, with 10 vertical atmospheric levels and a monthly time step. Outputs have been regridded to a daily time step with a 0.5° × 0.5° grid resolution. The model uses an increase of CO_2 at a rate of 1% per year from 1990 levels to 2100 (Boer and Denis 1997). The direct forcing effect of sulfate aerosols is also included by increasing the surface albedo (Reader and Boer 1998) based on loadings from the sulfur cycle model of Langner and Rodhe (1991).

The second model, developed by the Hadley Centre for Climate Prediction (HADCM2SUL), has a spatial resolution of 2.5° × 3.75° with 19 vertical atmospheric levels (Cullen 1993) and produces monthly outputs that have been reconfigured to a daily time step with a 0.5° × 0.5° grid resolution. The model uses an increase of CO_2 at a rate of 1% per year from 1990 levels to 2100 and includes sulfate aerosol inputs (IS92d).

Both the Hadley and Canadian simulations used 1895 as the initial year and ran to 1993 using observed increases in greenhouse gases and sulfate aerosol. Greenhouse forcing was increased at a rate of 1% per year from the present to the end of the 21st century, an emissions rate roughly equivalent to the IS92a scenario of the Intergovernmental Panel on Climate Change. The climate variables from each scenario were averaged over their last 30 years of simulation to allow use by equilibrium models, such as MAPSS. These 30-year averages approximate a 2 × CO_2 scenario, although the GCMs were clearly not in equilibrium at that time, having attained only about 50% to 65% of their eventual temperature increase (Gates et al. 1996).

The two scenarios are quite different (Table 4), spanning nearly the range of temperature change exhibited by the

Table 3. Results of VEMAP 1 biochemistry model simulations for changes in NPP and total carbon storage. Results shown here are for the linked predictions in which the redistribution of biomes from the biogeography models are used as input, along with altered climate and doubled CO_2, to predict NPP and C storage (VEMAP members 1995). BBGC, Biome-BGC; CEN, CENTURY; TEM, Terrestrial Ecosystem Model.

Model combination		Percentage change in total annual NPP			Percentage change in total carbon storage		
		OSU	GFDL	UKMO	OSU	GFDL	UKMO
BBGC	BIOME2	+7.4	+21.7	+0.4	–13.2	–9.5	–34.7
	DOLY	+5.6	+20.1	–0.1	–18.1	–13.6	–36.4
	MAPPS	+11.9	+20.4	–0.7	–8.3	–13.9	–39.4
CEN	BIOME2	+11.3	+18.4	+12.2	–0.8	+12.6	–1.8
	DOLY	+26.0	+20.4	+14.7	+9.8	+17.7	+7.8
	MAPPS	+15.6	+29.2	+20.3	+17.0	+20.4	–1.5
TEM	BIOME2	+27.0	+38.5	+27.8	+11.9	+25.7	0.0
	DOLY	+33.1	+39.0	+33.2	+19.7	+25.3	+12.5
	MAPPS	+39.7	+37.2	+32.4	+32.3	+32.2	+1.7

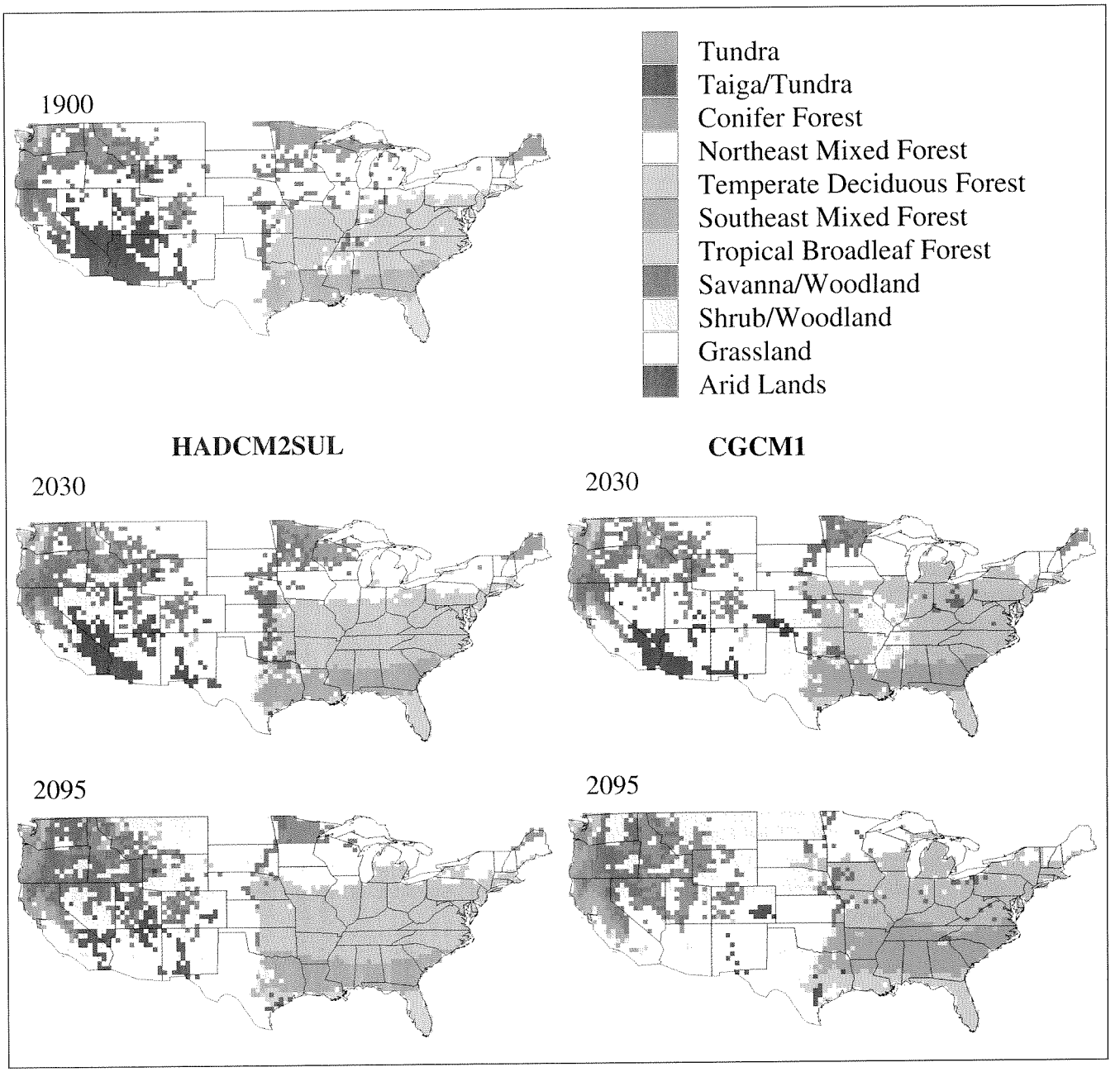

Figure 2. MC1-simulated change in vegetation distribution for 11 major vegetation types under two future climate scenarios.

older equilibrium scenarios. The Hadley scenario exhibits only modest warming (3.3°C) by the end of the next century with a considerable increase in precipitation (23%), while the Canadian scenario is much warmer (5.8°C) with only a moderate increase in precipitation (17%). Notably, the Canadian scenario shows a small decrease in precipitation over the first three decades to about 2030, with increases thereafter. Both scenarios produce increased precipitation in the Southwest, more extreme in the Canadian scenario, centered in southern California and extending into the Great Basin. Both models show slight drying in the Northwest, more so in the Hadley. South Texas shows decreased rainfall in both models, but extending much farther north with deeper declines in the Canadian. Both scenarios show increased precipitation in the upper Midwest. However, the Hadley scenario shows increased precipitation over most of the eastern US forests, except along the Gulf coast and in southern Florida, while the Canadian scenario shows large decreases in precipitation east of the Appalachian Mountains, with as much as a 30% decline in the Southeast, grading to a small decline in New England. Both models show the most warming over the continental interior, centered over the central Rockies in the Hadley and over the Great Plains in the Canadian scenario.

Predictions of forest biome redistribution. Predictions from the MC1 model using the two new transient climate scenarios (Figure 2) are broadly consistent with the previous equilibrium simulations of VEMAP 1 as described

Table 4. Average US annual temperature and precipitation changes compared with 1961–1990 means.

Scenario	2025–2034 Temperature (°C)	2025–2034 Precipitation (%)	2090–2099 Temperature (°C)	2090–2099 Precipitation (%)
HADCM2SUL	1.4	6	3.3	23
CGCM1	2.1	–4	5.8	17

by Hansen et al. (2001). One significant area of disagreement is in the degree of conversion of forests to grassland and savanna–woodland in the eastern United States. Under the Canadian scenario, MC1 creates a large but temporary expansion of grasslands into the temperate deciduous forest by 2030 (Figure 2), with reversion to forest occurring by 2095. Smaller areas of grassland and shrubland persist throughout the East. In contrast, MAPSS (Hansen et al. 2001) predicts a major expansion of savanna and grassland in the southeastern United States. Another DGVM from the VEMAP 2 models, LPJ, also produced conversions of southeastern forests to savannas under the Canadian scenario, but with LPJ, as with MAPSS, they remain as savannas and grasslands.

Under the Hadley scenario, MC1 predicts no conversion of southeastern forests, and all models (MAPSS, MC1, LPJ) under both scenarios produce forest expansions into the Upper Midwest Prairie Peninsula in concert with the increased precipitation in that region by the end of the 21st century. Over much of the eastern United States, expansions and contractions of forest land must be considered provisional because of the dominant role of agriculture and other land uses in determining vegetative cover.

In the West, MC1 produces conversions of shrub lands to tree–savannas in California and other parts of the Southwest under both scenarios, and an increase in the broadleaf component of Northwest conifer forests. The importance of arid lands is also greatly reduced. All forest zones in the West shift upslope under all simulations. On some temperate mountain ranges, entire alpine and subalpine life zones could be eliminated (Hansen et al. 2001). However, lower elevation, water-limited ecotones could shift up or down, depending on the overall regional water balance. Under both the Hadley and Canadian scenarios, the increased rainfall in the Southwest tends to counter increases in temperature, and low-elevation ecotones either remain stable or shift downslope in some areas. Yet, with moderate drying in northern Washington, lower forest ecotones may shift slightly upslope. It must be emphasized that these model results rely on the increased water-use efficiency assumed from elevated CO_2 concentrations. Some early results of the FACE experiment indicate that conifers may not experience such increased WUE (DeLucia et al. 1999). If that is the case, then western forests could be at considerably greater risk from moisture stress than these results would suggest (VEMAP members 1995).

Predicted changes in forest carbon storage. Total live vegetation carbon storage within the coterminous United States (Table 5) increases with all VEMAP phase 2 models under the Hadley scenario. Under the Canadian scenario, all the biogeochemical models (TEM, CENTURY, BIOME-BGC) simulate gains in live vegetation carbon over the United States of approximately 3–14 Pg, but MC1 simulates a decline in vegetation carbon of about 2–4 Pg. Total carbon, live and dead, largely mirrors the live vegetation responses in MC1. Dynamic vegetation type and dynamic fire simulation are the primary reasons for the different carbon responses of the two classes of models (biogeochemical and DGVM).

The average gains and losses of carbon across the coterminous United States mask regional changes (Figure 3). Under the Hadley scenario, about 20% of current forest area could experience some level of carbon loss, while the remaining 80% may experience increased storage (Figure 3a). Under the

Table 5. Changes in carbon storage for the coterminus United States in 2030 and 2095, as predicted by the VEMAP models using the two transient climate change scenarios described in the text. Baseline period is 1961–1990. Changes are given for forest vegetation, total forest carbon, all vegetation, and total carbon. Values are expressed in Pg.

Change in carbon	Model	Hadley 2030	Hadley 2095	Canadian 2030	Canadian 2095
For forest vegetation	BBGC	3.9	11.1	2.9	8.5
	Century	0.5	3.1	0.3	3.0
	TEM	3.2	9.0	2.3	10.5
	MC1	0.7	4.4	–2.1	–2.3
Total forest carbon	BBGC	3.3	10.7	2.0	7.1
	Century	0.2	3.2	0.2	3.2
	TEM	2.8	9.3	2.0	9.8
	MC1	3.0	11.4	–4.8	–2.7
For all vegetation	BBGC	4.7	13.2	3.8	11.1
	Century	0.4	3.3	0.2	3.2
	TEM	4.5	11.9	3.8	14.0
	MC1	1.0	4.5	–1.7	–2.1
Total	BBGC	4.1	12.9	3.0	10.2
	Century	0.3	3.5	0.2	3.5
	TEM	4.8	14.4	4.4	14.9
	MC1	3.9	10.5	–0.9	–3.8

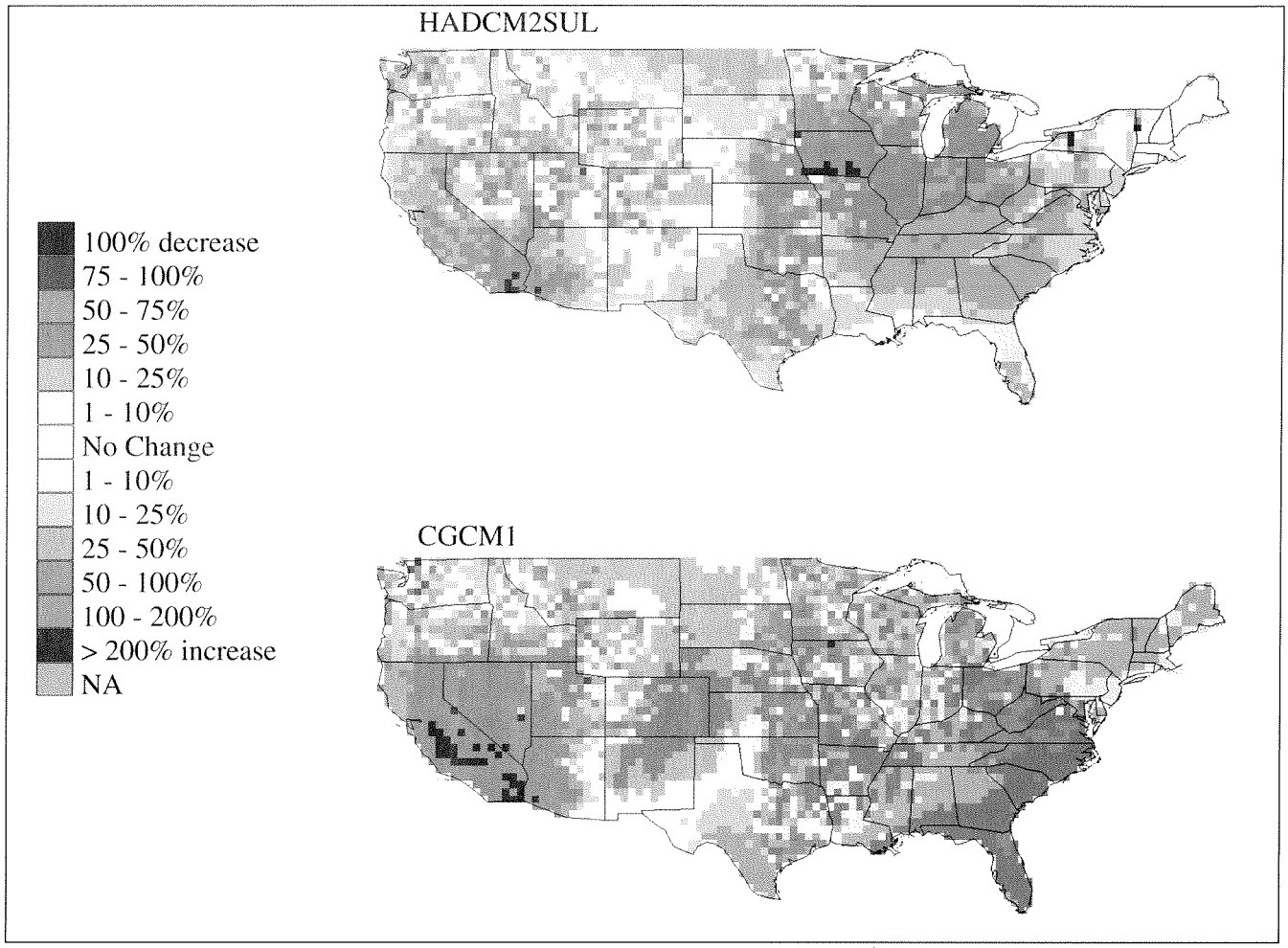

Figure 3. Percentage change in live vegetation carbon density for the period 2090–2099, as simulated by the MCI model under two future climate scenarios.

much warmer Canadian scenario, MC1 predicts that closer to 50% of current forest area could experience drought-induced loss of carbon. Reductions in carbon storage are especially severe in the eastern and southeastern United States, where losses are predicted to approach 75% in some cases. When results from MAPSS runs under the equilibrium climate scenarios from VEMAP 1 are combined with MC1 results from the two transient scenarios, there appears to be a consistent trend in the relationship between higher temperatures under $2 \times CO_2$ conditions and the fraction of forest area predicted to experience reductions in carbon storage (Figure 4). Once again, these potentials for carbon loss and gain will be modified by land-use practices, especially in the East.

An increase in the importance of fire is predicted.

Unlike MAPSS, the MC1 model is able to simulate fire occurrence, severity, and size as a direct function of fuel and weather conditions by incorporating current approaches to large-scale fire modeling (Lenihan et al. 1998). These algorithms have successfully predicted extreme fire periods in the 1910s, 1930s, and 1950s, as well as the Yellowstone fire in 1988. MC1 predicts a trend of increasing biomass consumed under both scenarios throughout the 21st century (Figure 5). Under both scenarios, fire is predicted to increase in frequency over most of the West, due largely to increased fuel loads from increased precipitation. The eastern US forests do not normally experience the severe fire regimes of the West because of considerable summer rainfall and high humidity. Under the Hadley scenario, fires remain an insignificant feature of eastern forests. However, under the Canadian scenario, several large fires begin emerging in the Southeast over the course of the next three to four decades because of increasing drought.

Carbon loss as a result of these fires is just the most extreme response in the worst areas, exacerbating large negative fluxes attributable to drought. Vegetation carbon, simulated by MC1, in the oak–hickory forests drops by about 60% by about 2040 and recovers by 2100 to a level of only about two-thirds present carbon density (Figure 3b). The Southeast is not expected to experience quite as dramatic a carbon reduction from fire, but still loses about one-third of its vegetation carbon from drought stress by around 2025 and never recovers to a higher level. By contrast, in the Upper Midwest Prairie Peninsula, the frequency and magnitude of fires

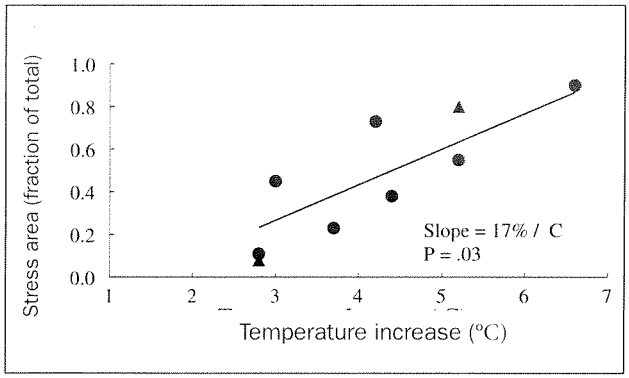

Figure 4. Area of current forests, which is simulated to undergo drought-induced reductions in carbon density under seven future climate scenarios as a function of the simulated increase in temperature over the coterminous United States at the time of equivalent 2 × CO_2 forcing (near the middle to end of the 21st century). Dots are MAPSS simulations. Triangles are MC1 simulations.

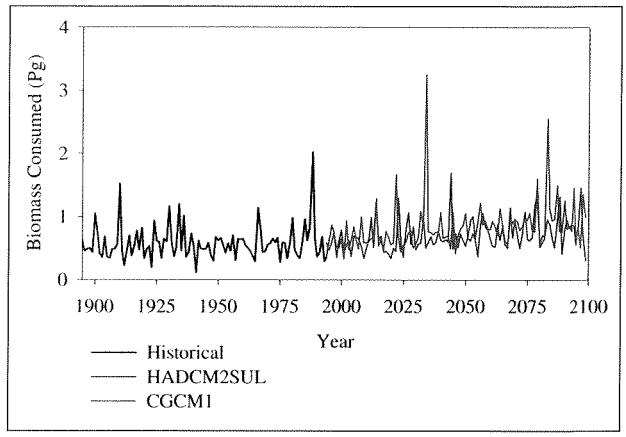

Figure 5. Simulated (MC1) total biomass consumed by fire over the coterminous United States under historic and two future climates. The fire simulations are for potential vegetation and do not consider historic fire suppression activities. However, grid cells with more than 40% agriculture have been excluded from the calculation (Bachelet et al. 2001).

decrease and the region gains in carbon density from increased precipitation. The fires simulated for the Prairie Peninsula are, of course, overestimates because the region is largely agricultural. Even so, the simulations do indicate the degree of stress, or change in stress, for the region.

Trajectories and timing. At least one hypothesis emerges across scenarios and ecological models from these collective results. Early in any future global warming, while temperature increases are still relatively modest, forests may be more productive and their storage of carbon may increase, in part because of CO_2 fertilization (Neilson and Drapek 1998). However, as temperatures continue to increase, the CO_2 effect may be overwhelmed by exponential increases in evapotranspiration or reductions in precipitation or both. In the case of reduced precipitation, there could be a threshold response resulting in a shift from increased productivity to a rapid, drought-induced dieback (e.g., MC1 under CGCM1), resulting in a release of carbon back to the atmosphere, with implications for the climate. Areas potentially susceptible to this are the Pacific Northwest and the Southeast. This hypothesis assumes a monotonic increase in both temperature and precipitation. However, as seen with both new, transient scenarios, interdecadal variations in precipitation can override the benefits of elevated CO_2 or the negative impacts of elevated evaporative demand caused by higher temperatures.

Under the CGCM1 scenario, vegetation decline, as simulated by MC1, begins almost immediately and continues with increasing fire intensity and frequency, both in the western and eastern US forests, for about the next three to four decades, driven in part by decreased rainfall (Table 4). Biomass consumed over the United States exhibits an increasing trend in both scenarios (Figure 5), beginning with the initiation of the scenario and increasing to the end of the next century, but with far more severe fires in the Canadian scenario. Under the Hadley scenario, fires also begin increasing almost immediately in the western United States, even though vegetation carbon density is simulated to increase over the entire United States.

Water resources. Vegetation dynamics are tightly coupled with hydrologic processes, comprising a complex set of interactions between vegetation water-use efficiency, soil characteristics, snow dynamics, and climate (Dale 1997). With increased temperatures, longer growing seasons, and more leaf area, vegetation may transpire more water, even with CO_2-induced increases in water-use efficiency, leaving less runoff for irrigation or domestic uses.

This complex interaction can be seen in MAPSS predictions for changes in LAI and runoff averaged from the seven VEMAP 1 static climate change scenarios. MAPSS predicts significant decreases in LAI in the Upper Midwest, Great Lakes, and northeastern regions, with moderate increases in other areas (Figure 6; Neilson and Marks 1994). Loss of LAI in the North and East is great enough to reduce transpiration, even in a longer growing season, such that runoff increases. In the Southeast and Great Plains, very large fractional reductions in runoff are predicted, in part because of moderate increases in LAI. The Ohio and Tennessee Valleys lie between regions of decreased moisture in the southeastern United States and regions of increased moisture in the North, so the prospects are uncertain. The entire Mississippi drainage basin could see as much as a 20% decrease in annual runoff, averaged across all seven model scenarios (with a range of +2% to –40%). Implications for shipping, irrigation, and domestic water uses would be profound. The Northwest, California, and the Great Basin could see large increases in runoff, primarily in winter.

In areas with considerable summer rainfall, that is, east of the Rockies and in the Southwest, changes in vegetation and

changes in runoff tend to be negatively correlated (i.e., decreased vegetation is associated with increased runoff, and increased vegetation is associated with decreased runoff) (Figures 6, 7). In contrast, both vegetation and runoff are predicted to increase in the West.

Runoff in the West is largely snowmelt dominated and, under a global warming scenario, generally increases in the winter. With moderate warming, there is sufficient soil moisture recharge such that, with a longer growing season, forest growth may be enhanced. However, with more pronounced climate warming, runoff is likely to increase but forests may still experience drought-induced dieback because of the stress of summertime warming.

Models of other stressors and their interactions with climate

The VEMAP program was designed to examine the effects of temperature, precipitation, and CO_2 interactions on ecosystem distribution and function. Other individual models have addressed these interactions as well, and a few have been developed to examine the other stressors not included in the VEMAP exercise, such as N deposition and ozone. Those models summarized here have been applied regionally over a subset of the contiguous United States. Responses to N deposition and ozone can be on the same order as responses to climate change, suggesting that a complete analysis of forest ecosystem response to global change may need to include these additional factors.

PnET. PnET (photosynthesis and evapotranspiration) is an uncalibrated model (that is, parameters are not calibrated) designed to simulate carbon, nitrogen, and water dynamics in temperate and boreal forest ecosystems. It has been tested and applied at the stand and watershed (Aber et al. 1995, 1996, Aber and Driscoll 1997) and regional (Ollinger et al. 1998) scales; the model has recently been extended to include the effects of ozone (Ollinger et al. 1997). Regional applications include estimates of climate change and ozone effects for the northeastern and southeastern United States.

For the northeastern region, PnET-II has been used to predict the interactive effects of changes in temperature, precipitation, and $2 \times CO_2$ (realized as a doubling of water-use efficiency; Aber et al. 1995). Predictions were made using older climate change scenarios (+6°C, –15% precipitation for the northeastern United States). Results for this region were similar to those obtained from the VEMAP models. Combining all three factors completely alleviated water stress and caused a 10%–20% increase in production and an average 15% decrease in water yield.

In the southeast, PnET-II was combined with the biogeographic model DISTRIB (Iverson and Prasad 1998) to assess the impact of climate change on forest productivity and distribution and the economic impacts across the region (McNulty et al. 2000). Using the HADCM2SUL climate scenario, southern pine forest distribution was predicted to move northward into southern Illinois and along the coast into southern Pennsylvania. Productivity would also shift northward, with the largest increases in productivity occurring throughout Tennessee. Although predicted total forest productivity increased within the region, parts of the southern Gulf Coast showed reduced growth.

The regional effects of ozone on forest production have been predicted using PnET-II modified to include the distribution of this pollutant throughout a forest canopy and its physiological effects on rates of net photosynthesis (Ollinger et al. 1998). Using ambient climate and comparing the effects of current ground-level ozone concentrations with a no-ozone control, PnET predicted a 1%–16% reduction in NPP, and a 3%–21% reduction in wood production for deciduous forests across the Northeast under current ozone levels. Interesting interactions between ozone and drought effects were revealed. Ozone events tended to occur during times of high temperature and drought. Drought reduced stomatal conductance and hence ozone uptake, providing partial protection against ozone effects. Ozone-induced reductions in growth were highest in the southern part of the region where concentrations were highest, and on soil with high water holding capacity where drought stress was minimal.

In contrast, PnET predicts increased growth in response to increases in N deposition, with increases in N leaching loss attenuated over a long period of time because of slow recycling through soils. Effects of interannual variability in climate on N leaching-loss rates largely mask any progressive increase in N losses over decadal time steps (Aber and Driscoll 1997).

TREGRO. TREGRO is a detailed short-time-step model of the physiological responses of trees to climate drivers and ozone. Developed in conjunction with a set of intensive experimental manipulations with seedlings and saplings, TREGRO has been calibrated for application to several different forest stand conditions.

Initial experiments and model design were conducted with seedlings of red spruce which, as a low-conductance species, shows relatively little response to ozone. Initial runs predicted only an 8% reduction in growth with $3 \times$ ambient-ozone treatment (at Ithaca, NY; Laurence et al. 1993). Weinstein and Yanai (1994) used TREGRO to predict that the interactive effects of ozone stress and magnesium deficiency would be less than the sum of the individual stresses. Retzlaff et al. (1997) applied TREGRO to a 160-year-old maple tree in Ithaca, and again showed that a $2 \times$ current-ozone treatment (Ithaca, NY) results in only a 4% reduction in total carbon gain.

In a regional assessment of two different types of ponderosa pine, Constable and Taylor (1997) showed a linear decrease in net photosynthesis with increasing exposure (ppm per hr); the slower-growing type with lower stomatal conductance was less affected. A related study, focused on conditions in Corvallis, Oregon, tested the combined effects of CO_2 (more than 200 ppm), ozone (increased by 0.5, 1.0, and $2.0 \times$ current level), and temperature (+4°C). CO_2 alone increased growth by 29%, temperature alone by 13%, and both com-

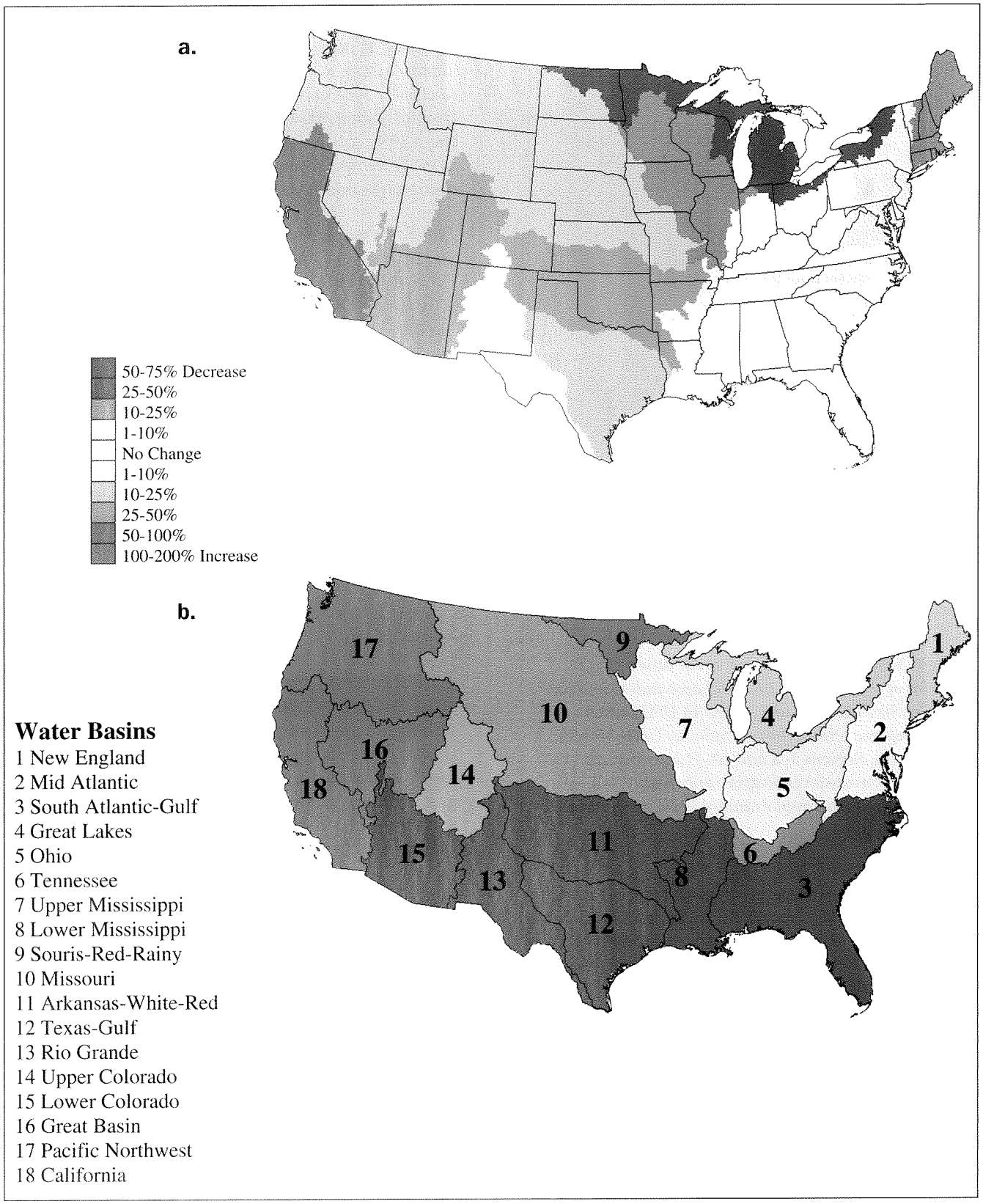

Figure 6. Average simulated change in (a) LAI (leaf area index) and (b) runoff by the MAPSS model over seven future climate scenarios for the 18 USGS water resource regions within the coterminous United States. See Figure 7 for mean and range within each region.

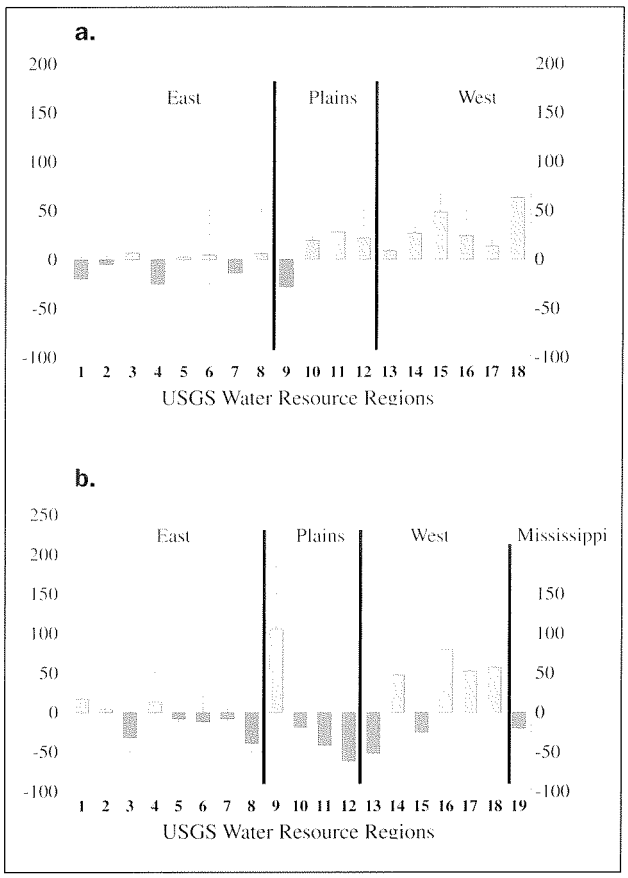

Figure 7. Mean and range across seven future climate scenarios of change in (a) LAI (leaf area index) and (b) runoff by the MAPSS model for the 18 USGS water resource regions within the coterminous United States (see Figure 6). Regions 5–8 and 10–11 have been summed to provide an indication of potential change over the entire Mississippi drainage basin, designated 19 in the figure.

bined by 49%. The three levels of ozone reduced growth by 1%, 19%, and 39%, respectively. Increased CO_2 reduced stomatal conductance and hence conferred some protection from ozone. The combined set of maximum treatments resulted in a nearly neutral effect on growth.

UTM/FORET/PTAEDA2. This combination of models has been applied to the question of ozone effects on NPP for southern pine forests (Luxmoore et al. 1997). The modeling structure involves an hourly time-step physiology model (UTM) which calculates water and carbon balances and is linked to the FORET model of tree competition and growth. Estimated tree growth is converted to site index values, which are then used to drive the forest management model (PTAEDA2).

Empirical data on the effects of ozone on loblolly pine photosynthesis were used to drive the model, and an assumption of loss of stomatal control over conductance following extreme ozone events was also included. Under these conditions, this combination of models was run for 5 years (1988–1992) using ambient climate and ozone data. Significant reductions in leaf area were predicted in high ozone years (especially 1988 and 1992). Total stand respiration was increased by about 6% and net photosynthesis was reduced by about 10%. Loss of stomatal control resulted in an increase in evapotranspiration of nearly 18% and total wood production was reduced by about 6%.

ITE Edinburgh model. This model, developed by Thornley and others, is a very short time-step (10 minutes), detailed physiological model of the effects of environmental drivers on plant physiology. In one application for forest plantations in the United Kingdom, the model was applied to test the interactive effects of changes in CO_2 and temperature over two forest rotations (Thornley and Cannell 1996). Results are similar to those reported above for other temperate humid forest systems. An increase in temperature alone (+3°C) resulted in increased water stress and reductions in growth. Increasing CO_2 alone removed all water stress and increased growth. Increased CO_2 in N-rich sites resulted in increased LAI, and on N-poor sites, in increased root production. Increased CO_2 also reduced conductance and so reduced transpiration, increasing water yield. Nitrogen leaching losses were also predicted to decline. Overall, the combination of increased CO_2 and temperature was predicted to increase forest production.

Unanswered questions and future research

Although many basic physiological relationships between climate change and plant growth have been addressed since the inception of the national global change research program in the early 1990s, understanding of the interactions between stresses on individual trees, and especially on multiple environmental stress interactions at the forest level, is still very limited. Specific examples include the interaction between atmospheric CO_2 and soil water and nutrient limitations on forest productivity, carbon sequestration, and species composition; the interactions between CO_2 and tropospheric O_3 on plant water-use efficiency; the migration rates of tree species under climate change; the rate of ecosystem establishment under climate change; and improved integration of forest process models that are used to predict future conditions.

In addition to increased understanding of the mechanism associated with climate change impacts on forests, improved and enhanced emphasis needs to be placed on long-term monitoring of forest composition and growth. These databases are critical to accurately developing the baseline from which future scenarios are calculated, and for use in validating model prediction of current conditions. A combination of permanent ground-based forest monitoring plots and improved remote sensing technologies could be instrumental in characterizing future US forests.

Compared with older, static GCM runs, the newer, dynamic climate scenarios used in this assessment predict a smaller increase in average US temperature during the next century. Biogeochemical model algorithms incorporate the effect of elevated atmospheric CO_2 into the models through increased water-use efficiency or other mechanisms. Generally, these conditions result in more productive forests across the United States. Looking across a wide range of scenarios, it appears that modest warming could result in carbon gains in most forest ecosystems in the coterminus United States. However, under the warmer scenarios, forests in the Southeast and Northwest could experience drought-induced losses of carbon, possibly through enhanced fire frequency and intensity. Much of the increased forest growth and carbon storage is based on incomplete or untested model integration between climate, forest vegetation, and soil interactions. For example, if there is no long-term CO_2 fertilization effect, then model predictions of a greener world are likely to be in error.

Potential gains and losses of carbon in some regions will be subject to land use patterns, especially conversions between forests and agricultural use. Current land-use patterns will also affect the expression of disturbances such as drought and fire. There may be opportunities for carbon sequestration in some regions currently under agriculture, such as the Upper Midwest. However, such conversions must be considered in the context of regional water resources which could be reduced if the full potential for carbon gain is allowed.

Even if US forests become more productive over the next century, there will very likely be a transitional period which could include increased fire, plant, and animal displacement (Hansen et al. 2001), as well as changes in the economic forest base (Irland et al. 2001). Fires are predicted to increase in the interior dry forests and parts of the Northwest under both transient scenarios. Under the Canadian scenario, fires could become a very significant feature of eastern US forests, although current land-use patterns could limit fire spread.

Acknowledgments

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