

## MODELING PATTERNS OF NONLINEARITY IN ECOSYSTEM RESPONSES TO TEMPERATURE, CO<sub>2</sub>, AND PRECIPITATION CHANGES

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**Abstract.** It is commonly acknowledged that ecosystem responses to global climate change are nonlinear. However, patterns of the nonlinearity have not been well characterized on ecosystem carbon and water processes. We used a terrestrial ecosystem (TECO) model to examine nonlinear patterns of ecosystem responses to changes in temperature, CO<sub>2</sub>, and precipitation individually or in combination. The TECO model was calibrated against experimental data obtained from a grassland ecosystem in the central United States and ran for 100 years with gradual change at 252 different scenarios. We primarily used the 100th-year results to explore nonlinearity of ecosystem responses. Variables examined in this study are net primary production (NPP), heterotrophic respiration ( $R_h$ ), net ecosystem carbon exchange (NEE), runoff, and evapotranspiration (ET). Our modeling results show that nonlinear patterns were parabolic, asymptotic, and threshold-like in response to temperature, CO<sub>2</sub>, and precipitation anomalies, respectively, for NPP, NEE, and  $R_h$ . Runoff and ET exhibited threshold-like pattern in response to both temperature and precipitation anomalies but were less sensitive to CO<sub>2</sub> changes. Ecosystem responses to combined temperature, CO<sub>2</sub>, and precipitation anomalies differed considerably from the responses to individual factors in terms of response patterns and/or critical points of nonlinearity. Our results suggest that nonlinear patterns in response to multiple global-change factors were diverse and were considerably affected by combined climate anomalies on ecosystem carbon and water processes. The diverse response patterns in nonlinearity have profound implications for both experimental design and theoretical development.

**Key words:** CO<sub>2</sub>; evapotranspiration; global change; grassland; heterotrophic respiration; net ecosystem carbon exchange; net primary production; nonlinear pattern; precipitation; runoff; temperature.

### INTRODUCTION

Global climate change usually involves simultaneous and continuous changes in atmospheric CO<sub>2</sub> concentration, earth surface temperature, and precipitation over a time of decades and centuries (IPCC 2001). Changes in the climate-forcing variables likely cause nonlinear responses of ecosystem structure and functioning, and alter ecosystem services to human society. Research has been done mostly with two discrete treatment levels of one or two factors to quantify effects of global change on ecosystem processes and mechanisms (Shaver et al. 2000, Weltzin et al. 2003, Ainsworth and Long 2004, Rustad 2006). The results from those experiments have no information on nonlinearity in response to climate change. Indeed, the Intergovernmental Panel on Climate Change (IPCC 2001) projected wide ranges of climate scenarios for each of the global-change factors. Manipulative experiments are not very feasible with numerous treatment levels for multiple global-change factors. Thus, the use of models can be of particular importance to examine how ecosystems could respond nonlinearly

to a range of potential future climates (e.g., temperature, CO<sub>2</sub>, and precipitation).

It is commonly acknowledged that ecosystem responses to global climate change are nonlinear, including accelerating, abrupt, and potentially irreversible changes (Ackerly and Bazzaz 1995, Gill et al. 2002, Burkett et al. 2005, Reid et al. 2005). Ecosystem nonlinearity is now becoming an increasingly important focus of global-change research (Pielke et al. 2003, Mayer and Rietkerk 2004), which was identified as high-priority research across the U.S. Federal government (Lucier et al. 2006). The Millennium Ecosystem Assessment (Reid et al. 2005) raised significant research needs to improve understanding of nonlinear changes in ecosystems, and this has been listed as one of the most important uncertainties hindering decision making. Meanwhile, several international programs have focused on nonlinear and threshold responses to climate change (Körner 2000, Pielke et al. 2003; see also Global Change and Terrestrial Ecosystems [GCTE] and International Geosphere-Biosphere Programme [IGBP], information *available online*).<sup>2,3</sup> More importantly, nonlinear responses have explained some of the apparent contradictory

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results observed in previous climate change studies (Zak et al. 1993, Rustad et al. 2001). Therefore, ecosystem nonlinearity is a vital and challenging component of global-change science, which may have an impact on how we design experiments, build models, and perceive ecosystem dynamics in a changing world (J. Reynolds, *unpublished manuscript*).

However, few experimental studies have examined nonlinear responses to global change factors on ecosystem carbon processes, even a single climate-change factor. For example, soil carbon storage and net nitrogen (N) mineralization in an intact C<sub>3</sub>–C<sub>4</sub> grassland of central Texas (USA) responded nonlinearly to a subambient-to-superambient CO<sub>2</sub> gradient (Mielnick et al. 2001, Gill et al. 2002). Responses to three levels of soil-gradient warming (i.e., 2.5°, 5.0°, and 7.5°C) in a northern hardwood forest were also nonlinear with respect to soil respiration and leaf-litter decomposition (Mchale et al. 1998). To date, there have been no manipulative experiments to examine nonlinear responses to a range of treatment levels for simultaneous changes in multiple global change factors such as temperature, CO<sub>2</sub>, and precipitation. Such experiments are also not very feasible in the near the future due to cost limitation and ecosystem complexities.

Quantitative ecosystem modeling can be of particular advantage in examining nonlinear response patterns (Reid et al. 2005, Groffman et al. 2006), though only a few studies have been carried out. For example, Luo et al. (1998) examined diverse nonlinear patterns of photosynthesis in response to a single CO<sub>2</sub> gradient due to relative changes in specific leaf area and leaf nitrogen concentration for soybean (*Glycine max*). Ackerley and Bazzaz (1995) revealed nonlinearity of community growth and reproduction in response to the CO<sub>2</sub> gradient based on plant competition of four species. We are aware of only one modeling study to examine ecosystem nonlinear responses to simultaneous changes in temperature, CO<sub>2</sub>, and precipitation using a dynamic global vegetation model (DGVM) within a region of Amazonia (Cowling and Shin 2006). However, this study mainly focused on threshold responses in tropical rain forest ecosystems, there were only three CO<sub>2</sub> scenarios (e.g., –100, control, and +100 ppmv [parts per million by volume]). It is not clear how other ecosystems such as grasslands may respond to a range of levels of multiple global change factors and what response patterns of nonlinearity would be on ecosystem carbon and water processes.

In our present modeling study we used a terrestrial ecosystem (TECO) model to examine nonlinear patterns of ecosystem carbon and water dynamics in response to a range of individual and simultaneous changes in temperature, CO<sub>2</sub>, and precipitation. The TECO model was calibrated against experimental data obtained from a grassland ecosystem in the central United States. Climate-change scenarios varied gradually within 100 years. Variables of carbon and water cycles examined in

the study are net primary production (NPP), heterotrophic respiration ( $R_h$ ), net ecosystem carbon exchange ( $NEE = NPP - R_h$ ), runoff, and evapotranspiration (ET). We also discuss implications of experimental studies and model assumptions.

## MATERIALS AND METHODS

### *Model description*

The terrestrial ecosystem (TECO) model evolves from a terrestrial carbon sequestration (TCS) model (Luo and Reynolds 1999) and was designed to examine ecosystem responses to perturbations in global-change factors such as elevated CO<sub>2</sub>, warming, and altered precipitation. The model has been extensively applied to the modeling study at the Duke Forest (Chapel Hill, North Carolina, USA) CO<sub>2</sub>-enrichment experiment (Luo et al. 2001a, 2003, Xu et al. 2006). The details of the TECO model are described in E. Weng and Y. Luo (*unpublished manuscript*). Here we provide only a brief overview.

The TECO model has four major components: a canopy photosynthesis submodel, a soil water dynamic submodel, a plant growth submodel, and a soil carbon transfer submodel (Fig. 1). The canopy photosynthesis and soil-moisture dynamics submodels were simulated at the hourly time step, while the plant growth and soil carbon transfer submodels ran at a daily step. Temperature-driven changes in phenology and the length of growing seasons were simulated on a carbon-gain-based scheme (Arora and Boer 2005). Acclimation of physiological and ecological processes to warming and elevated CO<sub>2</sub> was not imposed on model runs unless it was simulated internally via changes in nutrient dynamics or water stress.

The canopy-photosynthesis submodel is a multi-layer process-based model that mainly evolved from the model developed by Wang and Leuning (1998), to simulate canopy conductance, photosynthesis, and energy partitioning by calculating radiation transmission based on Beer's law. For each layer, foliage is divided into sunlit and shaded leaves. Leaf photosynthesis is estimated based on the coupled Farquhar photosynthesis model (Farquhar et al. 1980) and the Ball-Berry stomatal-conductance model as described by Harley et al. (1992). The soil water dynamic submodel stratifies soil into 10 layers. The soil water content of these layers is determined by mass balance between water influx and efflux. The water influx is precipitation for the surface layer and percolation for deeper layers. The water efflux includes evaporation, transpiration, and runoff. Evaporation rate is mainly controlled by the water content of the first soil layer and evaporative demand of the atmosphere. Transpiration changes the water content of the layers where roots reach. In our model runs, rooting depth in grassland was assumed as 70 cm, reaching to the fourth soil layer. The roots had a constant distribution ratio in the four soil layers based on observed root profiles in grasslands from the scientific literature (Jackson et al. 1996, Barrett 2002).

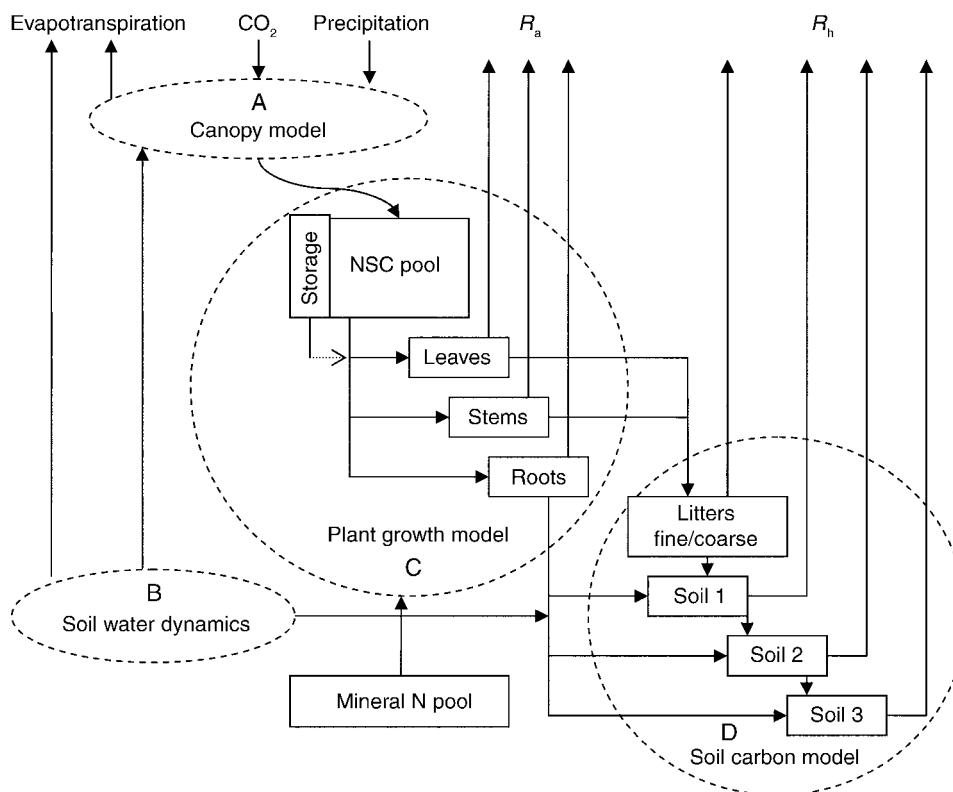


FIG. 1. Schematic diagram of structure of terrestrial ecosystem (TECO) model. Boxes represent pools, and the dashed circles and ovals represent four submodels (A–D). NSC is nonstructural carbon;  $R_a$  is autotrophic respiration including leaf, stem, and root respiration; and  $R_h$  is heterotrophic respiration including litter and soil organic matter (SOM) decomposition (Z. Weng and Y. Luo, unpublished manuscript).

The plant-growth submodel simulates carbon allocation and phenology following ALPHAPHA model (Denison and Loomis 1989) and CTEM (Canadian terrestrial ecosystem model; Arora and Boer 2005), respectively. Allocation of assimilates over the plant components depends on growth rates of leaves, stems, and roots, and varies with phenology. Phenology is represented by annual variation of leaf-area index (LAI). Leaf onset is initiated by growing degree days (GDD). Litterfall is induced by low temperature and soil drought. In the carbon-transfer submodel, a soil profile is divided into three layers with carbon movement from upper to lower layers in this study. Carbon inputs to the soil from plant residues are partitioned into these three layers based on the soil carbon-transfer part of the VAST (vegetation and soil carbon transfer) model (Barrett 2002).

*Study site*

The study site was located at the Kessler’s Farm Field Laboratory (KFFL) in McClain County, Oklahoma, USA (34°59’ N, 97°31’ W), ~40 kilometers southwest of the Norman campus of the University of Oklahoma. It is an old-field tallgrass prairie abandoned from agriculture 30 years ago and without grazing for 25 years. The grassland is dominated by three  $C_4$  grasses, *Schizachyrium scoparium*, *Sorghastrum nutans*, and *Eragrostis*

*curvula*, and two  $C_3$  forbs, *Ambrosia psilostachya* and *Xanthocephalum texanum*. Mean annual temperature is 16.3°C, with monthly air temperature ranging from 3.3°C in January to 28.1°C in July. Mean annual precipitation is 915 mm (Oklahoma Climatological Survey). A silt loam soil in the grassland includes 35.3% sand, 55.0% silt, and 9.7% clay. The soil belongs to part of the Nash-Lucien complex with neutral pH, high available water capacity, and a deep, moderately penetrable root zone (U.S. Department of Agriculture 1979).

*Input data*

Daily climate variables used in this study were from the MESONET station of Washington, Oklahoma (2000 to 2005 data set), including air temperature, soil temperature, vapor-pressure deficit, relative humidity, precipitation, and incident photosynthetically active radiation. Equilibrium state was accomplished by running the model using repeated cycles of the six-year climate set. Simulations were run from bare ground for 1000 years, at which time climate-change scenarios were imposed.

*Model validation*

In this grassland we used soil respiration, above-ground biomass (AGB), belowground biomass (BGB),

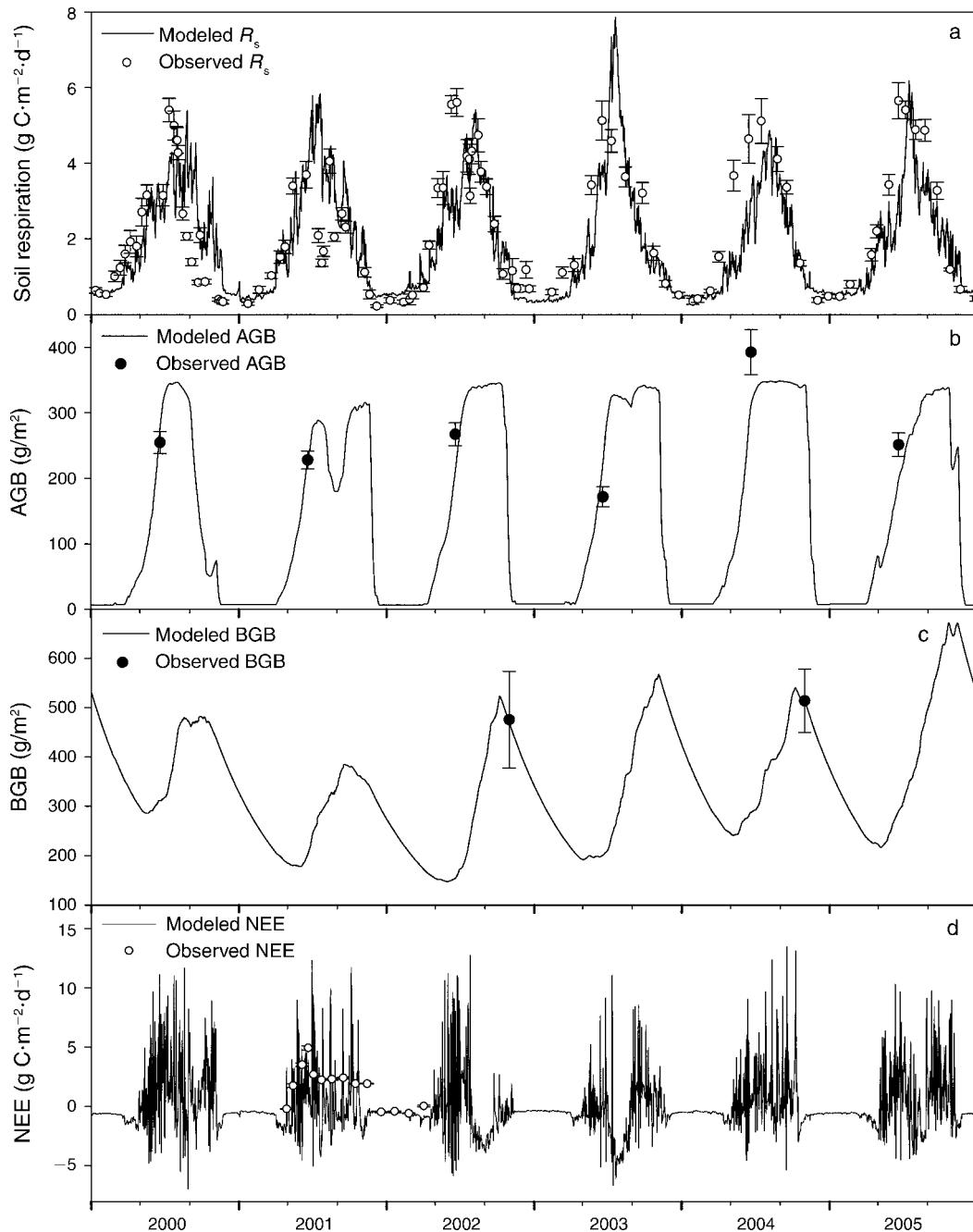


FIG. 2. Observed (circles) vs. simulated (lines) daily (a) soil respiration, (b) aboveground biomass (AGB), (c) belowground biomass (BGB), and (d) net ecosystem exchange of carbon (NEE) in Oklahoma (USA) grassland over six years. Error bars denote  $\pm$ SE.

and net ecosystem exchange of carbon (NEE) to validate the simulated values. Observed soil respiration was measured approximately once a month using LI-COR 6400 (LI-COR, Lincoln, Nebraska, USA) with soil CO<sub>2</sub> flux chamber (Luo et al. 2001b, Wan et al. 2005, Zhou et al. 2006, 2007). Observed aboveground biomass was measured once a year and belowground biomass was only determined in October 2002 and 2004 (Wan et al.

2005; Y. Luo, B. Sherry, X. Zhou, and S. Wan, *unpublished manuscript*). NEE was measured monthly in 2001 (X. Liu and Y. Luo, *unpublished data*). For all these variables, the simulated results are in good agreement with observational data except an overprediction of soil respiration in summer 2001 (Fig. 2). However, paired *t* tests between simulated and observed soil respiration indicate no significant difference ( $P = 0.21$ ).

TABLE 1. Scenarios examined in this study.

Global-change factors	Treatment levels†
Temperature (°C)‡	-2, 0, +2, +4, +6, +8, +10
CO <sub>2</sub> concentration (%)§	-20, 0, +30, +60, +100, +140
Precipitation (%)	-40, -20, 0, +30, +60, +100

† Positive or negative values represent absolute increases or decreases in temperature (°C) and percentages of increases or decreases compared to the control for CO<sub>2</sub> concentration and precipitation.

‡ Zero (0) represents the current condition (i.e., control), and mean air temperature for this study is 16°C.

§ Zero (0) represents 350 ppm by volume of the CO<sub>2</sub> concentration (range: 280–840 ppmv).

|| Zero (0) represents the current condition (i.e., control), and annual precipitation is 804 mm (range: 482–1608 mm).

Modeling scenarios

Our experimental simulations involved each climate anomaly individually and in combination (i.e., temperature, CO<sub>2</sub>, and precipitation). Temperature anomaly influences all ecosystem processes by soil and air temperature. CO<sub>2</sub> anomaly affects them by stomatal conductance. Precipitation anomaly affects ecosystem processes by soil water content dynamics. Multifactor interactions occur through a series of feedbacks

involving leaf physiology, foliar N concentration, carbon allocation, biomass production, soil moisture availability, litter C:N ratios, decomposition, soil N supply, and plant N demand. To evaluate the individual and combined effects of temperature, CO<sub>2</sub>, and precipitation, we conducted a total of 252 simulations (including all possible interactions of the climate anomalies and control) (Table 1). All anomalies were changed gradually (mean changes within 100 years) starting in 2000 and ending by 2100. Because dynamic responses from 2000 to 2100 to changes in different scenarios were not the main focus of this study and were similar to other studies (Campbell et al. 1997, Hanson et al. 2005), we only present modeling results of ecosystem responses at the 100th-year data for NPP, R<sub>h</sub>, NEE, runoff, and ET to examine nonlinear patterns.

RESULTS

Nonlinear responses to single factor changes

Simulated NPP (net primary production), R<sub>h</sub> (heterotrophic respiration), and NEE (net ecosystem exchange of carbon) all show parabolic-curve responses to temperature anomalies from -2°C to +10°C compared to current condition (Fig. 3a, d). NPP and R<sub>h</sub> increased

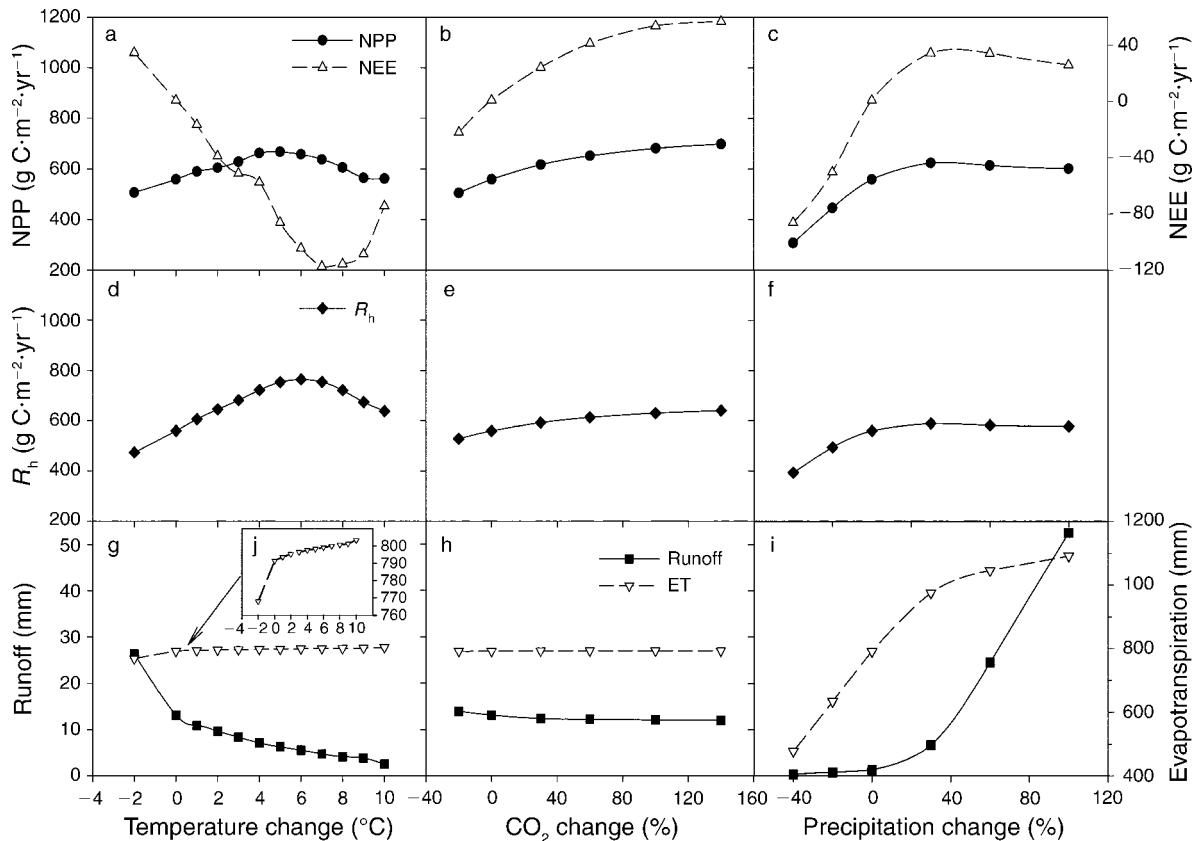


FIG. 3. Responses of net primary production (NPP), heterotrophic respiration (R<sub>h</sub>), net ecosystem exchange (NEE), runoff, and evapotranspiration (ET) to single-factor changes in temperature (a, d, g), CO<sub>2</sub> (b, e, h), and precipitation (c, f, i). Runoff in panel (i) has been divided by 10. Inserted panel (j) represents response of ET to temperature at a fine scale from 760 to 810 mm.

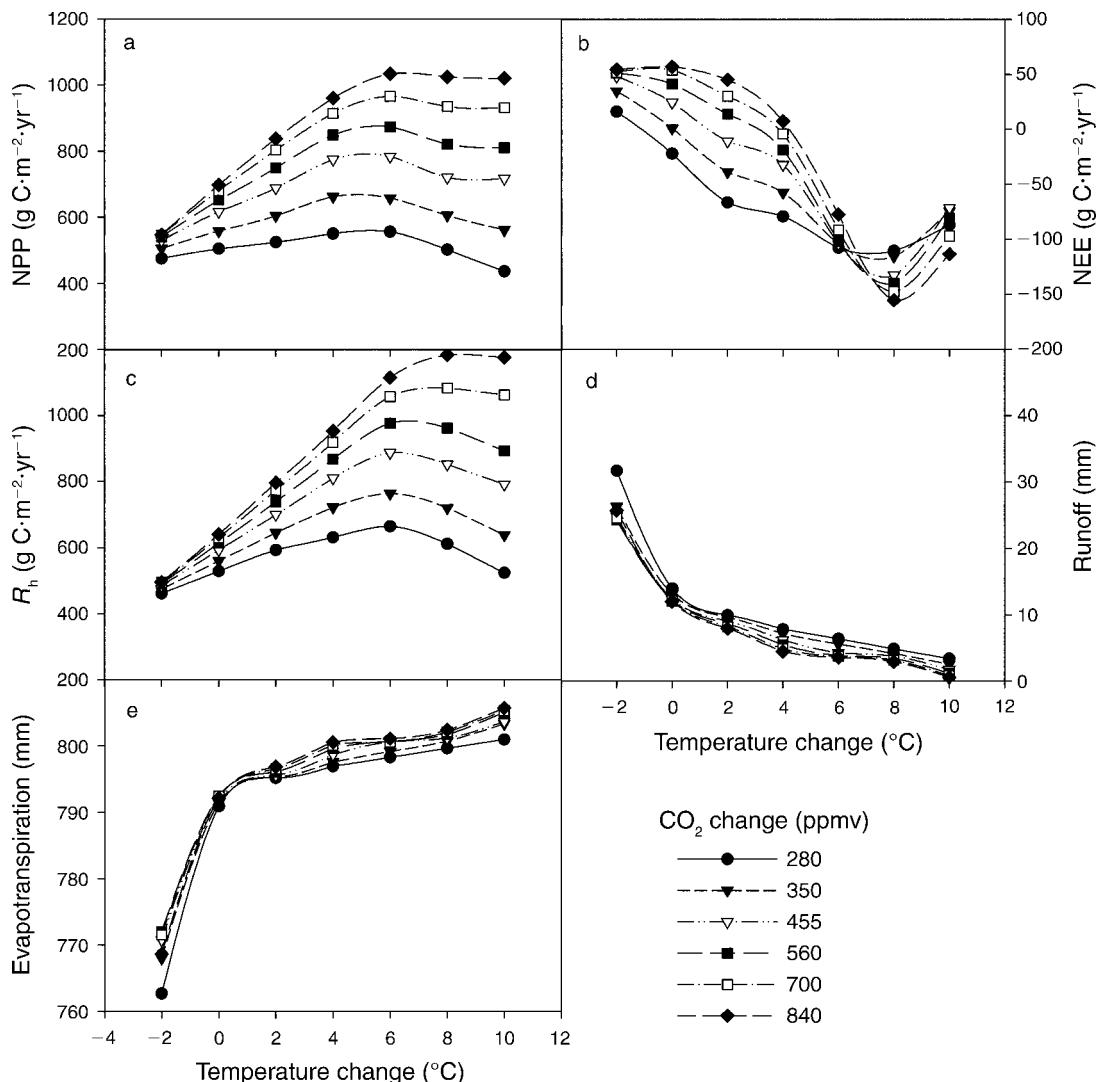


FIG. 4. Responses of (a) NPP, (b) NEE, (c)  $R_h$ , (d) runoff, and (e) ET to simultaneous changes in temperature and  $\text{CO}_2$  (ppmv is parts per million by volume). See Fig. 3 for explanation of abbreviations.

with temperature, reached a peak at  $+5^\circ\text{C}$  (NPP) or  $+6^\circ\text{C}$  ( $R_h$ ), and then declined, while NEE had an adverse trend with a lowest value at  $+7^\circ\text{C}$ . Increases in  $\text{CO}_2$  concentration from 280 to 840 ppmv stimulated NPP,  $R_h$ , and NEE with an asymptotic curve (Fig. 3b, e). However, responses of NPP,  $R_h$ , and NEE to precipitation changes from  $-40\%$  to  $+100\%$  compared to current condition display threshold-like curves (Fig. 3c, f), which increased with precipitation at the beginning and then reached a plateau. If we define “threshold” as a point at which there is an abrupt change in response to external stimuli, our modeling results indicate that precipitation threshold values were about  $+30\%$  for NPP and NEE and near current condition for  $R_h$ .

For runoff and ET (evapotranspiration) of water cycle, response patterns to individual temperature and precipitation changes were threshold-like, while the

response to  $\text{CO}_2$  changes was less sensitive (Fig. 3g–j). Runoff decreased in response to increasing temperature while ET increased, but both with similar threshold values near current conditions. Runoff and ET responded positively to precipitation changes but with different threshold values, which were near current condition for runoff and about  $+30\%$  for ET.

#### *Nonlinear responses to simultaneous changes in multiple factors*

Changes in  $\text{CO}_2$  concentration not only affected turning points or threshold values of temperature responses but also varied nonlinear response shapes for NPP,  $R_h$ , and NEE compared to the ambient  $\text{CO}_2$  (350 ppmv, Fig. 4). Specifically, with increasing  $\text{CO}_2$  concentration from 280 to 840 ppmv, turning points of temperature responses increased by  $1^\circ\text{C}$  from  $+5^\circ$  to

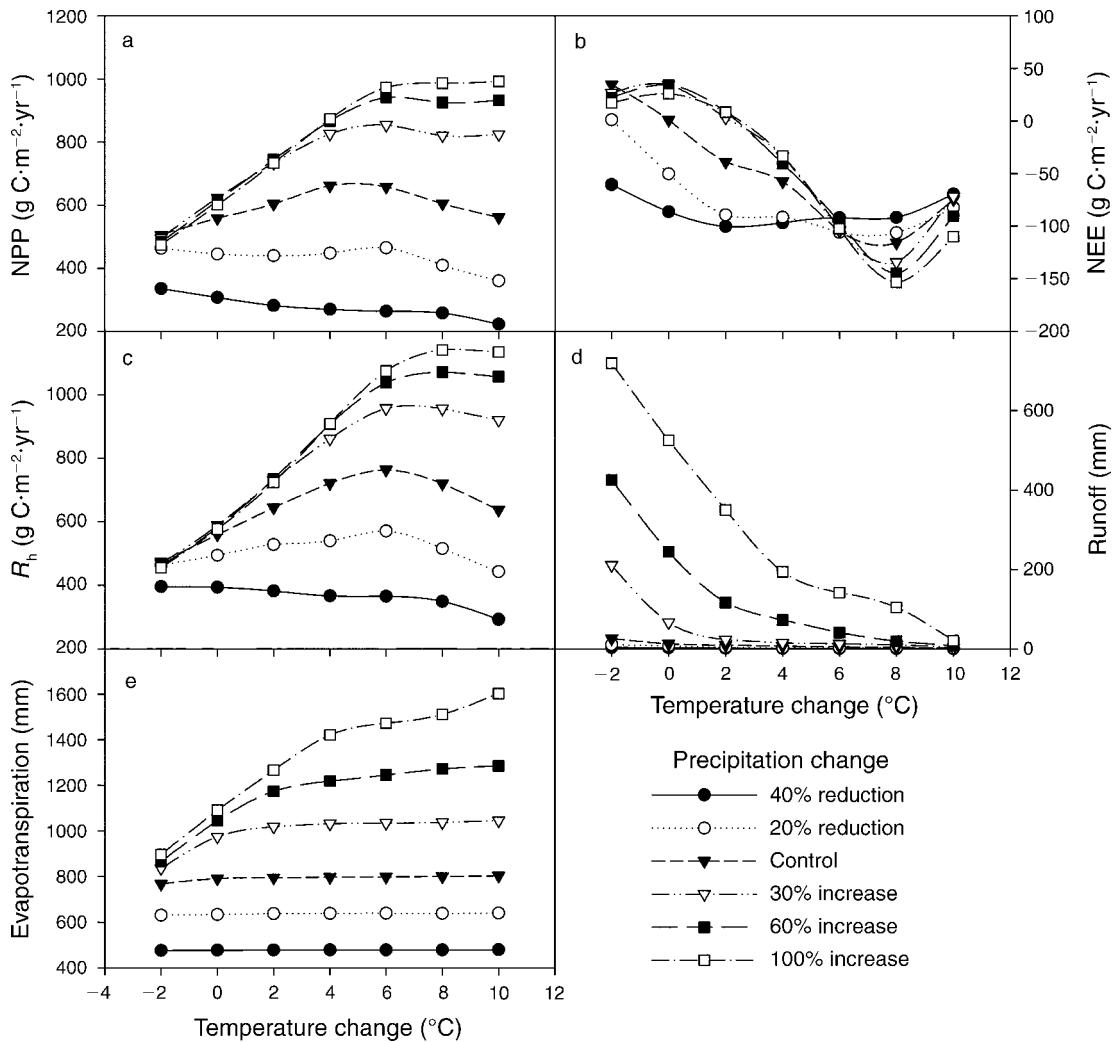


Fig. 5. Responses of (a) NPP, (b) NEE, (c)  $R_h$ , (d) runoff, and (e) ET to simultaneous changes in temperature and precipitation. See Fig. 3 for explanation of abbreviations.

+6°C for NPP and from +6° to +7°C for  $R_h$ . Nonlinear patterns of temperature responses shifted from parabolic patterns below 560 ppmv to threshold-like curves above 700 ppmv (Fig. 4a, c). The lowest values of NEE were in +6°C under 280 ppmv of CO<sub>2</sub> concentration and +8°C above 560 ppmv compared to +7°C in the control (CO<sub>2</sub> = 350 ppmv) (Fig. 4b). However, there were no interactive effects of temperature and CO<sub>2</sub> on runoff and ET (Fig. 4d, e).

Similarly, with increasing precipitation from -40 to +100%, both response curves and threshold points were also affected (Fig. 5). Temperature response curves were relatively insensitive under -40% of precipitation, were parabolic under -20% and current condition, and became threshold-like above +30% for NPP and  $R_h$  (Fig. 5a, c). The lowest values of NEE were in +2°C under -40% and -20% of precipitation and +8°C above +30% compared to +7°C in the control (Fig. 5b). Responses of runoff and ET to temperature anomalies were relatively

insensitive under -40%, -20%, and current condition of precipitation and became threshold-like patterns above +30% (Fig. 5d, e). Temperature threshold values increased from 1°C under +30% to 4°C under +100% of precipitation for both runoff and ET. With increasing CO<sub>2</sub> concentration, precipitation response curves did not vary, while their threshold values decreased from about +30% of precipitation under 280 ppmv to current condition under 840 ppmv for NPP, NEE, and  $R_h$  (Fig. 6a-c).

For simultaneous changes in temperature, CO<sub>2</sub>, and precipitation, we only show NPP and NEE for the carbon cycle due to the similar trend between NPP and  $R_h$  under three CO<sub>2</sub> concentrations, representing preindustrial, current, and future conditions. The three factors interactively changed response patterns and turning points or threshold values for NPP and NEE (Fig. 7). For example, temperature turning points or threshold values of NPP did not change with increasing

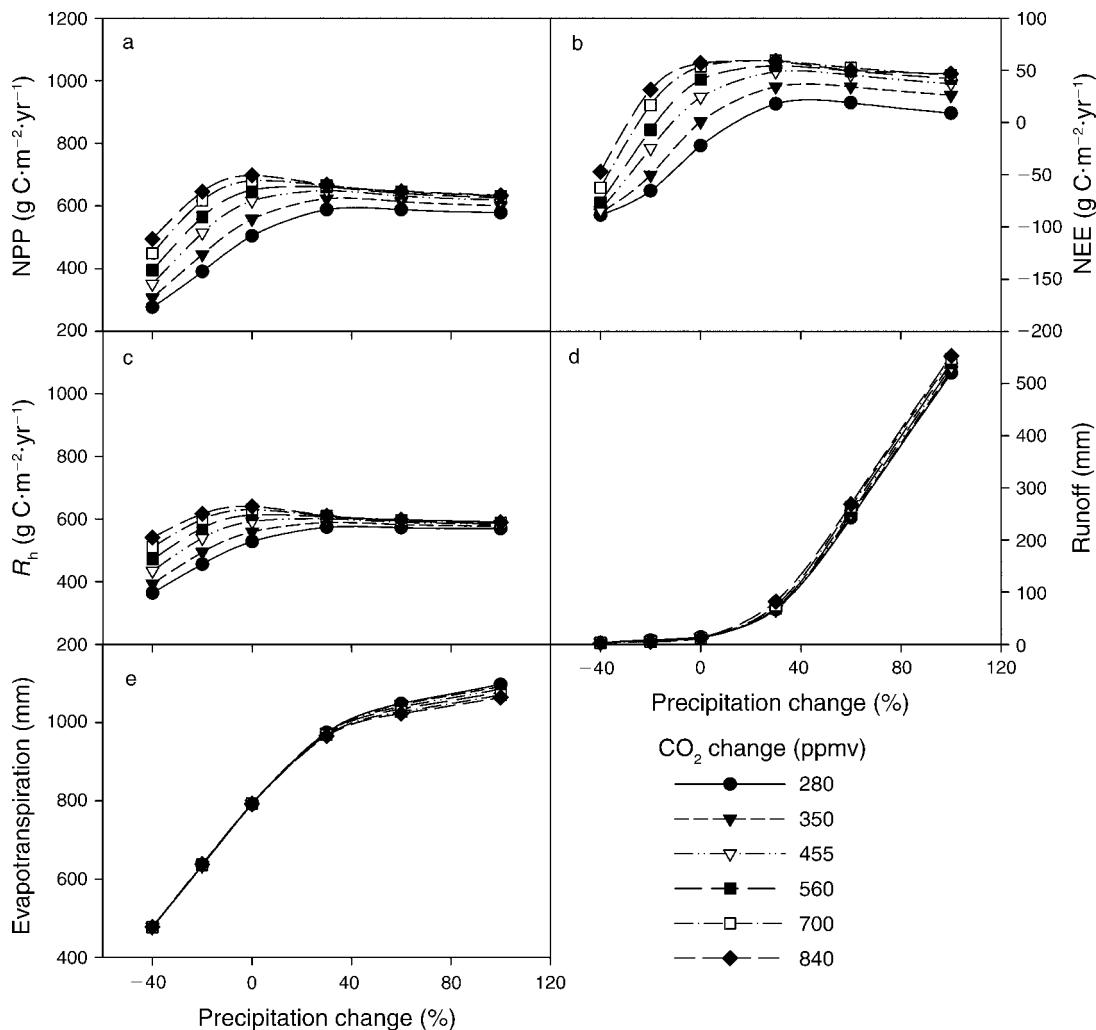


FIG. 6. Responses of (a) NPP, (b) NEE, (c)  $R_h$ , (d) runoff, and (e) ET to simultaneous changes in precipitation and  $\text{CO}_2$ . See Fig. 3 for explanation of abbreviations.

precipitation under 280 ppmv of  $\text{CO}_2$  concentration, increased from  $+5^\circ$  to  $+6^\circ\text{C}$  under 350 ppmv, and increased from  $+5^\circ$  to  $+8^\circ\text{C}$  under 700 ppmv (Fig. 7a, c, e). The lowest values of NEE were  $+2^\circ\text{C}$  at  $-40\%$  of precipitation under 280 and 350 ppmv, while it was  $6^\circ\text{C}$  under 700 ppmv (Fig. 7b, d, f). However,  $\text{CO}_2$  concentration did not significantly affect responses of runoff and ET to simultaneous changes in temperature and precipitation (Fig. 8).

#### DISCUSSION

Nonlinear changes have commonly occurred in ecosystems and their services (e.g., Burkett et al. 2005, Reid et al. 2005, Groffman et al. 2006). Our modeling analysis demonstrates diverse nonlinear patterns of ecosystem carbon and water dynamics in response to global change factors. Response patterns of net primary production (NPP), heterotrophic respiration ( $R_h$ ), and net ecosystem exchange of carbon (NEE) were in

parabola, asymptotic, and threshold-like shapes to individual changes in temperature,  $\text{CO}_2$ , and precipitation, respectively (Fig. 3a–f). Runoff and evapotranspiration (ET) also responded nonlinearly to temperature and precipitation anomalies with a threshold-like pattern but were less sensitive to changing  $\text{CO}_2$  (Fig. 3g–j). Combinations of temperature,  $\text{CO}_2$ , and precipitation anomalies interactively affected nonlinearity by changing response patterns (Figs. 4, 5, 7, and 8) and/or shifting critical points of nonlinearity (e.g., turning points or threshold values, Figs. 4–7). The nonlinear dynamics and multifactor interactions of ecosystem carbon and water processes greatly complicate the interpretation and predictability of ecosystem-level responses. Our modeling study indicates that a diversity of nonlinear patterns in response to multiple global-change factors and effects of combined climate anomalies should be of concern in choosing scenarios of

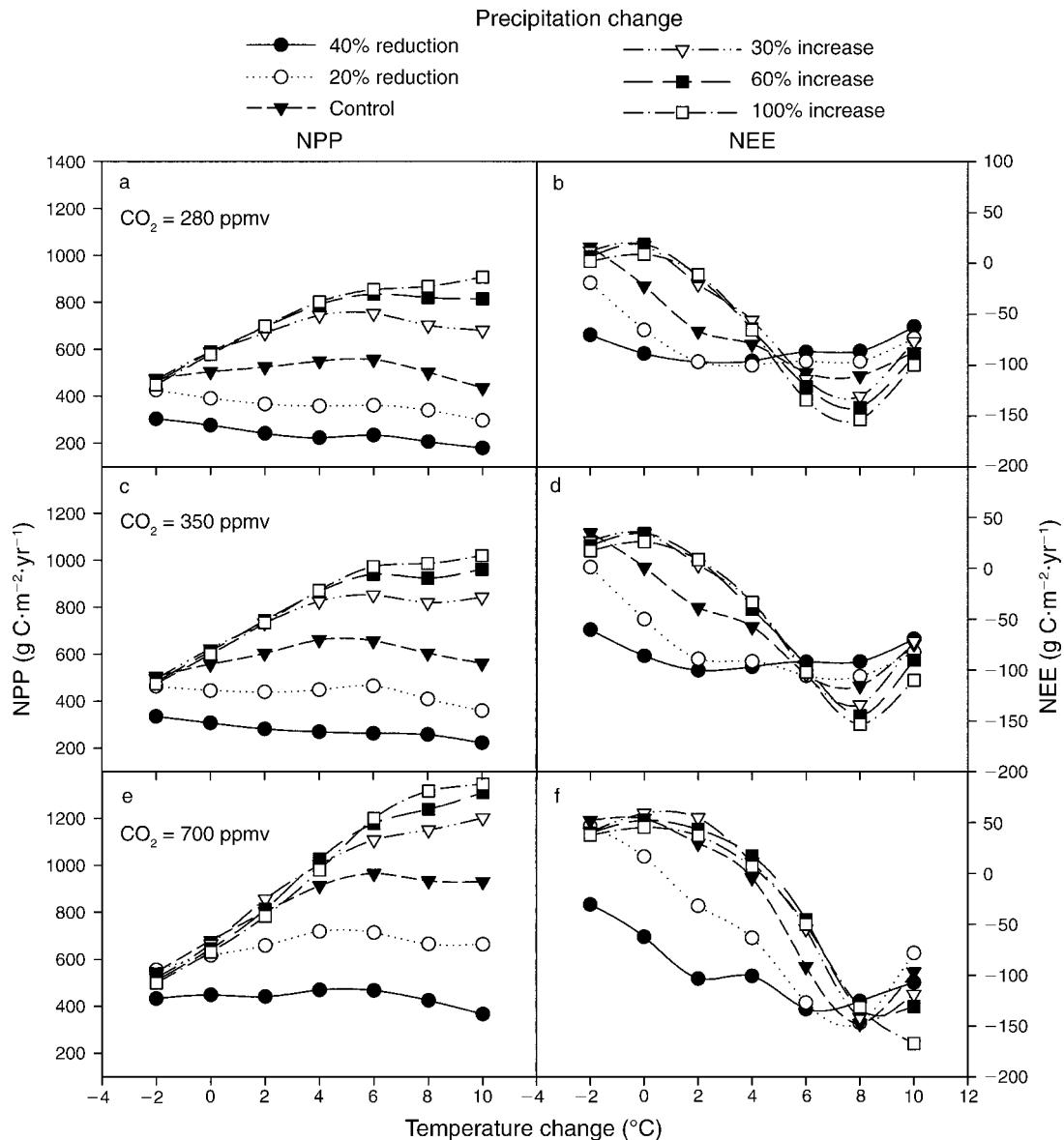


FIG. 7. Responses of NPP (a, c, e) and NEE (b, d, f) to simultaneous changes in temperature, CO<sub>2</sub>, and precipitation. See Fig. 3 for explanation of abbreviations.

climate change to predict ecosystem responses and to set up new experiments.

*Nonlinear responses to single factor changes*

Our results of model simulations exhibit different patterns of nonlinear responses to individual changes in temperature, CO<sub>2</sub>, and precipitation for NPP, R<sub>h</sub>, NEE, runoff, and ET. A parabolic pattern in response to temperature change was observed in NPP and R<sub>h</sub> (Fig. 3a, d). At a low temperature range, warming stimulated both plant biomass growth and soil respiration due to extended growing season and enhanced N-mineralization rates (Rustad et al. 2001, Hanson et al. 2005, Wan et al. 2005), leading to increases in the two fluxes with

temperature. At a high temperature range the stimulation of warming declined with increasing temperature due to soil moisture limitation (Drake et al. 1997), because the effects of climate warming on production and decomposition were strongly dependent on interactions with soil moisture (Ise and Moorcraft 2006). Our results were consistent with that under three levels of soil-gradient warming in a northern hardwood forest, in which soil respiration and leaf litter decomposition were less in +7.5°C than +2.5° and +5°C (McHale et al. 1998). However, R<sub>h</sub> was more responsive to warming than was NPP (Kirschbaum 2000), resulting in a decrease in NEE with increasing warming at a low temperature

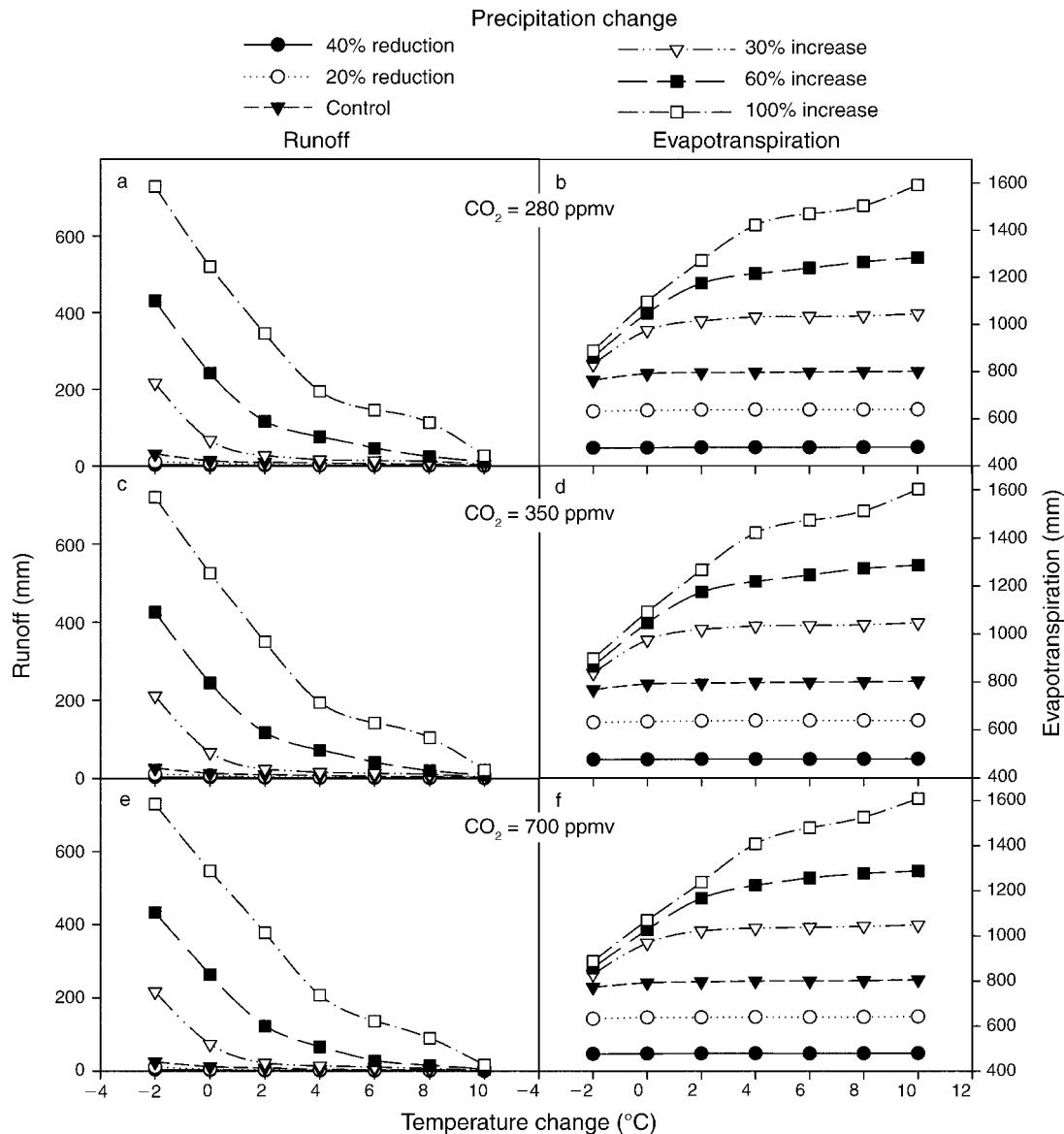


FIG. 8. Responses of runoff (a, c, e) and ET (b, d, f) to simultaneous changes in temperature,  $CO_2$ , and precipitation. See Fig. 3 for explanation of abbreviations.

range and slight recovery at a high temperature range (Fig. 3a).

The responses of NPP, NEE, and  $R_h$  to a gradient of  $CO_2$  levels were in an asymptotic shape (Fig. 3b, e). The stimulated effects were similar to observed results from a manipulative experiment in central Texas for a continuous gradient of  $CO_2$  from 200 to 550  $\mu\text{mol/mol}$  (Mielnick et al. 2001, Gill et al. 2002, Polley et al. 2003, 2007). Along that gradient,  $CO_2$  enrichment increased photosynthesis (Mielnick et al. 2001), biomass production (Polley et al. 2003), net carbon uptake (Gill et al. 2002), and ecosystem respiration (Polley et al. 2006). A further enhancement of  $CO_2$  supply may reduce the stimulated effects on the rate of uptake due to

$CO_2$  saturation to photosynthesis and then diminishing  $CO_2$  sensitivity (Körner 1995, Lambers et al. 1998). Furthermore, increased plant demand for N and reduced foliar N concentrations enhanced with increasing  $CO_2$  concentration, and then altered litter C:N ratios and decomposition rates to affect NPP, NEE, and  $R_h$  (Johnson 1999, Ainsworth and Long 2004). However, the compiled response patterns of plant processes (e.g., photosynthesis) along  $CO_2$  gradients were diverse, with the positive, negative, nonmonotonic, and nonsignificant (flat) ones largely due to photosynthetic acclimation and specific-species responses (Ackerley and Bazzaz 1995, Luo et al. 1998). Our model was built within an ecosystem framework and did not impose acclimation of

ecological processes to climate change unless it was simulated internally via changes in nutrient dynamics or water stress, resulting in only asymptotic response patterns to changing CO<sub>2</sub>.

The threshold-like pattern occurred for NPP, NEE,  $R_h$ , runoff, and ET in response to precipitation change (Fig. 3c, f, i). Precipitation threshold values are about +30% for NPP, NEE, and ET and near-current condition (+0%) for  $R_h$  and runoff. The threshold response curves indicate that a relatively rapid change is occurring in the carbon and water fluxes currently or in the near future. Once ecosystems pass the threshold, recovery to the original state may take decades or centuries and may sometimes be impossible (Reid et al. 2005). To date, little information was available in manipulative precipitation experiments, although similar threshold response patterns have been reported along natural rainfall gradients (Austin 2002, Austin and Sala 2002). In a rainfall-manipulation experiment with decreasing water input by rainout shelters, Yahdjian and Sala (2006) showed that aboveground NPP and plant density linearly increased with precipitation, which was consistent with our results at the low-precipitation range. Similarly, runoff and ET also have a threshold response pattern to temperature change. Their temperature threshold values are near current condition.

*Nonlinear response to simultaneous changes  
in multiple factors*

Ecosystem responses to combined temperature, CO<sub>2</sub>, and precipitation anomalies differed considerably from the responses to individual factors in terms of patterns or critical points of nonlinearity (Figs. 4–8). For example, responses of NPP and  $R_h$  to changes in temperature at ambient CO<sub>2</sub> (350 ppm) and precipitation (804 mm) can be described by a parabolic curve (Fig. 3a, d). The parabolic patterns were gradually transformed to threshold-like patterns as CO<sub>2</sub> concentration increased from 280 ppm to 840 ppm (Fig. 4a, c) or as precipitation increased from the ambient level to the doubled level (Fig. 5a, c). The parabolic patterns at ambient precipitation were, however, transformed to a linear pattern when precipitation decreased 40% from the ambient level (Fig. 5a, c). The transformation from the parabolic to threshold-like patterns as CO<sub>2</sub> or precipitation increased resulted from the fact that increased resource availability alleviated adverse effects of high temperature on NPP and  $R_h$ . Increased CO<sub>2</sub> concentration usually resulted in reduced stomatal conductance, increased water-use efficiency (WUE), and enhanced N mineralization and plant N uptake under elevated CO<sub>2</sub> (Drake et al. 1997, Johnson 1999, Lilley et al. 2001, Ainsworth and Long 2004, Wall et al. 2006). Changes in those processes would minimize adverse effects of soil drying and water stress under high temperature. With increasing CO<sub>2</sub> concentration, CO<sub>2</sub> saturation to photosynthesis (Körner 1995, Lambers et al. 1998), increased plant demand for N, and

reduced foliar N concentrations (Johnson 1999, Ainsworth and Long 2004) may result in shifts of temperature response patterns from parabolic to threshold-like curves (Fig. 4).

Increasing precipitation certainly offset negative effects of high temperature, resulting in higher turning points of nonlinearity (Fig. 5). However, a reduction in precipitation caused large changes in temperature response curves and became more flat compared to ambient precipitation because it enhanced water stress irrespective of climate warming (Ise and Moorcraft 2006). Temperature response curves of runoff and ET also varied largely with increasing precipitation because the terrestrial ecosystem (TECO) model only simulated changes in precipitation amount but not its variability, resulting in large runoff and ET under increasing precipitation (Fig. 5d, e). With increasing CO<sub>2</sub> concentration, precipitation threshold values of NPP, NEE, and  $R_h$  decreased due to water saving effects of CO<sub>2</sub> enrichment on stomatal conductance and WUE (Drake et al. 1997). The interaction of combined temperature, CO<sub>2</sub>, and precipitation anomalies was complicated through both changing response patterns and turning points of nonlinearity (Figs. 7 and 8). The mechanisms discussed above (i.e., one- or two-factor changes) led us to understand these changes in response patterns of carbon and water fluxes and critical points of nonlinearity in this grassland.

To date, there was no experimental evidence on ecosystem nonlinear patterns in response to multiple treatment levels of combined climate-change anomalies, though several mesocosm experiments (e.g., chamber and tunnel) have exposed specific plants to three levels of both temperature and CO<sub>2</sub> (Hadley et al. 1995, Usami et al. 2001, He et al. 2005). Those results only showed that the interactive effects of warming and elevated CO<sub>2</sub> resulted in a larger growth enhancement than warming alone in the one-year experiment. The short-term results could reveal large uncertainty in predicting long-term ecosystem responses to climate change based on leaf- or plant-level response (Körner 1995). The only model study, by Cowling and Shin (2006), showed that temperature threshold values decreased with increasing precipitation in Amazonian tropical rainforests. In contrast, temperature threshold values increased with increasing precipitation in this study due to decreasing water stress (Ise and Moorcraft 2006, Wall et al. 2006). The different responses may result from the difference in models (DGVM [dynamic global vegetation model] vs. TECO) and ecosystem types (tropical forest vs. grassland). With very limited data sets, it is too early to rigorously evaluate consistency between model simulations and between modeling and experimental results.

*Implications for experimental studies*

Our modeling results from numerous scenarios provide insight as to how ecosystems might respond to a broad range of global-change factors compared to

responses from manipulative experiments with limited treatment levels. Thus, our study will offer suggestions for experimental studies on ecosystem responses to multiple global-change factors, at least in three aspects. First, as expected, our results exhibit ecosystem nonlinearity in response to global-change factors. However, most experiments were currently manipulated in two treatment levels of one or two factors. Although those results provided single-factor pulse response under climate change and/or two-factor interaction, there was no information on ecosystem nonlinearity along the gradients of climate change. Thus, caution should be taken on interpretation of results. Linear interpolation or extrapolation of experimental results may yield large errors. For example, if the nonlinear pattern was parabolic in response to temperature (Fig. 3a), the same response magnitude occurred under two treatment levels (e.g., 3° and 7°C for NPP).

Second, the nonlinear patterns of ecosystem carbon and water dynamics in response to individual changes in temperature, CO<sub>2</sub>, and precipitation were different. The diverse patterns indicate the necessity of conducting experimental studies with individual gradient of temperature, CO<sub>2</sub>, and precipitation changes. Although some experiments have included field manipulations, e.g., a continuous gradient of CO<sub>2</sub> from 200 to 550 ppmv in central Texas (Gill et al. 2002), the range under experimental manipulation was narrower compared to the Intergovernmental Panel on Climate Change (IPCC) projection (~668–734 ppmv in 2100; IPCC 2001). The differential responses may occur between the low range and high range of climate-change factors (Fig. 3).

Third, the combined two- or three-factor anomalies substantially changed nonlinear patterns and/or shifted critical points of nonlinearity on ecosystem carbon and water processes compared to single-factor changes. The substantial changes would make it very difficult to infer ecosystem responses to multifactor global change from single-factor experimental results. It is also not very feasible to conduct multisite, multifactorial experiments with a range of treatment levels due to ecosystem complexities and cost limitation. However, simple, well-designed multifactor experiments are necessary to better capture complex interactive processes, to provide useful inputs and model validation for theoretical development, and in turn to improve models. Such experimental results combined with the modeling output may guide future global-change research. For example, How many treatment levels are needed to reveal nonlinear responses for two-factor climate changes? What should the interval be for each of the treatment levels? Furthermore, new experiments are needed that explicitly account for nonlinear patterns generated from feedback mechanisms and threshold behavior.

#### *Model assumptions*

Model simulation results show diverse nonlinear patterns in response to individual and simultaneous

global changes on ecosystem carbon and water processes. The diversity of nonlinear responses reflects the fact that natural ecosystems may have different responses to multiple global-change factors (Scheffer et al. 2001, Burkett et al. 2005), which were well simulated by the structure of the TECO model. However, ecosystem biogeochemical models share a similar structure of carbon and water flows but have different functions to relate the rate variables that control the flows to changes in temperature, CO<sub>2</sub>, and precipitation, resulting in large simulation uncertainties of ecosystem response to global change (Burke et al. 2003). Thus, the modeling results may change with the functions in various models. It is very critical to examine and improve various response functions.

Although global climate change largely affects ecosystem structure and function and impacts the natural resources on which humans depend, it has to be considered that vegetation may acclimate and adapt to changing climate conditions (Luo et al. 1998, 2001b, Hanson et al. 2005, Rustad 2006). In addition, changes in community composition would be expected because plant species exhibit markedly different response patterns to climate change (Ackerly and Bazzaz 1995). However, the acclimation mechanisms and the changes in vegetation composition were not incorporated into the model for this study. Further research has to incorporate them into our TECO model to improve ecological forecasting and inform decision makers on managing the conditions leading to nonlinear responses and subsequent changes to ecosystem services. (Carpenter et al. 1999, Scheffer et al. 2001).

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