

Modeled interactive effects of precipitation, temperature, and [CO₂] on ecosystem carbon and water dynamics in different climatic zones

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Abstract

Interactive effects of multiple global change factors on ecosystem processes are complex. It is relatively expensive to explore those interactions in manipulative experiments. We conducted a modeling analysis to identify potentially important interactions and to stimulate hypothesis formulation for experimental research. Four models were used to quantify interactive effects of climate warming (T), altered precipitation amounts [doubled (DP) and halved (HP)] and seasonality (SP, moving precipitation in July and August to January and February to create summer drought), and elevated [CO₂] (C) on net primary production (NPP), heterotrophic respiration (R_h), net ecosystem production (NEP), transpiration, and runoff. We examined those responses in seven ecosystems, including forests, grasslands, and heathlands in different climate zones. The modeling analysis showed that none of the three-way interactions among T , C , and altered precipitation was substantial for either carbon or water processes, nor consistent among the seven ecosystems. However, two-way interactive effects on NPP, R_h , and NEP were generally positive (i.e. amplification of one factor's effect by the other factor) between T and C or between T and DP. A negative interaction (i.e. depression of one factor's effect by the other factor) occurred for simulated NPP between T and HP. The interactive effects on runoff were positive between T and HP. Four pairs of two-way interactive effects on plant transpiration were positive and two pairs negative. In addition, wet sites generally had smaller relative changes in NPP, R_h , runoff, and transpiration but larger absolute changes in NEP than dry sites in response to the treatments. The modeling results suggest new hypotheses to be tested in multifactor global change experiments. Likewise, more experimental evidence is needed for the further improvement of ecosystem models in order to adequately simulate complex interactive processes.

Keywords: climate change, heterotrophic respiration, net ecosystem production, net primary production, runoff, transpiration

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Introduction

Global change manifests itself through simultaneous changes in multiple environmental factors. Because of land-use change and fossil fuel combustion, the atmospheric CO₂ concentration has increased from 280 ppm in preindustrial time (Neftel *et al.*, 1982; Friedli *et al.*, 1986) to ~380 ppm at present and is expected to reach 700 ppm or more towards the end of the 21st century (Solomon *et al.*, 2007). As a consequence of rising CO₂ and other greenhouse gases, the Earth's surface temperature has increased by 0.76 °C in the past 150 years and is expected to increase by 1.5–6.4 °C by the end of the 21st century (Solomon *et al.*, 2007). Climate warming is expected to spatially and temporally alter precipitation regimes. Global precipitation is anticipated to increase by about 0.5–1% per decade in this century globally (Solomon *et al.*, 2007). At regional scales, for example, air temperature in the US Great Plains is predicted to increase by 2–4 °C with doubling of present CO₂ concentration (Long & Hutchin, 1991) and precipitation is expected to increase by 16–22% per decade and to be delivered in heavier rainfall events (Kunkel *et al.*, 1999).

Concurrent changes in multiple factors potentially trigger complex interactive influences on ecosystem structure and functioning (Fuhrer, 2003). Shaw *et al.* (2002), for example, showed that elevated CO₂ suppressed the effects of increased temperature, precipitation, and nitrogen deposition on net primary production (NPP) in a Californian annual grassland. That result indicated that the multifactor effects can differ greatly from simple combinations of single-factor responses. Conversely, interactive effects of multiple global change factors on soil CO₂ efflux have not been observed in most studies (Edwards & Norby, 1998; Lin *et al.*, 2001; Niinistö *et al.*, 2004; Zhou *et al.*, 2006). Thus, evaluating multifactor interactions in influencing ecosystem structure and functioning is critical to understand their response to global change in the real world. Indeed, when interactive effects (i.e. amplification or depression of one factor's effects by the other factors) dominate over main effects of single factors (i.e. differences in observed variables between treatment levels and control of one factor), results from single-factor experiments become less useful for understanding ecosystem changes. When interactive effects are minor relative to main effects, results from single-factor experiments are useful and cost-effective in informing us of potential ecosystem responses to multifactor global change.

Ecosystem responses to multifactor global change are regulated by complex, nonlinear processes (Zhou *et al.*, 2008). For example, warming can directly influence primary production in terrestrial ecosystems by changing plant photosynthesis and growth (Shaver *et al.*,

2000; Luo, 2007). Warming can also indirectly affect plant growth and production by extending the length of the growing season and changing plant phenology (Price & Waser, 1998; Sherry *et al.*, 2007; Slaney *et al.*, 2007), changing the spring thawing dates (Bergh & Linder, 1999), increasing soil nitrogen mineralization and availability (Rustad *et al.*, 2001; Melillo *et al.*, 2002; Strömngren & Linder, 2002), reducing soil water content (Harte & Shaw, 1995; Wan *et al.*, 2002), and shifting species composition and community structure (Harte & Shaw, 1995). Similarly, altered precipitation and elevated [CO₂] can trigger a variety of feedback processes to indirectly affect ecosystem structure and functioning (e.g. Knapp *et al.*, 2002; Luo *et al.*, 2004). However, a very limited experimental capability exists to separate the feedback processes and then evaluate their relative importance in influencing ecosystem responses to global change.

We conducted this modeling study to examine interactive effects of multifactor global change on ecosystem carbon and water processes. The study was motivated by the fact that multifactor experiments are usually expensive and cannot be conducted in many ecosystems due to financial constraints. To make multifactor experiments more effective, modeling can help stimulate hypothesis formation in their initial phases, and then extrapolate experimental results, once available, from several limited sites to other ecosystems, wider geographic areas and into the future. In the past decades, many ecosystem models have been developed (e.g. Parton *et al.*, 1987; Comins & McMurtrie, 1993; Rastetter *et al.*, 1997; Sitch *et al.*, 2003), validated by experimental results, and applied to examine ecosystem responses to global change (Cramer *et al.*, 2001; Luo *et al.*, 2001; Hanson *et al.*, 2005). Many of the models are designed to reflect general understandings of ecosystem processes in the scientific communities and provide insights into interactive effects of multifactor global change on ecosystem processes (Norby & Luo, 2004).

Instead of general model sensitivity analysis, this study used four ecosystem models to mimic experimental manipulations of doubled [CO₂], warming (by 2 °C), and altered precipitation (doubled – DP, halved – HP, and changed seasonality – SP) and then to simulate ecosystem responses to the manipulations. Using a standard statistical approach, we partitioned model outputs into main vs. interactive effects of the three factors on NPP, heterotrophic soil respiration (R_h), net ecosystem exchange (NEP = NPP – R_h), transpiration, and runoff. The analysis was conducted for seven ecosystems to identify patterns of ecosystem responses under diverse climatic and hydrologic regimes and vegetation types (cf. Gerten *et al.*, 2008 for more discussion). The four models used are well described in literature, two of them primarily developed for global-

scale analysis and two for ecosystem- and regional-scale studies. Implications of the modeling results were discussed in the context of future multifactor experimental studies and model improvement.

Methods

Models and study sites

This study used four ecosystem models to simulate responses of carbon and water processes to altered precipitation, warming, and elevated [CO₂] at seven sites. The companion paper by Gerten *et al.* (2008) describes the models and sites in detail. The following text provides a brief overview of them.

The four models are the Lund–Potsdam–Jena (LPJ) Dynamic Global Vegetation Model (Sitch *et al.*, 2003; Gerten *et al.*, 2004), the daily-time-step version of CENTURY (DAYCENT) model, the Terrestrial Ecosystem (TECO) model (Luo & Reynolds, 1999; Weng & Luo, 2008), and the ORCHIDEE Dynamic Global Vegetation Model (Krinner *et al.*, 2005). LPJ, TECO, as well as ORCHIDEE use a Farquhar photosynthesis scheme coupled with a transpiration scheme to simulate canopy photosynthesis and transpiration. NPP is the difference between canopy photosynthesis and autotrophic respiration. The latter is dependent on biomass amounts, specific respiration rates, and regulated by temperature. All four models have multiple plant, litter and soil carbon pools. R_h is computed from decomposition of litter and soil organic matter, which is regulated by soil temperature and moisture. Runoff is calculated from ecosystem water balance among precipitation, soil evaporation, canopy transpiration, and changes in soil water content in soil layers. Temperature-driven changes in phenology and the length of growing seasons are simulated on a carbon-gain based scheme (Arora & Boer, 2005) in the TECO model. Acclimation of physiological and ecological processes to warming and elevated [CO₂] was not imposed on model runs unless it was simulated internally via changes in nutrient dynamics or water stress. The models have been shown to capture well the interannual dynamics of carbon fluxes for the sites under investigation (Gerten *et al.*, 2008).

The seven sites are the Flakaliden conifer forest (Sweden) in the boreal region, a heathland at Mols Bjerge (Denmark), a heathland within Clocaenog forest (Wales, UK) with high rainfall, an oak-dominated temperate forest near Walker Branch (Tennessee, USA), the Konza tallgrass prairie dominated by perennial grasses (Kansas, USA), an annual-dominated grassland at the Jasper Ridge Biological Preserve (California, USA), and the tropical Tapajós National Forest (Brazil). These sites

are distributed in latitude from 2°90'S to 64°07'N, mean annual temperature from 2.3 to 25.7°C, and mean annual precipitation from 642 to 1555 mm. The sites represent different climatic and hydrologic regimes and vegetation types [see Gerten *et al.* (2008) for more description of each site].

Simulation scenarios

Daily climate data from 1990 to 2003 from all seven sites were used to drive the four models (Gerten *et al.*, 2008). The models were run for 980 years by repeating the observation time series 70 times to bring the long-term carbon stores into equilibrium before simulation treatments were applied. This study examined main and interactive effects of three factors: precipitation, temperature, and atmospheric CO₂ concentration. The precipitation treatment had four levels: ambient, doubled amount (DP), halved amount (HP), and altered seasonality (SP). SP created a summer drought scenario by moving precipitation in July and August to January and February. The CO₂ treatment had two levels: ambient at 360 ppmv (parts per million volumetrically) and elevated [CO₂] (C) at 720 ppmv. The temperature treatment also had two levels: control, and warming (T) by 2°C. The time series of temperature and precipitation constructed from observed daily climate time series over a 14-year period (1990–2003) at the seven sites was used for the control runs [detailed scenario description in Gerten *et al.* (2008)]. Thus, this study examined complete combinations of the three factors (four levels of precipitation × two levels of temperature × two levels of [CO₂] = 16 scenarios), which was partitioned into five main effects, seven two-way interactions, and three three-way interactions plus one mean at control.

The five main effects referred to changes in ecosystem attributes in response to treatments of single factors of DP, HP, SP, T, and C, respectively. The seven two-way interactive terms were (1) increased temperature and elevated [CO₂] ($T \times C$), (2) increased temperature and doubled precipitation ($T \times DP$), (3) increased temperature and halved precipitation ($T \times HP$), (4) increased temperature and changed seasonality of precipitation ($T \times SP$), (5) elevated [CO₂] and doubled precipitation ($C \times DP$), (6) elevated [CO₂] and halved precipitation ($C \times HP$), and (7) elevated [CO₂] and changed seasonality of precipitation ($C \times SP$). The three three-way interactive terms were (1) increased temperature and elevated [CO₂] and doubled precipitation ($T \times C \times DP$), (2) increased temperature and elevated [CO₂] and halved precipitation ($T \times C \times HP$), and (3) increased temperature and elevated [CO₂] and changed seasonality of precipitation ($T \times C \times SP$).

Analysis of main and interactive effects

Percent responses of NPP, R_h , transpiration, and runoff in each treatment were calculated relative to control treatment values. Modeled NEP (net ecosystem production) was obtained by the subtraction of simulated R_h from simulated NPP and presented as absolute values instead of percent changes as for NPP and R_h . Standard errors were estimated from simulated values of NPP, R_h , NEP, transpiration, and runoff by the four models. To avoid over-interpretation of modeled values, rigorous significance tests were not attempted and instead consistent patterns of responses among ecosystems identified.

To help illustrate the method of calculation of main and interactive effects, we present a notation system in Table 1 for simulated NPP ($\text{g C m}^{-2} \text{yr}^{-1}$) results from TECO under different treatments of doubled precipitation (DP), elevated temperature (T), and elevated [CO₂] concentration (C) at Jasper Ridge. (Averages of simulated values by the four models are presented in Results and may not match with calculated values in this example.) Using this notation system, a standard statistical method (Sahai & Ojeda, 2004) calculates the main effects of the three factors as follows:

$$\begin{aligned} DP &= P_2T_1C_1 - P_1T_1C_1 \\ &= 417 - 345 \\ &= 72 \text{ g C m}^{-2} \text{ yr}^{-1} \\ T &= P_1T_2C_1 - P_1T_1C_1 \\ &= 92 \text{ g C m}^{-2} \text{ yr}^{-1} \\ C &= P_1T_1C_2 - P_1T_1C_1 \\ &= 113 \text{ g C m}^{-2} \text{ yr}^{-1}. \end{aligned}$$

The main effects of HP and SP can be similarly estimated. A two-way interaction between DP and T is the subtraction of the main effects of DP and T from the effect of the joint DP plus T treatment and was calculated by

$$\begin{aligned} T \times DP &= (P_2T_2C_1 - P_1T_1C_1) - DP - T \\ &= (537 - 345) - 72 - 92 \\ &= 28 \text{ g C m}^{-2} \text{ yr}^{-1}. \end{aligned}$$

Similarly, the two-way interactions between DP and C , or between T and C , were calculated by

$$\begin{aligned} C \times DP &= (P_2T_1C_2 - P_1T_1C_1) - DP - C \\ &= 15 \text{ g C m}^{-2} \text{ yr}^{-1} \\ T \times C &= (P_1T_2C_2 - P_1T_1C_1) - T - C \\ &= 30 \text{ g C m}^{-2} \text{ yr}^{-1}. \end{aligned}$$

A three-way interaction among DP, T , and C is the subtraction of the effect of the joint DP, T , and C

Table 1 Notation system for studying main effects, two- and three-way interactions of precipitation, temperature, and CO₂ on simulated net primary production (NPP) ($\text{g C m}^{-2} \text{yr}^{-1}$) at Jasper Ridge using the Terrestrial Ecosystem (TECO) model

Treatment	Precipitation			
	Ambient (P_1)		Doubled (P_2)	
	Notation	Value	Notation	Value
Ambient temperature (T_1) and ambient CO ₂ (C_1)	$P_1 \times T_1 \times C_1$	345	$P_2 \times T_1 \times C_1$	417
Warming (T_2) and ambient CO ₂ (C_1)	$P_1 \times T_2 \times C_1$	437	$P_2 \times T_2 \times C_1$	537
Ambient temperature (T_1) and elevated CO ₂ (C_2)	$P_1 \times T_1 \times C_2$	458	$P_2 \times T_1 \times C_2$	545
Warming (T_2) and elevated CO ₂ (C_2)	$P_1 \times T_2 \times C_2$	580	$P_2 \times T_2 \times C_2$	689

treatment from all the combined two-way interactions and main effects of the three factors and was calculated by

$$\begin{aligned} T \times C \times DP &= (P_2T_2C_2 - P_1T_1C_1) \\ &\quad - DP \times T - DP \times C - T \times C - DP - T - C \\ &= -6 \text{ g C m}^{-2} \text{ yr}^{-1}. \end{aligned}$$

Similarly, main effects were calculated along with two- and three-way interactions for T and C with half precipitation (HP) and altered seasonality of precipitation (SP). Note that although this example showed smaller values for high-order interactions, three-way interactions can be larger than two-way interactive or main effects (e.g. the three-way interactive effect among temperature, elevated [CO₂], and halved precipitation on respiration at Tapajós in Fig. 2).

Because calculated main and interactive effects varied with different models at different sites, a method was developed to evaluate relative magnitudes of the two- or three-way interactions. The relative magnitude for the two-way interaction (I^2) between DP and T , for example, was calculated by the following equation:

$$\begin{aligned} I^2(\%) &= \frac{T \times DP}{(|DP| + |T|)/2} \times 100 \\ &= \frac{28}{(|72| + |92|)/2} \times 100 \\ &= 34. \end{aligned} \tag{1}$$

The above equation expresses the magnitude of the two-way interaction relative to a mean of the absolute main effects of the two factors. $I^2 = 34\%$ means that the two-way interaction adds 34% of the mean value of

single-factor effects to the effect of joint T and DP treatment. Similarly, the relative magnitude of the three-way interaction (I^3) among DP, T , and C was evaluated by the following equation:

$$I^3(\%) = \frac{T \times C \times DP}{(|DP| + |T| + |C|)/3} \times 100$$

$$= \frac{-6}{(|72| + |92| + |132|)/3} \times 100 \quad (2)$$

$$= -6.$$

$I^3 = -6\%$ means that the three-way interaction of DP, T , and C is 6% of the mean single-factor effects. The above two equations work well in most cases. When the main effects approached zero and the interactive effects were large, there were 9, 0, 8, 3, and 8 out of 280 simulated I^2 or I^3 values that were larger than 200%, respectively, for NPP, R_h , NEP, runoff, and transpiration. Those values were deleted from the calculation of means and standard errors among the four models to avoid abnormally large error bars of I^2 or I^3 .

Results

Net primary production (NPP)

At all study sites, modeled NPP was stimulated by doubled precipitation (DP) and elevated $[\text{CO}_2]$ (C), depressed by halved precipitation (HP) and summer drought (SP), and unresponsive to warming by 2°C (T) except at Flakaliden and Clocaenog (Fig. 1). When two factors were combined, NPP increased under T and DP, T and C , or C and DP; decreased under T and HP; and did not consistently change under T and SP, C and HP, or C and SP across the seven sites and among the four models. The combination of the three factors T , C , and DP resulted in the highest increase in NPP across the sites. The combination of T , C , and SP stimulated NPP at Jasper Ridge, Walker Branch, Tapajós, and Clocaenog but did not lead to a consistent change in the other three sites.

Interactive effects of T with C or DP on NPP were mostly positive (Fig. 2a), indicating that warming reinforced effects of elevated $[\text{CO}_2]$ and doubled precipitation on NPP despite the minor effect of warming itself. However, the interactive effects of T and HP were usually negative, suggesting that warming aggravated water stress caused by halved precipitation. The other two-way and all the three-way interactions were small in magnitude and not consistent among sites (Fig. 2a).

Among the seven sites, the ecosystem at Clocaenog was generally the least responsive to almost all the treatments of individual or combined factors (Figs 1 and 2). Error bars indicate variation in simulated NPP responses to the treatments among the four models.

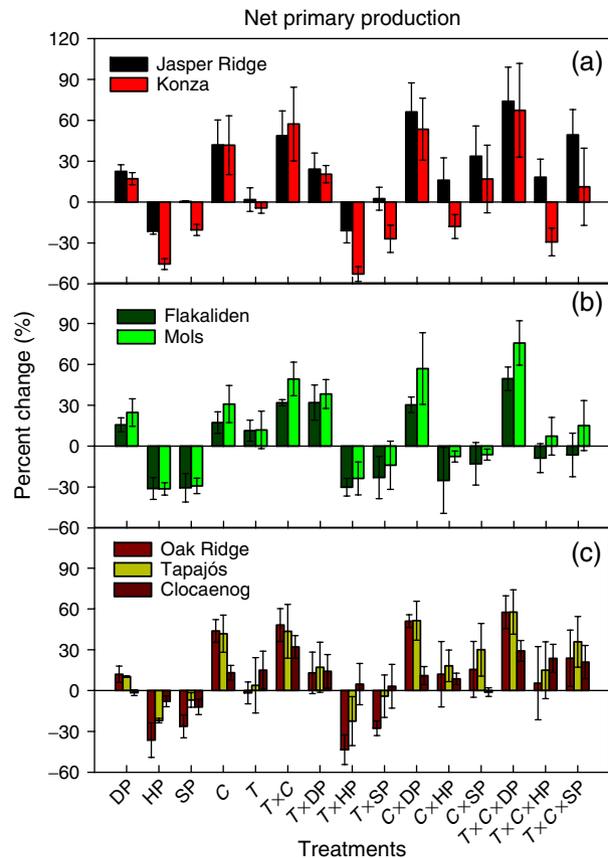


Fig. 1 Percent changes relative to control in modeled net primary production (NPP) in response to treatments of doubled precipitation (DP), halved precipitation (HP), summer drought (SP), elevated CO_2 (C), elevated temperature (T), and their combinations at Jasper Ridge and Konza (a), Flakaliden and Mols (b), Walker Branch, Tapajós and Clocaenog (c). Data indicate the mean ± 1 SE calculated from simulated values of NPP by the four models.

They were usually small for the main effects of individual factors and large for the interactive effects because of differences in response functions and parameterization among models.

Heterotrophic respiration (R_h)

The overall response pattern of modeled R_h to the treatments (Fig. 3) was similar to that for NPP (Fig. 1). However, the magnitude of R_h responses was somewhat smaller than that for the NPP responses partly because R_h had larger baseline values than NPP. Specifically, modeled R_h consistently increased under DP, C , and T but decreased under HP and SP in comparison with that under control (Fig. 3). The two-factor combinations of T and C , T and DP, or C and DP consistently stimulated respiration whereas the joint T and HP

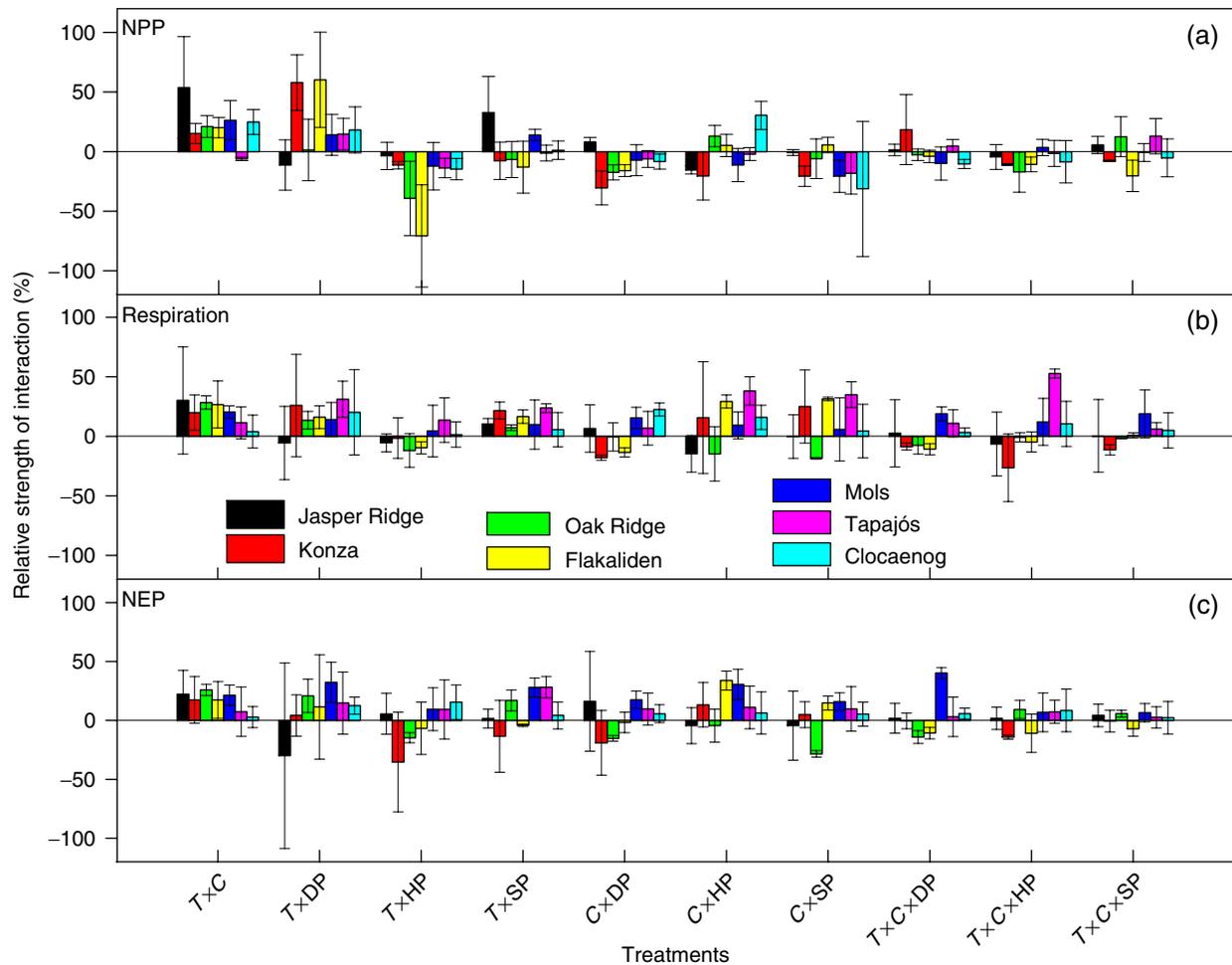


Fig. 2 Relative strength of two- or three-way interactive effects on net primary production (NPP) (a), heterotrophic respiration (R_h) (b), and net ecosystem production (NEP) (c) among doubled precipitation (DP), halved precipitation (HP), summer drought (SP), elevated CO₂ (C), elevated temperature (T) at Jasper Ridge, Konza, Flakaliden, Mols, Walker Branch, Tapajós, and Clocaenog. The relative strengths of interactive effects are calculated according to Eqns (1) and (2) (see text). Data were presented in the same way as in Fig. 1.

treatment decreased it. The three-factor joint treatment with T , C , and DP strongly enhanced respiration. The joint treatments of T and C with either HP or SP did not cause consistent responses among the sites.

The three wet sites – Walker Branch, Tapajós, and Clocaenog – demonstrated relatively small responses to all the treatments, probably due to their high baseline respiration rates under control (data not shown). The models showed that Jasper Ridge grassland and Mols heathland responded most positively to DP, C , and their combinations with T . The modeled response of Konza prairie to HP was most negative. The created summer drought scenario under SP did not affect R_h at Jasper Ridge where little precipitation occurred in summer months from May to October under the Mediterranean climate.

Similar to the patterns of NPP, the interactive effects of T with C or DP were mostly positive on R_h (Fig. 2b).

The other two-way or all the three-way interactive effects on R_h were inconsistent among the seven sites and were highly variable among the models.

Net ecosystem production (NEP)

Modeled NEP was the highest at the Tapajós tropical forest site and the second highest at the Konza prairie and Oak Ridge temperate forest with treatments of elevated CO₂ alone or in combination with other factors (Fig. 4). The three sites were also most negatively responsive to HP, SP, and T alone or in combination, whereas the other four sites, with NEP less than 50 g C m⁻² yr⁻¹, responded minimally to the treatments. The interactive effects of T with C or DP were generally positive on NEP (Fig. 2c). No consistent patterns emerged across the sites for the other two-way and all the three-way interactive effects on NEP.

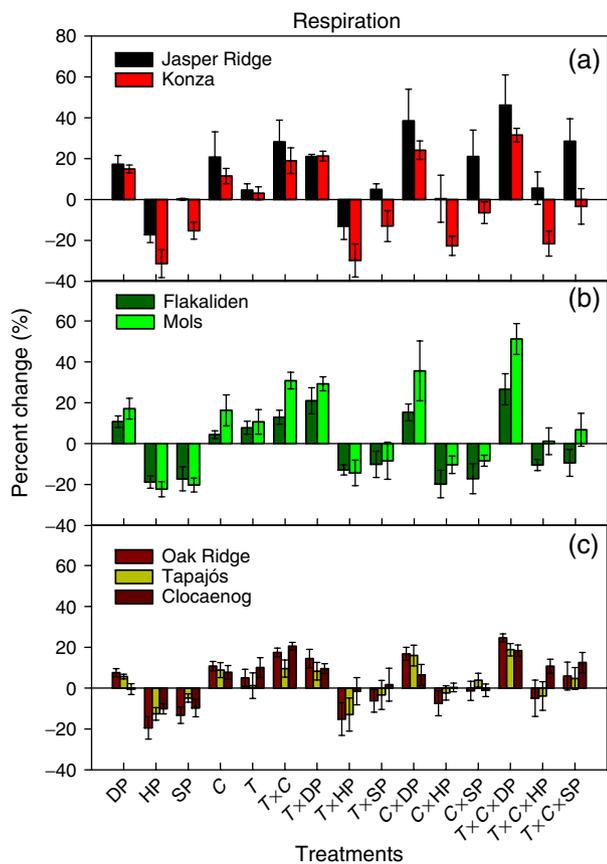


Fig. 3 Percent changes relative to control in modeled heterotrophic respiration (R_H) in response to treatments of doubled precipitation (DP), halved precipitation (HP), summer drought (SP), elevated CO_2 (C), elevated temperature (T), and their combinations at Jasper Ridge and Konza (a), Flakaliden and Mols (b), and Walker Branch, Tapajós, and Clocaenog (c). Data were presented in the same way as in Fig. 1.

Transpiration and runoff

In comparison to that under control conditions, modeled transpiration decreased by 20–60% when precipitation was halved (HP) alone or in combination with C and T (Fig. 5). The modeled transpiration increased by approximately 20% at Jasper Ridge, Konza prairie, Tapajós, and Mols when precipitation was doubled alone (DP). The joint treatment of DP and T increased transpiration by 20–40%. Elevated $[CO_2]$ (C) alone reduced transpiration by 10–20% at all the sites except Jasper Ridge whereas warming (T) alone increased it by 5–10%. The changed seasonality in precipitation (SP) with summer drought reduced transpiration by 10–20% at all sites with the exception of Jasper Ridge and Walker Branch. HP alone or in combination had relatively stronger effects on transpiration than DP.

The interactive effects of T with C or DP and C with HP or SP on transpiration were generally positive

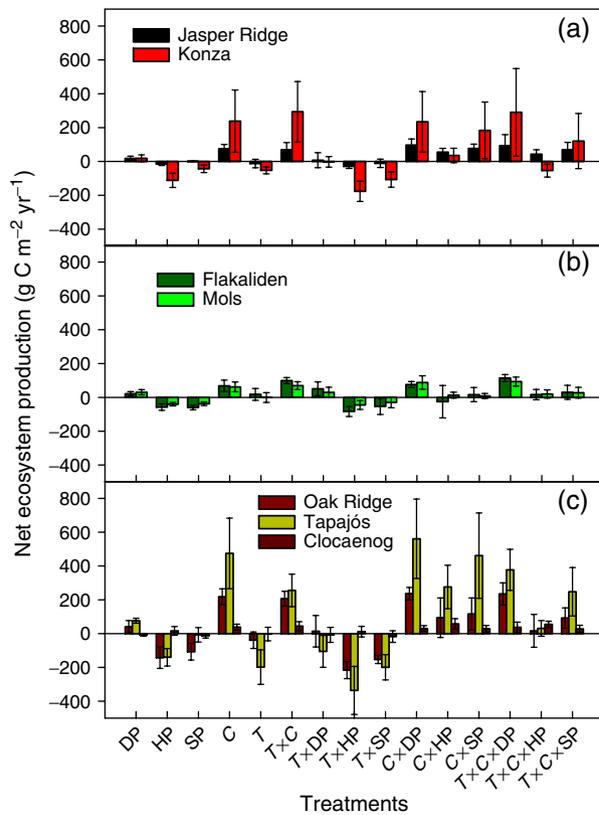


Fig. 4 Difference ($g\ C\ m^{-2}\ yr^{-1}$) in modeled net ecosystem production (NEP) in response to treatments of doubled precipitation (DP), halved precipitation (HP), summer drought (SP), elevated CO_2 (C), elevated temperature (T), and their combinations at Jasper Ridge and Konza (a), Flakaliden and Mols (b), and Walker Branch, Tapajós, and Clocaenog (c). The NEP differences are calculated by subtracting simulated NEP at each of the treatments from that under control. Data were presented in the same way as in Fig. 1.

across the sites (Fig. 6a). The interactive effects were, however, mostly negative between T and HP, between T and SP, or between C and DP at the seven sites. The three-way interactive effects among T and C with either DP or HP or SP were not substantial in magnitude or consistent among the sites.

Runoff under DP alone or in combination with C or T was nearly five times greater at Konza and 150–300% of that under control at the other six sites (Fig. 7), indicating that added water was mostly lost with smaller fractions being used by plants. Runoff decreased by more than 100% under HP alone or in combination with T and/or C at all the sites. Thus, runoff was the most sensitive to changes in precipitation amounts among all the processes examined in this study. SP, C, and T, and their combinations, all had relatively minor effects on runoff (Figs 6b and 7). The interaction was slightly

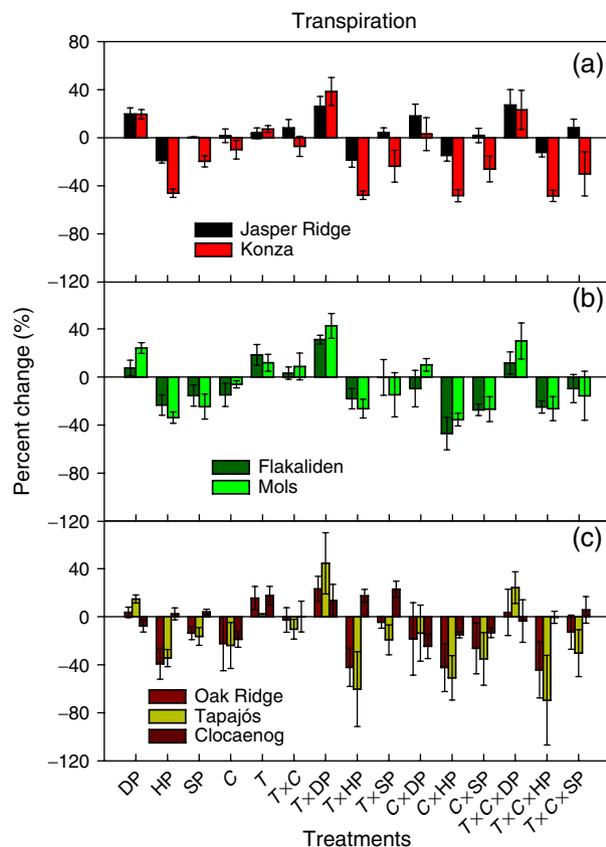


Fig. 5 Percent changes in modeled transpiration in response to treatments of doubled precipitation (DP), halved precipitation (HP), summer drought (SP), elevated CO₂ (C), elevated temperature (T), and their combinations at Jasper Ridge and Konza (a), Flakaliden and Mols (b), Walker Branch, Tapajós, and Clocaenog (c). The percent changes are all relative to that under control. Data were presented in the same way as in Fig. 1.

positive between *T* and HP across all seven sites and tended to be negative between *T* and C, between *T* and DP, between C and HP, and between C and SP.

Discussion

To stimulate hypothesis formulation for global change research, this modeling study evaluated interactive effects of multiple factors (i.e. climate warming, rising atmospheric CO₂ concentration, and altered precipitation amounts and seasonality) on ecosystem carbon and water dynamics. In ecosystems where interactive effects of multiple factors dominate over main effects of single factors, results from single-factor experiments will not reliably predict dynamics under global change. For this reason, multifactor experiments are essential to understand ecosystem changes. By contrast, in ecosystems where interactive effects are minor relative to main

effects, potential ecosystem responses to multifactor global change can be inferred from results of single-factor experiments. In this case, multifactor experiments would be less critical to the understanding of ecosystem responses. This modeling exercise attempted to shed light on relative importance of main and interactive effects.

Main and interactive effects of multiple factors on carbon processes

All four models simulated relatively robust main effects of individual factors, in that NPP and *R_h* increased under warming (*T*), doubled precipitation (DP), and elevated [CO₂] (C) but decreased under halved precipitation (HP) and summer drought (SP). Those results were qualitatively consistent with observations in manipulative experiments. For example, elevated [CO₂] usually increased photosynthesis and NPP (cf. Saxe *et al.*, 1998; Luo *et al.*, 2006), soil respiration (Luo *et al.*, 1996; Zak *et al.*, 2000), and net ecosystem carbon storage (Jastrow *et al.*, 2005; Lichter *et al.*, 2005; Luo *et al.*, 2006). Simulated responses of NPP to elevated [CO₂], however, were higher than observed responses at Jasper Ridge (Dukes *et al.*, 2005). Apart from the CO₂ effect, experimental warming stimulated plant biomass growth, soil respiration, and net nitrogen mineralization (Saxe *et al.*, 1998; Rustad *et al.*, 2001; Wan *et al.*, 2005; Zhou *et al.*, 2006; Luo, 2007). In addition, NPP usually increased with added precipitation and decreased with reduced precipitation and altered seasonal precipitation (Fay *et al.*, 2003; Yahdjian & Sala, 2006). At Oak Ridge, for example, supplementation of throughfall by approximately 33% resulted in increases of basal-area growth by up to 70% for *Acer rubrum* and *Cornus florida* saplings over 7 years (Hanson *et al.*, 2003). Our simulations of the main effects of individual factors on ecosystem attributes appear to be relatively robust and therefore provide a basis for studying interactive effects of multiple global change factors.

Simulated interactive effects on NPP, *R_h*, and NEP that were generally consistent across the seven sites and among the models occurred only between *T* and C (positive), between *T* and DP (positive), and between *T* and HP (negative). None of the other two-way interactions or three-way interactions elicited responses of simulated NPP, *R_h* or NEP that were consistent among the models nor substantial in magnitude across the seven sites. The positive interactions of warming with elevated [CO₂] apparently resulted from various mechanisms. For example, CO₂ stimulation of photosynthesis was enhanced under warming (Long, 1991; Tjoelker *et al.*, 1998). Elevated [CO₂] reduced stomatal conductance, enhanced water use efficiency (Drake *et al.*, 1997), and thereby, usually increased soil water availability

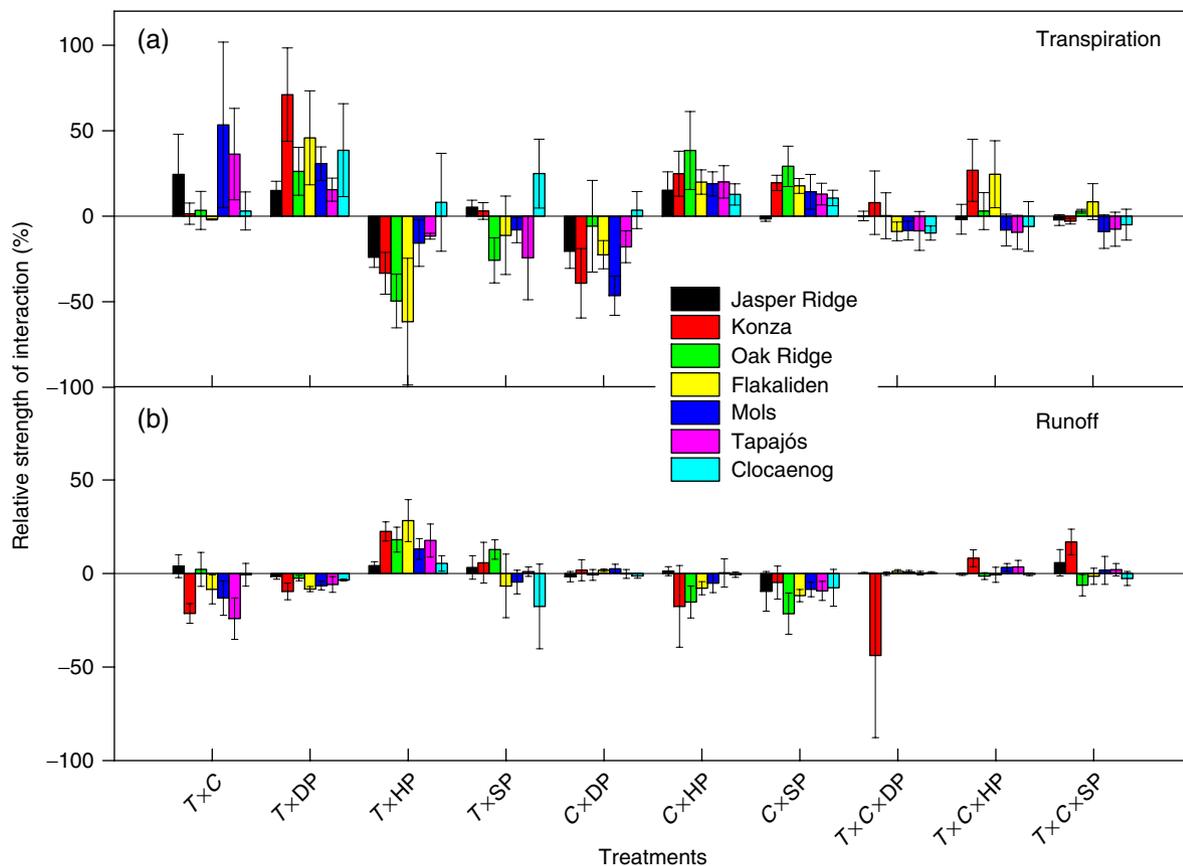


Fig. 6 Relative strength calculated according to Eqns (1) and (2) for two- or three-way interactive effects on transpiration (a) and runoff (b) among doubled precipitation (DP), halved precipitation (HP), summer drought (SP), elevated CO₂ (C), elevated temperature (T) at Jasper Ridge, Konza, Flakaliden, Mols, Walker Branch, Tapajós, and Clocaenog. Data were presented in the same way as in Fig. 1.

(Hungate *et al.*, 2002; Morgan *et al.*, 2004; Housman *et al.*, 2006). The plant physiological mechanisms and ecological processes induced by elevated CO₂ minimized the negative effects of soil drying and alleviate water stress under warming (Wall *et al.*, 2006), leading to the positive interactions between C and T found here. However, when water availability substantially decreased under HP, no positive interaction occurred with elevated [CO₂] probably because the water savings and/or drought avoidance mechanisms induced under elevated [CO₂] may not be adequate to fully compensate for the severe water limitation. The positive interactive effects between T and DP were expected because DP strongly increased soil water availability and so enhanced the response of water-limited ecosystem processes to warming [see also Gerten *et al.* (2008)]. The negative interaction between T and HP was due to the fact that soil drying under warming was exacerbated by reduced water availability.

Experimental evidence for interactive effects of multiple factors exists only for very limited sets of ecosystem processes from a few studies. Interactive effects were

found to be not significant for soil respiration between warming and increased precipitation (Zhou *et al.*, 2006), among elevated [CO₂], nitrogen supply, and plant diversity (Craine *et al.*, 2001), between elevated [CO₂] and temperature (Edwards & Norby, 1998; Niinistö *et al.*, 2004; Slaney *et al.*, 2007), and between elevated [CO₂] and [O₃] (Kasurinen *et al.*, 2004). Similarly, no significant interactive effects were found on grassland diversity and species composition in the first 3 years (Zavaleta *et al.*, 2003a, b) or NPP in the first 5 years (Dukes *et al.*, 2005) between elevated [CO₂], N deposition, added precipitation, and warming at Jasper Ridge. Interactive effects, however, were significant for NPP among elevated [CO₂], N deposition, added precipitation, and warming at Jasper Ridge in the third year of the experiment (Shaw *et al.*, 2002) and for litter production between elevated [CO₂] and nitrogen and between elevated [CO₂] and precipitation in the first 3 years (Zavaleta *et al.*, 2003b). Biomass growth and many plant physiological processes were also interactively affected by the combination of elevated [CO₂] and altered water availability in the Arizona free-air CO₂ enrichment

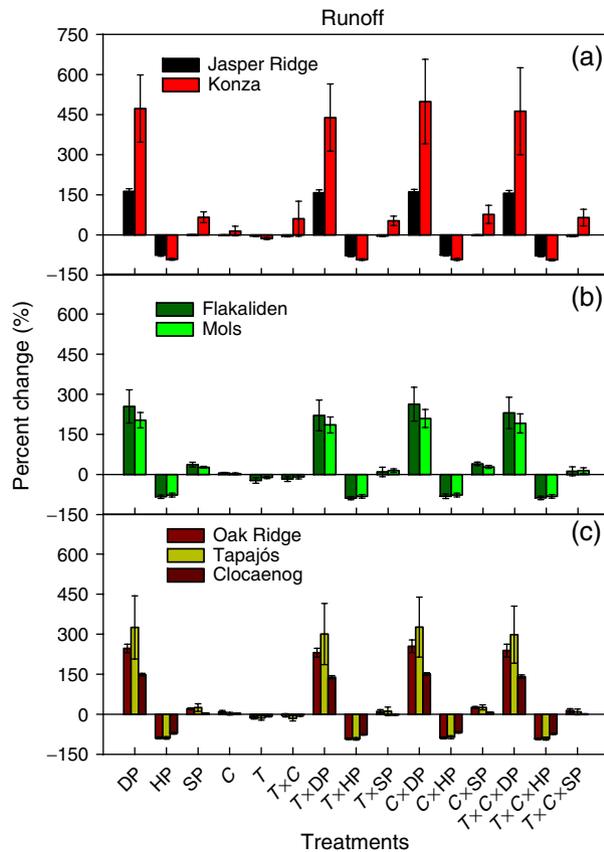


Fig. 7 Percent changes in modeled runoff in response to treatments of doubled precipitation (DP), halved precipitation (HP), summer drought (SP), elevated CO₂ (C), elevated temperature (T), and their combinations at Jasper Ridge and Konza (a), Flakaliden and Mols (b), and Walker Branch, Tapajós, and Clocaenog (c). The percent changes are all relative to that under control. Data were presented in the same way as in Fig. 1.

(FACE) experiment (Kimball *et al.*, 2001; Wall *et al.*, 2006). Overall, our modeling analysis captured the diverse interactions observed in experiments. A more rigorous evaluation of consistency between model simulations and experimental results is yet to be made as more experiments are conducted.

Main and interactive effects of multiple factors on water processes

Doubled precipitation (DP) resulted in increases in transpiration and runoff whereas halved precipitation (HP) reduced both of them [see Gerten *et al.* (2008) for more discussion]. Both the altered seasonality in precipitation (SP) and elevated [CO₂] generally increased runoff and decreased transpiration. Warming, by contrast, usually increased transpiration and decreased runoff. The modeled main effects of the five treatments were generally consistent with experimental observa-

tions. Elevated [CO₂] usually reduced stomatal conductance and consequently leaf and canopy transpiration (Housman *et al.*, 2006; Wall *et al.*, 2006). Soil evaporation and plant transpiration usually increased with temperature and thus water availability was reduced under experimental warming (Luo, 2007). Experimental warming by an additional 78 W m⁻² infrared radiation input, for example, increased evapotranspiration by 50–100% in fen and bog ecosystems in northeastern Minnesota (Bridgman *et al.*, 1999).

Modeled interactive effects were mostly positive on transpiration between T and DP or between T and C. This can be explained by the fact that warming increased vapor pressure deficit and potential transpiration, while doubled precipitation increased water availability. When the two factors were combined as one treatment, transpiration processes were reinforced, leading to positive interactions. Bridgman *et al.* (1999) showed a similar positive interaction in that elevated [CO₂] at the ambient temperature increased canopy aerodynamic resistance by 40–49% and reduced evapotranspiration by 14–16% of those under ambient [CO₂]. With rising temperature, these effects of elevated [CO₂] drastically decreased (Homma *et al.*, 1999), leading to a positive interaction between [CO₂] and temperature. The other modeled positive interactive effects on transpiration were between C and HP and between C and SP, largely due to the fact that CO₂-induced reduction in transpiration was usually stronger in dry than in wet environments (Housman *et al.*, 2006). The interactive effects on transpiration were negative between T and HP, between T and SP, or between C and DP. Under HP and SP, water loss via transpiration was mainly determined by water availability and may not be further stimulated by warming. Thus, the effects of warming with HP or SP were less than the sum of the main effects of individual factors. Although the modeled interactive effects were generally consistent with our present knowledge, few experimental measurements of transpiration and runoff from multifactor experiments are available to verify them.

Site and model differences

Across the seven sites, the driest ones showed the greatest modeled responses to changes in precipitation for NPP, R_h , transpiration, and runoff [as controlled primarily by water limitation, see Gerten *et al.* (2008)]. However, the absolute changes in NEP were greatest at the wet sites (e.g. Tapajós) and smallest at the cold sites (i.e. Flakaliden and Mols). The cold sites had relatively lower responses of NPP to elevated [CO₂] but had relatively higher responses of R_h to warming than the other sites. SP had strong negative effects on NPP, R_h , and

transpiration but minor positive effects on runoff (i.e. via increased winter runoff) at all sites except for Jasper Ridge where no precipitation occurred in summer.

This study showed that model agreement was generally high in terms of signs of modeled responses to multiple global change factors. Nonetheless, there were considerable deviations among individual models in simulated ecosystem responses to different scenarios of global change. For example, TECO simulated the smallest NEP at all sites except for Flakaliden due to equilibrated initial values of pool sizes by spin-up runs. The ORCHIDEE model simulated the highest runoff and lowest transpiration at all the sites except Walker Branch. The DAYCENT and LPJ models simulated much stronger reduction than TECO and ORCHIDEE in R_h in response to HP. The LPJ model yielded the strongest interactive effects between elevated $[CO_2]$ and increased temperature on all the five variables (positive on NPP, R_h , NEP and runoff and negative on transpiration) among the four models. The diverse responses to different global change scenarios generally resulted from differences in response functions and parameterizations (Gerten *et al.*, 2008). We need more experimental evidence to improve response functions and parameterizations in the future.

Implications for future experimental and modeling studies

Because the scenarios used in this study were rather stylized, the present modeling results offered suggestions for future experimental and modeling studies on ecosystem response to multifactor global change in several aspects. First, all four models produced substantial interactive effects of the three factors – CO_2 concentration, temperature, and precipitation – on ecosystem carbon and water processes. These interactions prevent the inference of ecosystem responses to multifactor global change from single-factor experimental results. It thus becomes essential to conduct multifactor experiments.

Second, none of the simulated three-way interactions among CO_2 concentration, temperature, and precipitation were substantial in magnitude or consistent among the seven ecosystems. This may be related to the fact that the models used in the analysis do not account for all potential interactions among the processes. Also, of the three factors considered – temperature, CO_2 concentration, and precipitation – all are still subject to substantial uncertainty in their model representations. Modeling ecosystem responses to drought, for example, remains a challenge because of the shortage of suitable experimental data. In most ecosystem models, processes of water uptake and stomatal limitation were represented only in simple forms (Hickler *et al.*, 2006; Knapp *et al.*, 2008). Nitrogen regulation of ecosystem

responses to rising atmospheric CO_2 concentration varied markedly among ecosystems and soil types (Luo *et al.*, 2004, 2006; Finzi *et al.*, 2007). Ecosystem responses to temperature changes cannot be fully represented in models because of complex and nonlinear regulatory mechanisms of plant and soil processes (Luo, 2007). We need more multifactor experiments to better capture complex interactive processes and subsequently to improve models.

Third, variable magnitudes in simulated two- and three-way interactions in this study could become rich ingredients of hypotheses for experimental studies. For example, simulated interactive effects between climate warming and elevated $[CO_2]$ and between warming and doubled precipitation are positive for NPP, R_h , and NEP. Those modeling results can become hypotheses to be tested in experiments. In a tallgrass prairie, for example, the interactive effect of warming and doubled precipitation on soil respiration was not significant (Zhou *et al.*, 2006). Our modeling analysis also suggests that none of the three-way interactions of warming, elevated $[CO_2]$, and altered precipitation amounts and seasonality were consistent among the models or substantial in magnitude across the seven sites for either carbon and water processes. If the three-way interactions were verified by experiments to be not significant, we may conduct more two-factor than three-factor experiments to advance our understanding of ecosystem responses to global change. Our analysis of ecosystem responses to multifactor global change may also be considerably simplified.

Fourth, the models simulated relatively larger responses of NPP, R_h , transpiration, and runoff to the global change factors for the dry than the wet ecosystems. However, the wet ecosystems had higher baseline rates of carbon and water cycling; their absolute responses of NEP to the treatments were larger than those of ecosystems in relatively low precipitation regimes. It appears, therefore, that more studies are needed in dry than wet ecosystems in terms of understanding vulnerability of ecosystems to global changes. It may be, however, more meaningful to study highly productive ecosystems if the research objective is to quantify large-scale changes in net ecosystem carbon storage in response to global change.

All implications of the current modeling results for future experimental research were drawn within the domain of a specific set of modeled perturbations. In the 21st century, climate warming is likely to increase local surface temperature by much more than the simulated $2^\circ C$ in most regions. Relative impacts of higher temperature increases on ecosystems may be different from the simulated ones in this study due to the nonlinear responses (Zhou *et al.*, 2008). It is impossible that precipitation would be doubled at the global

scale. However, this may well occur in some regions and in abnormal years. The doubled-precipitation scenario was used here to emphasize the responsiveness (or lack of it) to substantial increases in precipitation. Extrapolations and further utilization of the specific quantitative results from this modeling exercise to situations outside the simulation domain is unwarranted as the actual climatic changes need to be accounted for in reality. Nevertheless, the general trends of responses might be considered in evaluations of options of next-generation global change experiments and observations.

Conclusions

Simulated responses to the multiple factors were generally consistent among the models in terms of signs of modeled changes in the carbon and water processes. This reflects the fact that the structure of ecosystem biogeochemical models is fairly robust and built upon well-established experimental evidence that fluxes of carbon, nutrients, and water among compartments are largely donor pool-controlled (Parton *et al.*, 1987; Luo & Reynolds, 1999; Cramer *et al.*, 2001). However, the four models substantially deviated in simulated sensitivities of ecosystem responses to multifactor global change, probably because the models had different functions and parameter values to relate the rate variables of carbon and water fluxes to CO₂ concentration, temperature, and precipitation (or soil moisture content). As illustrated by Burke *et al.* (2003), different response functions and parameterizations can yield divergent modeled responses of ecosystems to environmental change. Thus, it is critical to improve various mechanistic response functions and model parameterization.

This modeling analysis illustrated variable magnitudes in simulated two- and three-way interactions, offering rich ingredients of hypotheses for experimental studies. Two-way interactive effects of climate warming with elevated [CO₂] and doubled precipitation, for example, were generally positive for simulated NPP, R_{lv} , and NEP but negative for simulated NPP between warming and halved precipitation. None of the three-way interactions among warming, elevated [CO₂], and altered precipitation was substantial for either carbon or water processes, or consistent among the seven ecosystems. Although several studies have examined some of the interactions, we need more experiments to examine interactive effects on a variety of ecosystem processes in different climate zones. If the three-way interactions are verified by experiments to be not significant as found in this modeling analysis, future analysis of ecosystem responses to multiple global change factors may be considerably simplified.

The analysis demonstrated that dry ecosystems were generally more responsive in relative terms to changes in atmospheric CO₂ concentration, temperature, and precipitation than wet ecosystems although the latter had larger absolute changes in net ecosystem exchange than the dry ecosystems. Therefore, dry ecosystems appeared to be more vulnerable to global change while the wet ecosystems had larger potential to alter terrestrial carbon balance.

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