

LETTER • OPEN ACCESS

Effects of rising atmospheric CO₂, climate change, and nitrogen deposition on aboveground net primary production in a temperate forest

To cite this article: Wen J Wang *et al* 2019 *Environ. Res. Lett.* **14** 104005

View the [article online](#) for updates and enhancements.



LETTER

OPEN ACCESS

RECEIVED
24 March 2019

REVISED
8 July 2019

ACCEPTED FOR PUBLICATION
11 July 2019

PUBLISHED
30 September 2019

Original content from this work may be used under the terms of the [Creative Commons Attribution 3.0 licence](#).

Any further distribution of this work must maintain attribution to the author(s) and the title of the work, journal citation and DOI.



Effects of rising atmospheric CO₂, climate change, and nitrogen deposition on aboveground net primary production in a temperate forest

Wen J Wang^{2,3,7,8}, Shuang Ma^{1,2,7}, Hong S He^{3,8}, Zhihua Liu⁴, Frank R Thompson III⁵, Wenchi Jin³, Zheng Fang Wu^{1,8}, Martin A Spetich⁶, Lei Wang², Song Xue², Wenguang Zhang² and Xianwei Wang²

¹ Key Laboratory of Geographical Processes and Ecological Security in Changbai Mountains, Ministry of Education, School of Geographical Sciences, Northeast Normal University, Changchun, 130024, People's Republic of China

² Northeast Institute of Geography and Agroecology, Chinese Academy of Sciences, Changchun, 130102, People's Republic of China

³ School of Natural Resources, University of Missouri, 203 ABNR Bldg, Columbia, MO, 65211, United States of America

⁴ CAS Key Laboratory of Forest Ecology and Management, Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang, 110016, People's Republic of China

⁵ USDA Forest Service, Northern Research Station, 202 ABNR Bldg, Columbia, MO, 65211, United States of America

⁶ Arkansas Forestry Science Laboratory, USDA Forest Service, Southern Research Station, PO Box 1270, Hot Springs, AR 71902 United States of America

⁷ Joint first authors: Wen J Wang and Shuang Ma contributed equally to this work.

⁸ Authors to whom any correspondence should be addressed.

E-mail: wangwenj@missouri.edu, heh@missouri.edu and wuzf@nenu.edu.cn

Keywords: carbon sink, forest productivity, ecosystem modeling, PnET, net primary production (NPP), temperate forest

Abstract

Temperate forests regrowing from historical land use and land cover change in the eastern US serve as carbon (C) sinks. Environmental drivers have been significantly altered (e.g. rising atmospheric CO₂ concentration, warmer temperature, and elevated nitrogen (N) deposition) and will have a wide range of impacts on future forest C sinks. However, the interactions among these environmental drivers are unclear and their effects are subject to uncertainty. We assessed the combined and interactive effects of rising CO₂ concentration, climate change (temperature, precipitation), and N deposition on forest aboveground net primary production (ANPP) and their relative contribution to ANPP changes of a temperate forest in the eastern US. We used a process-based ecosystem model PnET-day to simulate coupled cycles of C, water, and N of forest ecosystems. We found that (1) climate change exerted negative effects on ANPP ($-0.250 \text{ kg C m}^{-2} \text{ yr}^{-1}$) whereas rising CO₂ and N deposition enhanced ANPP ($+0.253$, $+0.014 \text{ kg C m}^{-2} \text{ yr}^{-1}$); (2) climate change interacted with rising CO₂ and N deposition to decrease ANPP (-0.032 , $-0.018 \text{ kg C m}^{-2} \text{ yr}^{-1}$); rising CO₂ and N deposition acted in synergy to increase ANPP ($+0.014 \text{ kg C m}^{-2} \text{ yr}^{-1}$); (3) changes in ANPP were mainly attributed to rising CO₂ and climate change whereas N deposition effects and any two- or three-factor interactive effects were relatively small. Our results suggest that the total negative effect sizes will not be offset by the total positive effect sizes, thus resulting in reductions in forest ANPP over the 21st century.

1. Introduction

Temperate forests, making up 25% of all forest area, sequester approximately 30% global carbon (C) emissions and store about 15% of global C (Martin *et al* 2001). The C sinks taken up by temperate forests have increased in the past decades primarily because of increasing density of biomass and great increases in forest area (Pan *et al* 2011). Recent studies generally agree that contemporary C sinks of temperate forests

in eastern US have been largely attributed to forest regrowth from historical land use and land cover change such as forest clearing, cropland expansion, and followed agricultural abandonment (Caspersen *et al* 2000, Pacala *et al* 2007). However, the future persistence and magnitude of C sinks of the temperate forests in the eastern US remain uncertain.

Environmental conditions have been significantly altered by human-induced activities over the past century and will continue to change in the future such as

rising atmospheric CO₂ concentration, warmer temperature, altered precipitation regimes, and elevated nitrogen (N) deposition (IPCC 2014). Both individually and interactively, these changes of environmental drivers have a wide range of impacts on future forest C sinks (Fekete *et al* 2017, Houtven *et al* 2019). Rising CO₂ concentration and warmer temperature will favor net primary productivity (NPP) and water use efficiency of trees and thus promote C sequestration (Fang *et al* 2014, Fernández-Martínez *et al* 2019), though the extent of CO₂ fertilization effects will depend upon other factors such as nutrients (de Vries *et al* 2017). Altered precipitation regimes such as increased drought stress will decrease tree growth and even trigger tree mortality under severe water limited conditions (Ibáñez *et al* 2018). Elevated N deposition is almost likely to increase tree growth, thus leading to higher C accumulation given that N is often the limiting nutrient in many forest ecosystems (Feng *et al* 2015, Maes *et al* 2019). However, the fertilization effects of elevated N deposition on tree growth are expected to saturate or even likely to decline with continuous N enrichment because of nonlinear responses of tree growth to accumulated N deposition (Tian *et al* 2016). These environmental drivers are also believed to act in synergy resulting significant interactive effects (Norby *et al* 2010, Dusenke *et al* 2019). For example, concurrent rise in CO₂ concentration and N deposition could bring out strong synergistic fertilization effects especially in the forest ecosystems with N limitation (O'Sullivan *et al* 2019). Understanding the combined effects of these environmental drivers is, therefore, needed to generate reliable projections of future forest C dynamics, which are essential for land managers and policy makers to design effective plans for natural resource conservation and adaptation strategies for climate change.

In our study, we assessed the combined effects of rising atmospheric CO₂ concentration, climate change (temperature, precipitation), and N deposition on aboveground net primary production (ANPP) of a temperate forest in the eastern US. We used a process-based ecosystem model PnET-day to simulate physiological responses of forest ecosystems to rising atmospheric CO₂, climate change, and elevating N deposition. We used PnET-day model because it simulates the coupled cycles of C, water, and N of forest ecosystems driven by daily environmental data (Aber *et al* 1996). It has been validated against inventory data and eddy-flux tower measurements and applied to various forests (Aber and Federer 1992, Aber *et al* 1996, Ryu *et al* 2008, Jin *et al* 2016). We addressed the following questions: (1) how forest ANPP will change under rising CO₂, climate change, and N deposition over the 21st century? and (2) what is the relative contribution of rising CO₂, climate change, N deposition, and the interaction of any two- and three-combination of

these three environmental drivers on forest ANPP changes?

2. Data and methods

2.1. Study area

Our study area included the Current River Hills ecological subsection (223 Af) within the Ozark Highland ecological section (223A) (McNab *et al* 2007) and was located in the US state of Missouri (figure 1). The study area covered approximately 810 000 hectares. It is a mature dissected plateau with dolomite and sandstone bedrock, and soils primarily developed from cherty limestones (McNab *et al* 2007). The climate is continental temperate with warm and humid summers and relatively dry and cold winters. The average annual temperature is 13.4 °C and average annual precipitation is 1100 mm.

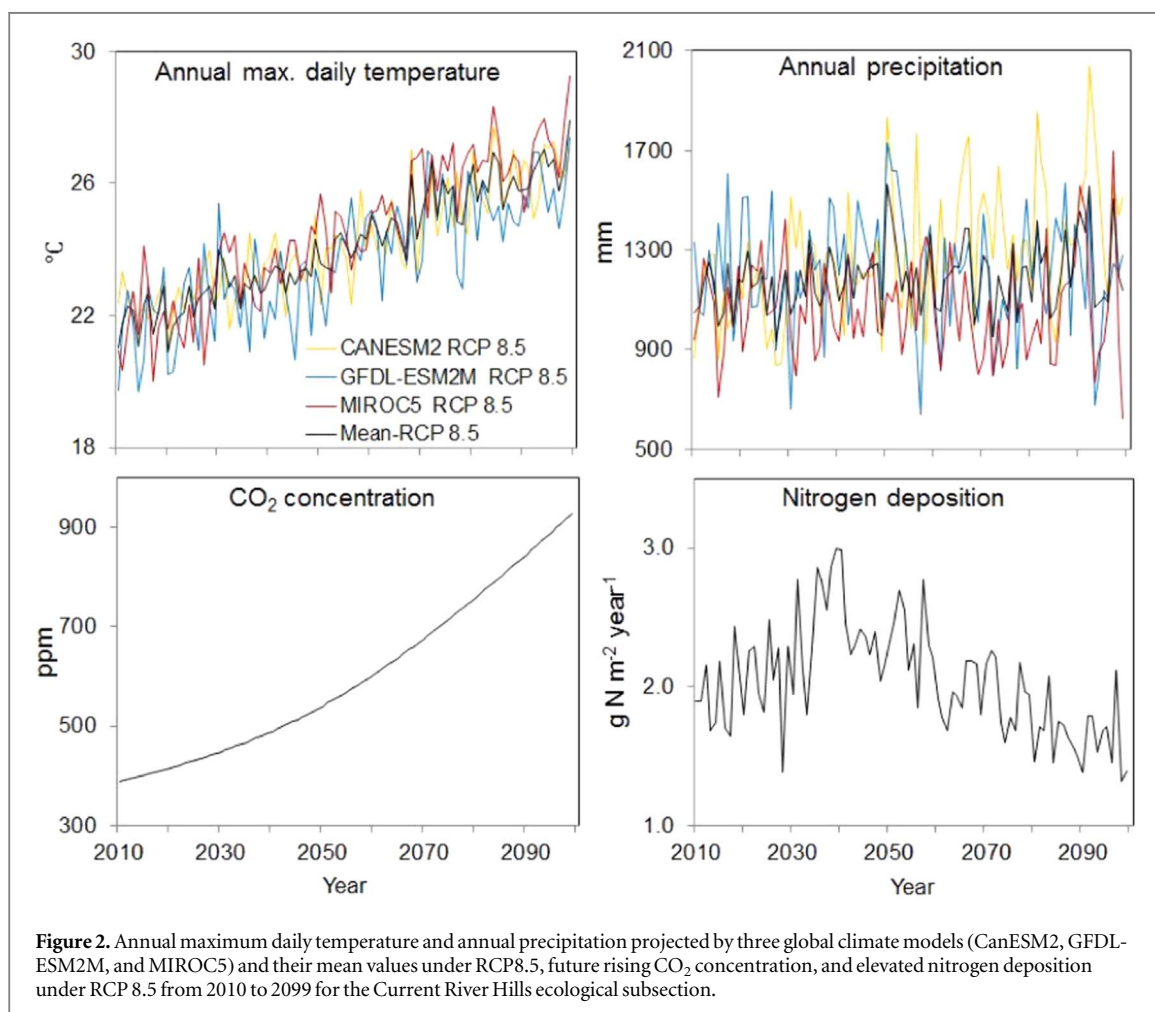
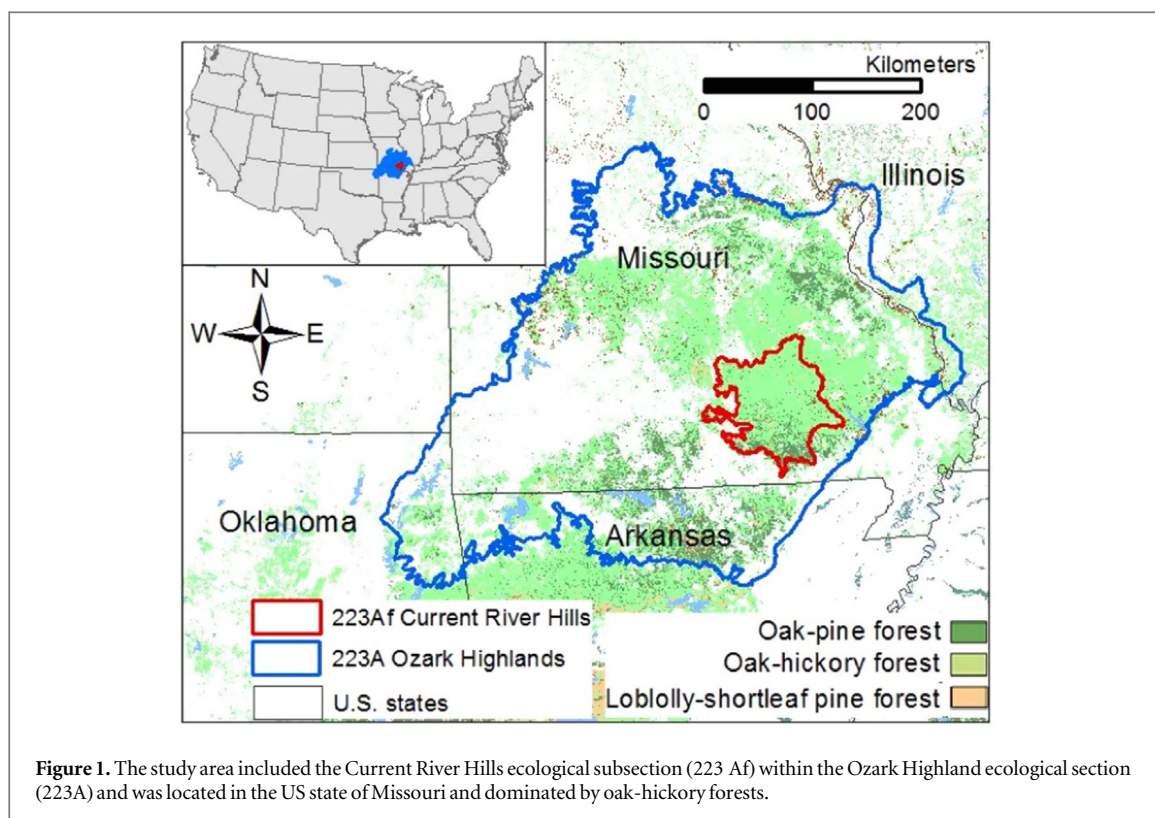
We chose the Current River Hills ecological subsection as the study area because it contained one of the largest blocks of forest in the eastern US (figure 1). This area was primarily composed of secondary upland oak-hickory and oak-pine forests. The dominant tree species included white oak (*Quercus alba* L.), black oak (*Q. velutina* Lamb.), scarlet oak (*Q. coccinea* Muenchh.), bitternut hickory (*Carya cordiformis* (Wangenh.) K. Koch), and pignut hickory (*C. glabra* Miller) (Shifley and Brookshire 2000). Oaks and hickories have been the dominant tree species for the past thousands of years and are the keystone species of major importance in maintaining biodiversity, ecosystem functions and services. Similar to many forests in the eastern US, current forests in the study area are regrowing from previous disturbances (mainly tree harvesting and agricultural abandonment) and the average stand age is approximately 70 years.

2.2. Modeling approach and experimental design

We designed a three-factor factorial experimental design with two levels of CO₂ concentration (current CO₂ concentration and future rising CO₂ concentration), four levels of climate (current climate and three climate change scenarios), and two levels of N deposition (current N and future elevated N deposition), resulting in total of 16 simulation scenarios. We treated the current CO₂ concentration, climate (temperature and precipitation), and N deposition scenario as the baseline scenario. We used PnET-day model to simulate the C, N and water dynamics of forest ecosystems for the 16 simulation scenarios.

2.2.1. Climate data and climate change scenarios

We included current climate and three climate change scenarios based on CanESM2, GFDL-ESM2M, and MIROC5 global climate models (GCMs) under the representative concentration pathway (RCP) 8.5 (Riahi *et al* 2007). Since the three GCMs projected different future climate change patterns, we were able



to generate a range of projections to incorporate uncertainties in future climate projections (figure 2, Rupp *et al* 2013).

We used daily maximum and minimum temperature, precipitation, and solar radiation for each climate scenario. We obtained the current climate data (1980–2009) for our study area at 1 km resolution from DAYMET (Thornton *et al* 2016). We downloaded the future climate data (2010–2099) for three climate change scenarios from the Coupled Model Intercomparison Project phase 5 (CMIP5, https://cmip.llnl.gov/cmip5/data_portal.html). Compared to the current climate scenario, three climate change scenarios projected the annual maximum daily temperature to increase by 4 °C–6 °C in 2070–2099 (figure 2), in which the CanESM2 and MIROC5 RCP 8.5 scenarios showed more dramatic increases than the GFDL-ESM2M RCP 8.5 scenario. Annual precipitation on average had relatively small anomalies from current climates with increased annual variations after 2050 (figure 2).

2.2.2. CO₂ concentration scenarios

We obtained the annual CO₂ concentration for the current CO₂ scenario (1980–2009) from Mauna Loa Observatory (<http://esrl.noaa.gov/gmd/obop/mlo/>). We used the atmospheric CO₂ concentration projection (2010–2099) under RCP 8.5 as the future rising CO₂ scenario (https://cmip.llnl.gov/cmip5/data_portal.html). CO₂ concentration under RCP 8.5 was projected to continue rising over 900 ppm and averaged 600 ppm over the 21st century (figure 2).

2.2.3. N deposition scenarios

We downloaded the N deposition data (1980–2009) for the current N deposition scenario from the National Atmospheric Deposition Program (<http://nadp.sws.uiuc.edu/committees/tdep/tdepmaps/>). Since RCP 8.5 did not have N deposition projections to the end of this century, we used the projections of atmosphere mass content of nitrate dry aerosol from 2006 to 2100 to derive the future N deposition based on the proportional relationship between N deposition and the atmosphere mass content of nitrate dry aerosol (Elliott *et al* 2009). Projected N deposition increased to 2040 followed by a decreasing trend and averaged 2.02 g m⁻² yr⁻¹ over the 21st century (figure 2).

2.3. PnET-day parameterization and validation

We used PnET-day model, an improved version of PnET-CN, to simulate the effects of rising CO₂ concentration, climate change, and N deposition on forest ANPP (<http://pnet.sr.unh.edu/>, Aber *et al* 1996, Ollinger *et al* 2002). PnET family models are process-based ecosystem models that simulate the C, water, and N dynamics of forest ecosystems (Aber and Federer 1992, Ollinger *et al* 2002). The core of

PnET-day was a daily time-step canopy submodel that simulated physiological processes of a multi-layered canopy using generalized leaf-trait relationships and vertical gradients in physical environmental conditions (Aber *et al* 1996). PnET-day model represented the vegetation using three major components: leaves, wood, and roots. It simulated the maximum potential net photosynthetic rate under light-saturated condition as a function of foliar N concentration and simulated water use efficiency (mg C fixed per g H₂O transpired) as a function of vapor pressure deficit. Based on these two principles, a link between C dynamics and water transpiration was established and the computation load for water transpiration was greatly reduced because it only depended on vapor pressure deficit. A complete N cycle in PnET-day model included N mineralization, nitrification, plant N uptake and leaching losses. Since PnET-day model simulated the interactions between C and N cycles, forest C sequestration was affected by both plant and soil N pools. The annual net primary productivity was summarized based on the net photosynthetic rate and the annual aboveground net primary productivity was allocated from the annual net primary productivity (Aber *et al* 1996).

We obtained the average water holding capacity for the entire subsection from Soil Survey Geographic Database (SSURGO, Soil Survey Staff 2014). We initialized the forests using average C mass of leaves, wood, and roots from forest inventory and analysis (FIA) data (O'Connell *et al* 2015). We used the generalized parameters for the broad-leaved deciduous forests (e.g. light attenuation constant, Q₁₀ for leaf respiration, minimum and optimum daytime temperature) from previous studies (Reich *et al* 1995, Aber *et al* 1996, Ollinger *et al* 2002). We derived the site-specific parameters (e.g. foliar N content, specific leaf weight, growing degree days to start or complete foliar production, max. or min. winter foliar biomass) based on previous studies (Aber and Federer 1992, Tjoelker *et al* 2001, Scheller and Mladenoff 2005, Ryu *et al* 2008, Xu *et al* 2009) and the eddy-flux tower measures in the Missouri Ozarks AmeriFlux (MOFLUX) site (doi.org/10.17190/AMF/1246081).

We used historical FIA data to validate model simulation results. We firstly initialized the forest ecosystems in PnET-day model using 136 FIA plots from the 2000 survey cycle and then run the model from 2000 to 2010 under the baseline scenario (with current climate, CO₂ and N deposition). We compared the average aboveground ANPP predicted by PnET-day model with the average ANPP estimated from FIA data over a 10 year period (2000–2010). Since FIA data did not contain ANPP information, we calculated three components: net C density increment from 2000 to 2010, aboveground mortality, and aboveground C removed due to disturbances; we then divided the sum of these three components by a time interval of 10 years to obtain the average ANPP. Predicted

average ANPP from PnET-day from 2000 to 2010 was $0.551 \text{ kg C m}^{-2} \text{ yr}^{-1}$, which was comparable to the observed average ANPP ($0.576 \text{ kg C m}^{-2} \text{ yr}^{-1}$) from FIA data for the same period. Thus, PnET-day model simulated consistent ANPP with observed field inventories in our study area. Finally, we reinitialized the PnET-day model using 142 FIA plots in the 2010 survey cycle and then simulated forest ecosystems from 2010 to 2099 for the 16 simulation scenarios.

2.4. Analysis of simulation results

We calculated the ΔANPP s for the simulation scenario i as the difference in ANPP between the simulation scenario i and the baseline scenario ($\text{ANPP}_i - \text{ANPP}_{\text{baseline}}$). We also calculated the average ΔANPP s for the period 2010–2100 for each simulation scenario. We averaged the ΔANPP s for the three climate change scenarios to focus on an average response, which was referred to as mean RCP 8.5 results.

We estimated the single-factor effect size of rising CO_2 concentration, climate change, or N deposition as the difference in ΔANPP s from 2010 to 2099 between the baseline scenario and the simulation scenario in which the single factor was only included; We calculated any two- and three-factor combined effect as the difference in ΔANPP s between the baseline scenario and the simulation scenario in which the given two or three factors were included simultaneously; We calculated any two-factor interactive effect by subtracting both two single-factor effects from the given two-factor combined effect; we finally calculated the three-factor interactive effect by subtracting both the three single-factor effects and three two-factor interactive effects from the three-factor combined effect (Temperli *et al* 2013). We averaged the single-factor effects, two- and three-factor interactive effects for the period 2010–2100 to represent the average effect sizes. Note that our analyses focused on average responses among three climate change scenarios and effect sizes rather than statistical significance.

3. Results

3.1. Temporal changes in ANPP under future scenarios

ΔANPP s varied greatly annually (figure 3) and averaged $-0.041 \text{ kg C m}^{-2} \text{ yr}^{-1}$ under the RCP 8.5 climates, future rising CO_2 and N deposition scenario over the 21st century (figure 4). ΔANPP s on average were overall less with climate change and greater with rising CO_2 and N deposition (figure 3). With climate change, the average ΔANPP was reduced by $0.250 \text{ kg C m}^{-2} \text{ yr}^{-1}$ under the mean RCP8.5 with greatest decreases under CanESM2 RCP 8.5 climate scenario followed by GFDL-ESM2M and MIROC5 RCP 8.5 climate scenarios, in comparison with the

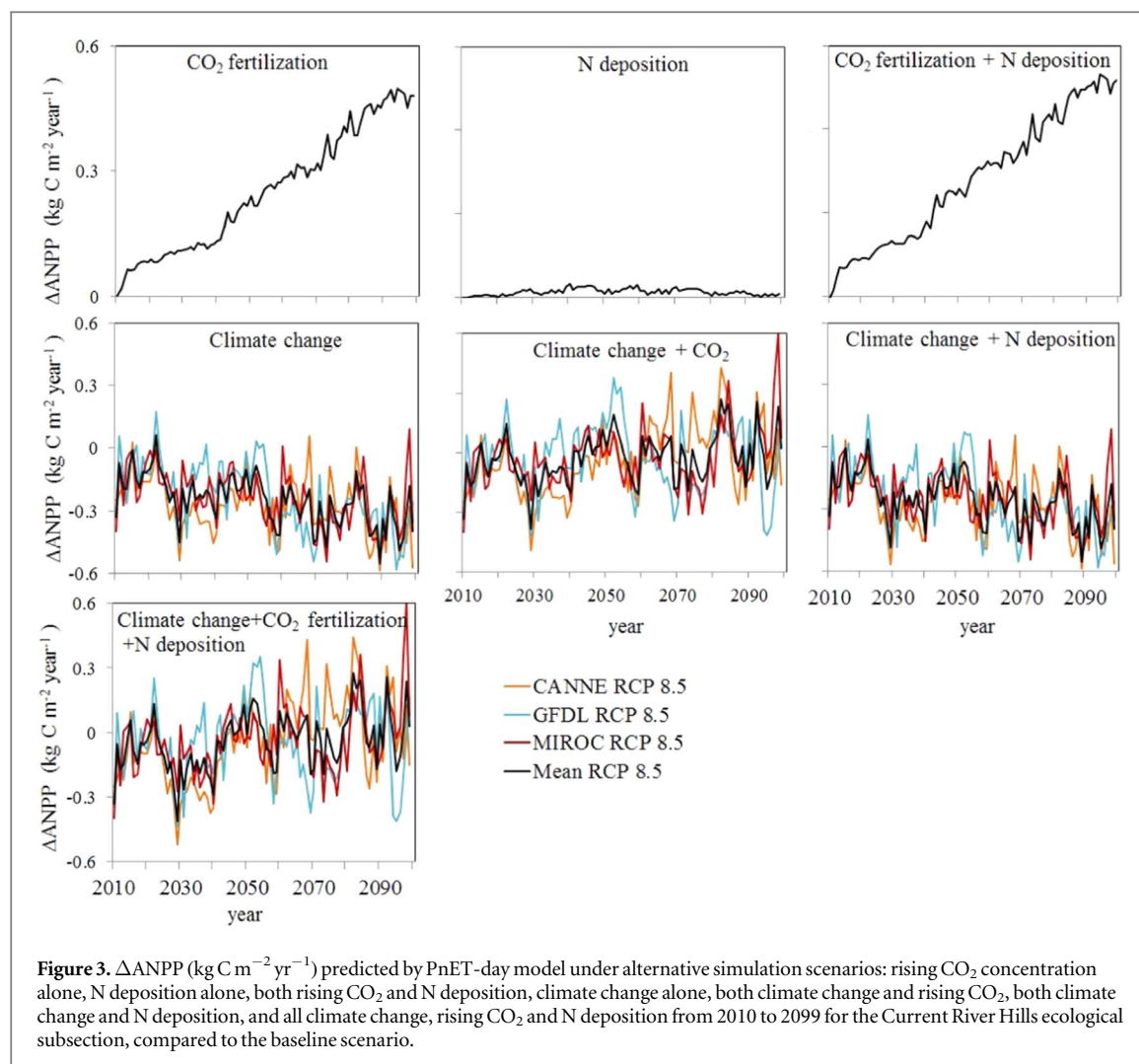
baseline scenario (figures 3 and 4). Future rising CO_2 and N deposition increased the ΔANPP by 0.253 and $0.014 \text{ kg C m}^{-2} \text{ yr}^{-1}$, respectively, compared with the baseline (figures 3 and 4). Climate change interacted with rising CO_2 and N deposition to reduce the average ΔANPP by 0.029 and $0.255 \text{ kg C m}^{-2} \text{ yr}^{-1}$, respectively, while rising CO_2 interacted with N deposition to increase the average ΔANPP by $0.28 \text{ kg C m}^{-2} \text{ yr}^{-1}$ (figure 4). The interaction of climate change, rising CO_2 and N deposition resulted in reductions in average ΔANPP by $0.041 \text{ kg C m}^{-2} \text{ yr}^{-1}$ (figure 4).

3.2. Interactive effects of rising CO_2 , climate change, and N deposition

The effect sizes of climate change on ΔANPP overall increased with great annual variation and averaged $-0.250 \text{ kg C m}^{-2} \text{ yr}^{-1}$ whereas the effect sizes of rising CO_2 continued increasing and averaged $0.253 \text{ kg C m}^{-2} \text{ yr}^{-1}$ (figures 5 and 6). The effect sizes of N deposition on ΔANPP increased by mid-century followed a decreasing trend and averaged $0.014 \text{ kg C m}^{-2} \text{ yr}^{-1}$ (figures 5 and 6). The average effect sizes for the interaction of rising CO_2 and climate change and the interaction of climate change and N deposition on ΔANPP were -0.032 and $-0.018 \text{ kg C m}^{-2} \text{ yr}^{-1}$, respectively (figure 6). The effect sizes for the interaction of rising CO_2 and N deposition on ΔANPP averaged $0.014 \text{ kg C m}^{-2} \text{ yr}^{-1}$ (figure 6). The average effect sizes for the interaction of climate change, rising CO_2 , and N deposition on ΔANPP were $-0.020 \text{ kg C m}^{-2} \text{ yr}^{-1}$ (figure 6). Thus, on average, the changes in ANPP were mainly attributed to rising CO_2 and climate change while the interactive effects of any two- and three-combination of rising CO_2 , climate change, and N deposition were relatively small. The total positive effect sizes (e.g. rising CO_2 , N deposition, the interaction of rising CO_2 and N deposition) were not enough to offset the total negative effect sizes (e.g. climate change, interaction of rising CO_2 and climate change), thus resulting in reductions in ANPP over the 21st century.

4. Discussion

It is important to note that our simulations are not to be interpreted as forecasts of future. Rather, we assessed the combined effects of three environmental drivers (rising CO_2 concentration, climate change, and N deposition) on forest ANPP and their relative contribution to ANPP changes. We found rising CO_2 and N deposition enhanced ANPP whereas climate change exerted negative effects on ANPP; rising CO_2 and N deposition acted in synergy to increase ANPP; climate change interacted with rising CO_2 or/and N deposition to decrease ANPP; future changes in ANPP were mainly attributed to rising CO_2 and climate

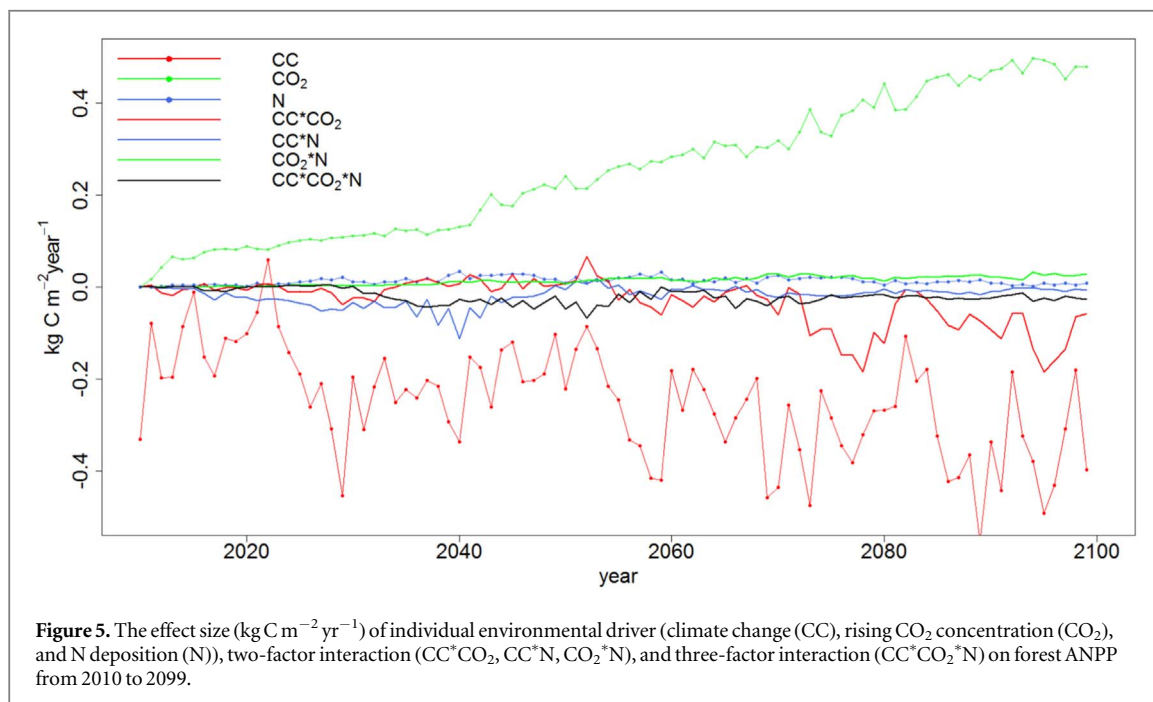
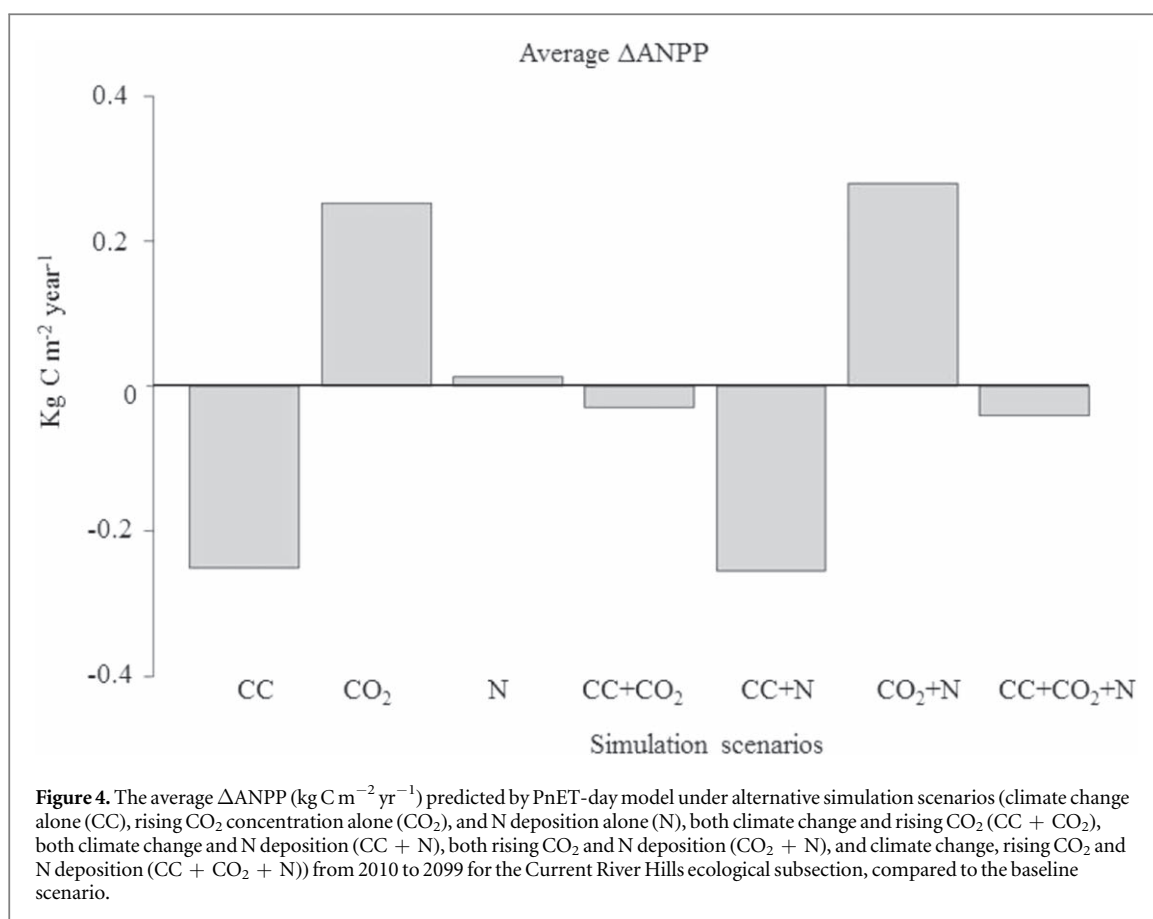


change whereas N deposition effects and any two- or three-factor interactive effects were relatively small.

The largest positive effects on ANPP was found for rising CO_2 concentration among three environmental drivers, which agree with many studies (Fernández-Martínez *et al* 2019, Tharammal *et al* 2019). Our results showed that, under current climates and N deposition level, ANPP with elevated CO_2 concentrations of 600 ppm increased by $0.253 \text{ kg C m}^{-2} \text{yr}^{-1}$ (21%). These estimates were similar to those of free-air CO_2 enrichment (FACE) experiments. For example, the FACE experiments conducted in four temperate forest sites in the Northern Hemisphere showed an average increase of 18% in NPP under the elevated CO_2 concentration (approx. 550 ppm) (Norby *et al* 2010). However, it is difficult to compare our results under higher CO_2 concentrations (>550 ppm) in a long timeframe with field-based forest ecosystem studies. We also found although CO_2 concentration kept increasing after 2080, most of CO_2 fertilization effects were found in the period of 2040–2080 with much smaller changes in Δ ANPP after 2080, suggesting CO_2 saturation effects. Enhanced photosynthesis under elevated CO_2 concentration may be reduced via physiological adjustments or limited by N availability

(Voelker *et al* 2016). It should be noted that the PnET model, similar to many other process-based models, scales up the leaf level responses to CO_2 fertilization directly to the ecosystem level, and thus our results should be considered to be at the upper bound of possible responses of forest ecosystems to rising CO_2 (Ollinger *et al* 2008).

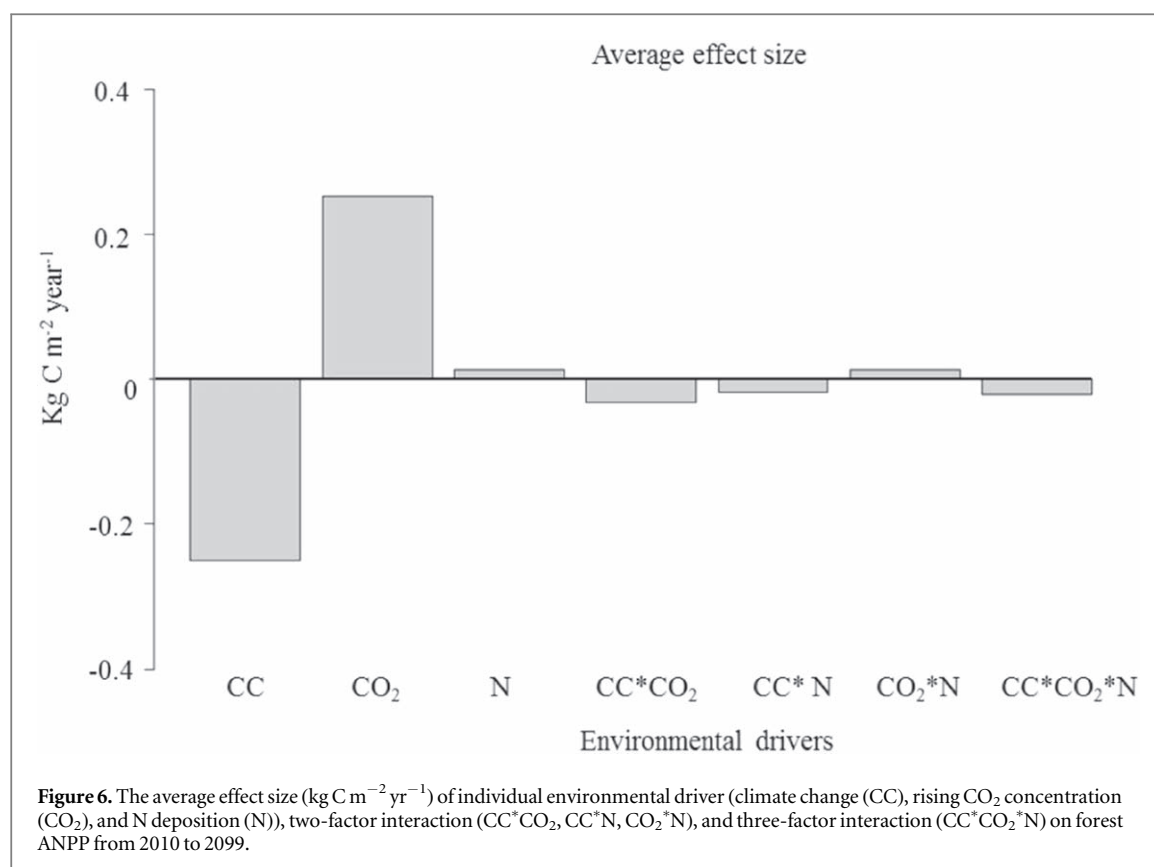
Climatic warming had a secondary effects on forest ANPP changes. ANPPs under the RCP 8.5 climates declined compared to those under current climates. Our results were consistent with predictions by Peters *et al* (2013) using PnET-CN model in Great Lakes forests in the northern US under the GFDL A1FI climate change scenario over the 21st century. However, Peters *et al* (2013) showed that ANPP was projected to slightly increase under the moderate climate change scenario PCM B1, which might indicate the saturation effects of warming climates. Moderate warming climates could enhance forest productivity by accelerating photosynthesis (Fang *et al* 2014, Bowling *et al* 2018) and lengthening growing season (Babst *et al* 2019). However, under more severe climate scenarios (e.g. RCP 8.5, GFDL A1FI), the negative effects of climate change could be because the elevated temperature was beyond the optimal temperature of photosynthesis



and thus caused photosynthetic rate to decline (Bagley *et al* 2015), and/or that the respiration increased with temperature (Ballantyne *et al* 2017), and/or that water was limited under extreme climate change scenario (Helman *et al* 2017), among other factors.

Among rising CO_2 concentration, climate change, and N deposition, our study suggested that N

deposition had the smallest effect on ANPP ($+0.043 \text{ kg C m}^{-2} \text{yr}^{-1}$). The interactive effects of N deposition with climate change and/or CO_2 fertilization were also relatively small compared to effects of CO_2 fertilization, climate change, and interaction of climate change and CO_2 fertilization. Our results generally agreed with some previous studies showing that



N deposition made only minor contributions to C sequestration in temperate forests (e.g. Fernández-Martínez *et al* 2017). However, our results differed with some field experimental studies of N fertilization (e.g. Lovett *et al* 2013, Etzold *et al* 2014) because most experiments had higher N deposition rates than those used in our study. For example, Lovett *et al* (2013) conducted 6 year increased N deposition experiments in southeastern New York State with an increased N deposition rate of $5 \text{ g N m}^{-2} \text{yr}^{-1}$, which did not significantly enhance ANPP for any tree species but significantly increased C stock in forest soils. This may be because only a small fraction of added N entered the trees, while most of added N remained in soil organic matter (Goodale 2017). This finding was supported by Etzold *et al* (2014) which showed that N deposition enhanced forest productivity with an increased N deposition rate of $2\text{--}3 \text{ g N m}^{-2} \text{yr}^{-1}$ and no further growth increased beyond that threshold. N can be absorbed directly into trees through canopies in temperate forests (Guerrieri *et al* 2015, Wang *et al* 2017a), however, in most forest models (including PnET) and field experiments, N enters the forest ecosystem in the forest soil surface, the effect of which may be different from that of equivalent N addition from atmospheric deposition.

Our study suggest the negative interactive effects of rising CO_2 and climate change on forest ANPP, which were consistent for observational and modeling studies that indicated the CO_2 fertilization effects on forest production were constrained by climate warming (e.g.

Fernández-Martínez *et al* 2019). The negative interactive effects may arise because of higher respiratory rates and drought stress under future warmer and drier climates. Rising CO_2 were expected to interact with elevated N deposition to increase forest production because N addition moderated N limitation (Norby *et al* 2010). Many forest ecosystem models are considered to have a tendency to overestimate the CO_2 fertilization effects because N limitation is not included in model formulations (He *et al* 2017, Fatichi *et al* 2019). However, PnET-day model was able to capture the effects of N on photosynthetic rate through simulating N cycles and its interaction with C cycles (Ollinger *et al* 2002).

It should be noted that there are several limitations in this study. First, PnET treats forest ecosystem as a lumped system consisting of different plant organs (e.g. roots, leaves), neither individual plant species nor functional types were represented; thus forest demographic processes and composition changes cannot be simulated. Most of temperate forests are relatively young and are typically 'regrown' from historical land management activities (e.g. harvest, agricultural abandonment) and are expected to continue taking up large amounts of C in the future (Reich and Frelich 2002). Recent studies suggest that age-driven forest demographic processes alone might play a larger role than growth enhancement from environmental changes (e.g. rising CO_2) (Liang *et al* 2015, Jin *et al* 2017, Wang *et al* 2017b, 2018, 2019, Pugh *et al* 2019). Secondly, PnET does not simulate effect of nutrients other than N, e.g. phosphorus (P), on ANPP. It has been suggested the models neglecting P limitations

may overestimate terrestrial C uptake (Fernández-Martínez *et al* 2017) and there could be interactions between N and P cycles (Schulte-Uebbing and de Vries 2017). Nevertheless, our modeling approach is well suited for assessing the effects of rising atmospheric CO₂ concentration, climate change, and N deposition on forest production. PnET-day model can be directly parameterized from forest inventory data and has been well validated against inventory data and eddy-flux tower measurements (e.g. Ryu *et al* 2008). With our modeling approach, we were able to incorporate the physiological responses of forest ecosystems to environmental changes through simulating coupled cycles of C, water, and N that would not be possible with some other models.

Acknowledgments

Funding for this work was provided by the National Natural Science Foundation of China (No. 41871045, No. 41801081), the Chinese Academy of Sciences (Y7H7031001), the Natural Science Foundation of Julian Province (20190201119JC, 20190103153JH), Key laboratory project of wetland ecology and environment, Chinese Academy of Sciences (O9B3017001), the USDA Forest Service Northern Research Station, the Department of Interior Northeast Climate Science Center graduate fellowship, and the University of Missouri-Columbia. Any data that support the findings of this study are included within the article.

References

- Aber J D and Federer C A 1992 A generalized, lumped-parameter model of photosynthesis, evapotranspiration and net primary production in temperate and boreal forest ecosystems *Oecologia* **92** 463–74
- Aber J D, Reich P B and Goulden M L 1996 Extrapolating leaf CO₂ exchange to the canopy: a generalized model of forest photosynthesis compared with measurements by eddy correlation *Oecologia* **106** 257–65
- Babst F, Bouriaud O, Poulter B, Trouet V, Girardin M P and Frank D C 2019 Twentieth century redistribution in climatic drivers of global tree growth *Sci. Adv.* **5** eaat4313
- Bagley J, Rosenthal D M, Ruiz-Vera U M, Siebers M H, Kumar P, Ort D R and Bernacchi C J 2015 The influence of photosynthetic acclimation to rising CO₂ and warmer temperatures on leaf and canopy photosynthesis models *Glob. Biogeochem. Cycles* **29** 194–206
- Ballantyne A *et al* 2017 Accelerating net terrestrial carbon uptake during the warming hiatus due to reduced respiration *Nat. Clim. Change* **7** 148–52
- Bowling D R, Logan B A, Hufkens K, Aubrecht D M, Richardson A D, Burns S P, Anderegg W R L, Blanken P D and Eiríksson D P 2018 Limitations to winter and spring photosynthesis of a Rocky Mountain subalpine forest *Agric. For. Meteorol.* **252** 241–55
- Caspersen J P, Pacala S W, Jenkins J C, Hurtt G C, Moorcroft P R and Birdsey R A 2000 Contributions of land-use history to carbon accumulation in US forests *Science* **290** 1148–51
- de Vries W, Posch M, Simpson D and Reinds G J 2017 Modelling long-term impacts of changes in climate, nitrogen deposition and ozone exposure on carbon sequestration of European forest ecosystems *Sci. Total Environ.* **605** 1097–116
- Dusenge M E, Duarte A G and Way D A 2019 Plant carbon metabolism and climate change: elevated CO₂ and temperature impacts on photosynthesis, photorespiration and respiration *New Phytol.* **221** 32–49
- Elliott E M, Kendall C, Boyer E W, Burns D A, Lear G G, Golden H E, Harlin K, Bytnerowicz A, Butler T J and Glatz R 2009 Dual nitrate isotopes in dry deposition: utility for partitioning NO_x source contributions to landscape nitrogen deposition *J. Geophys. Res.-Biogeosci.* **114** G04020
- Etzold S, Waldner P, Thimonier A, Schmitt M and Dobbertin M 2014 Tree growth in Swiss forests between 1995 and 2010 in relation to climate and stand conditions: recent disturbances matter *For. Ecol. Manage.* **311** 41–55
- Fang J Y, Kato T, Guo Z D, Yang Y H, Hu H F, Shen H H, Zhao X, Kishimoto-Mo A W, Tang Y H and Houghton R A 2014 Evidence for environmentally enhanced forest growth *Proc. Natl Acad. Soc.* **111** 9527–32
- Fatihci S, Pappas C, Zscheischler J and Leuzinger S 2019 Modelling carbon sources and sinks in terrestrial vegetation *New Phytol.* **221** 652–68
- Fekete I, Lajtha K, Kotroczo Z, Varbiro G, Varga C, Toth J A, Demeter I, Veperdi G and Berki I 2017 Long-term effects of climate change on carbon storage and tree species composition in a dry deciduous forest *Glob. Change Biol.* **23** 3154–68
- Feng Z Z, Rutting T, Pleijel H, Wallin G, Reich P B, Kammann C I, Newton P C D, Kobayashi K, Luo Y J and Uddling J 2015 Constraints to nitrogen acquisition of terrestrial plants under elevated CO₂ *Glob. Change Biol.* **21** 3152–68
- Fernández-Martínez M *et al* 2017 Atmospheric deposition, CO₂, and change in the land carbon sink *Sci. Rep.* **7** 9632
- Fernández-Martínez M *et al* 2019 Global trends in carbon sinks and their relationships with CO₂ and temperature *Nat. Clim. Change* **9** 73–81
- Goodale C L 2017 Multiyear fate of a N-15 tracer in a mixed deciduous forest: retention, redistribution, and differences by mycorrhizal association *Glob. Change Biol.* **23** 867–80
- Guerrieri R, Vanguelova E I, Michalski G, Heaton T H E and Mencuccini M 2015 Isotopic evidence for the occurrence of biological nitrification and nitrogen deposition processing in forest canopies *Glob. Change Biol.* **21** 4613–26
- He L M, Chen J M, Croft H, Gonsamo A, Luo X Z, Liu J N, Zheng T, Liu R G and Liu Y 2017 Nitrogen availability dampens the positive impacts of CO₂ fertilization on terrestrial ecosystem carbon and water cycles *Geophys. Res. Lett.* **44** 11590–600
- Helman D, Osem Y, Yakir D and Lensky I M 2017 Relationships between climate, topography, water use and productivity in two key Mediterranean forest types with different water-use strategies *Agric. For. Meteorol.* **232** 319–30
- Houtven G V, Phelan J, Clark C, Sabo R D, Buckley J, Thomas R Q, Horn K and Leduc S D 2019 Nitrogen deposition and climate change effects on tree species composition and ecosystem services for a forest cohort *Ecol. Monogr.* **0** e01345
- Ibáñez I, Zak D R, Burton A J and Pregitzer K S 2018 Anthropogenic nitrogen deposition ameliorates the decline in tree growth caused by a drier climate *Ecology* **99** 411–20
- IPCC 2014 *Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* IPCC 151
- Jin W C, He H S and Thompson F R 2016 Are more complex physiological models of forest ecosystems better choices for plot and regional predictions? *Environ. Modelling Softw.* **75** 1–14
- Jin W C, He H S, Thompson F R, Wang W J, Fraser J S, Shifley S R, Hanberry B B and Dijk W D 2017 Future forest aboveground carbon dynamics in the central United States: the importance of forest demographic processes *Sci. Rep.* **7** 41821
- Liang Y, He H S, Wang W J, Fraser J S, Wu Z and Xu J 2015 The site-scale processes affect species distribution predictions of forest landscape models *Ecol. Modelling* **300** 89–101
- Lovett G M, Arthur M A, Weathers K C, Fitzhugh R D and Templer P H 2013 Nitrogen addition increases carbon storage in soils, but not in trees, in an Eastern US deciduous forest *Ecosystems* **16** 980–1001

- Maes S L *et al* 2019 Environmental drivers interactively affect individual tree growth across temperate European forests *Glob. Change Biol.* **25** 201–17
- Martin P H, Nabuurs G J, Aubinet M, Karjalainen T, Vine E L, Kinsman J and Heath L S 2001 Carbon sinks in temperate forests *Annu. Rev. Energy Environ.* **26** 435–65
- McNab W H, Cleland D T, Freeouf J A, Keys J E, Nowacki G J and Carpenter C A 2007 Description of ecological subregions: sections of the conterminous United States *General Technical Report WO-76B* U.S. Department of Agriculture, Forest Service
- Nigh T A and Schroeder W A 2002 *Atlas of Missouri Ecoregions* (Jefferson City, MO: Missouri Department of Conservation)
- Norby R J, Warren J M, Iversen C M, Medlyn B E and McMurtrie R E 2010 CO₂ enhancement of forest productivity constrained by limited nitrogen availability *Proc. Natl Acad. Soc.* **107** 19368–73
- O'Connell B M 2015 *The Forest Inventory and Analysis Database: Database Description and User Guide for Phase 2, version 6.0.1*. Forest Inventory and Analysis National Program (www.fia.fs.fed.us/library/databasedocumentation/)
- O'Sullivan M, Spracklen D V, Batterman S, Arnold S R, Gloor M and Buermann W 2019 Have synergies between nitrogen deposition and atmospheric CO₂ driven the recent enhancement of the terrestrial carbon sink? *Glob. Biogeochem. Cycles* **33** 163–80
- Ollinger S V, Aber J D, Reich P B and Freuder R J 2002 Interactive effects of nitrogen deposition, tropospheric ozone, elevated CO₂ and land use history on the carbon dynamics of northern hardwood forests *Glob. Change Biol.* **8** 545–62
- Ollinger S V, Goodale C L, Hayhoe K and Jenkins J P 2008 Potential effects of climate change and rising CO₂ on ecosystem processes in northeastern US forests *Mitigation Adaptation Strateg. Glob. Change* **13** 467–85
- Pacala S W 2007 *The First State of the Carbon Cycle Report (SOCCR) The North American Carbon Budget and Implications for the Global Carbon Cycle* ed A W King *et al* (Asheville, NC: National Oceanic and Atmospheric Administration, National Climatic Data Center)
- Pan Y *et al* 2011 A large and persistent carbon sink in the world's forests *Science* **333** 988–93
- Peters E B, Wythers K R, Zhang S X, Bradford J B and Reich P B 2013 Potential climate change impacts on temperate forest ecosystem processes *Can. J. For. Res.-Rev. Can. Rech. Forestiere* **43** 939–50
- Pugh T *et al* 2019 Role of forest regrowth in global carbon sink dynamics *Proc Natl Acad. Soc.* **116** 4382–7
- Reich P B, Walters M B, Kloeppel B D and Ellsworth D S 1995 Different photosynthesis-nitrogen relations in deciduous hardwood and evergreen coniferous tree species *Oecologia* **104** 24–30
- Reich R B and Frelich L 2002 Temperate deciduous forests *Encyclopaedia of Global Environmental Change. The Earth System: Biological and Ecological Dimensions of Global Environmental Change* ed H A Mooney and J G Canadell vol 2 (Chichester, UK: Wiley) 565–9
- Riahi K, Grubler A and Nakicenovic N 2007 Scenarios of long-term socio-economic and environmental development under climate stabilization *Technol. Forecast. Soc. Change* **74** 887–935
- Rupp D E, Abatzoglou J T, Hegewisch K C and Mote P W 2013 Evaluation of CMIP5 20th century climate simulations for the Pacific Northwest USA *J. Geophys. Res.-Atmos.* **118** 10884–906
- Ryu S R, Chen J, Noormets A, Bresee M K and Ollinger S V 2008 Comparisons between PnET-day and eddy covariance based gross ecosystem production in two Northern Wisconsin forests *Agric. For. Meteorol.* **148** 247–56
- Scheller R M and Mladenoff D J 2005 A spatially interactive simulation of climate change, harvesting, wind, and tree species migration and projected changes to forest composition and biomass in northern Wisconsin, USA *Glob. Change Biol.* **11** 307–21
- Schulte-Uebbing L and de Vries W 2017 Global-scale impacts of nitrogen deposition on tree carbon sequestration in tropical, temperate, and boreal forests: a meta-analysis *Glob. Change Biol.* **24** E416–31
- Shifley S R and Brookshire B L E 2000 Missouri Ozark forest ecosystem project: site history, soils, landforms, woody and herbaceous vegetation, down wood, and inventory methods for the landscape experiment *General Technical Report NC-208* U.S. Dept. of Agriculture, Forest Service, North Central Forest Experiment Station 314
- Soil Survey Staff 2014 *Keys to Soil Taxonomy* 12th edn (Washington, DC: USDA-Natural Resources Conservation Service)
- Temperli C, Bugmann H and Elkin C 2013 Cross-scale interactions among bark beetles, climate change, and wind disturbances: a landscape modeling approach *Ecol. Monogr.* **83** 383–402
- Tharammal T, Bala G, Narayanappa D and Nemani R 2019 Potential roles of CO₂ fertilization, nitrogen deposition, climate change, and land use and land cover change on the global terrestrial carbon uptake in the twenty-first century *Clim. Dyn.* **52** 4393–406
- Thornton P, Thornton M M, Mayer B M, Wei Y, Devarakonda R S, Vose R S and Cook R B 2016 *Daymet: Daily Surface Weather Data on a 1-km Grid for North America, Version 3* (Oak Ridge, TN: ORNL DAAC) (<https://doi.org/10.3334/ORNLDAAC/1328>)
- Tian D H, Wang H, Sun J and Niu S L 2016 Global evidence on nitrogen saturation of terrestrial ecosystem net primary productivity *Environ. Res. Lett.* **11** 024012
- Tjoelker M G, Oleksyn J and Reich P B 2001 Modelling respiration of vegetation: evidence for a general temperature-dependent Q₁₀ *Glob. Change Biol.* **7** 223–30
- Voelker S L *et al* 2016 A dynamic leaf gas-exchange strategy is conserved in woody plants under changing ambient CO₂: evidence from carbon isotope discrimination in paleo and CO₂ enrichment studies *Glob. Change Biol.* **22** 889–902
- Wang R *et al* 2017a Global forest carbon uptake due to nitrogen and phosphorus deposition from 1850 to 2100 *Glob. Change Biol.* **23** 4854–72
- Wang W J *et al* 2017b Changes in forest biomass and tree species distribution under climate change in the northeastern United States *Landscape Ecol.* **32** 1399–413
- Wang W J *et al* 2018 Population dynamics has greater effects than climate change on tree species distribution in a temperate forest region *J. Biogeogr.* **45** 2766–78
- Wang W J *et al* 2019 Climate change and tree harvest interact to affect future tree species distribution changes *J. Ecol.* **107** 1901–17
- Xu C, Gertner G Z and Scheller R M 2009 Uncertainties in the response of a forest landscape to global climatic change *Glob. Change Biol.* **15** 116–31