



Interactive effects of seasonal drought and nitrogen deposition on carbon fluxes in a subtropical evergreen coniferous forest in the East Asian monsoon region

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ABSTRACT

Subtropical forests in the East Asian monsoon region function as considerable carbon sinks in the Northern Hemisphere. Forest ecosystems in this region have experienced intensified seasonal drought that has limited their carbon sequestration capacity, but increasing atmospheric nitrogen deposition has contrarily enhanced their capacity to act as carbon sinks. Understanding and quantifying the interactive effects of seasonal drought and nitrogen deposition on the carbon sequestration of subtropical forests is of great significance for accurately predicting future changes to the terrestrial carbon cycle. In this study, we used the Community Land Model Version 4.5 (CLM4.5) to investigate how carbon fluxes, i.e. gross primary productivity (GPP), ecosystem respiration (Re), and net ecosystem productivity (NEP), respond to seasonal drought and nitrogen deposition in an evergreen coniferous forest in southern China. Our results showed that reduced GPP during the drought in the summers of 2003 and 2007 weakened the forest's carbon sequestration capacity. The reduction in GPP mainly occurred at the sunlit canopy due to its higher sensitivity to soil water stress, and non-stomatal limitations played an important role in limiting leaf photosynthesis. The enhanced NEP by nitrogen deposition was attributed to increased plant growth, which could, in turn, be attributed to increases in leaf area. Interactions of seasonal drought and nitrogen deposition varied with drought severity. Interactive effects of the two drivers on GPP, Re, and NEP were additive under mild and moderate drought conditions but non-additive under severe drought. Their net effects on NEP shifted from +29% under mild and moderate drought conditions to -56% under severe drought. Our study highlights the importance of accounting for the interactive effects of seasonal drought and nitrogen deposition in assessing the carbon sequestration of subtropical forest ecosystems in the East Asian monsoon region.

1. Introduction

Subtropical forests in the East Asian monsoon region function as considerable carbon (C) sinks in the Northern Hemisphere, accounting for 8% of the global forest net ecosystem productivity (NEP) (Yu et al., 2014). Under the control of subtropical high over the western Pacific, summer droughts accompanied by heatwaves occur frequently in this

subtropical humid zone (Amulya et al., 2018; He et al., 2015), and significantly reduce carbon fluxes of forest ecosystems there and even the regional C budget (Liu et al., 2014; Saigusa et al., 2010; Sun et al., 2006; Xie et al., 2016). For example, a severe summer drought in southern China from July to August in 2013 caused a strong carbon uptake reduction of 101.54 Tg C, which was 39–53% of the annual net C sink of China's terrestrial ecosystems (Yuan et al., 2016). In this study

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we defined drought as a soil moisture deficit that restricts physiological processes such as photosynthesis and respiration (Baldocchi, 2008), because soil moisture deficit was found to be the main factor controlling carbon fluxes during seasonal drought in subtropical forests (Granier et al., 2007). Previous studies mainly focus on the investigation on how C and water fluxes respond to seasonal drought using eddy-covariance measurements (Liu et al., 2006; Song et al., 2006; Sun et al., 2006; Tang et al., 2014a,b; Wen et al., 2006, 2010; Yu et al., 2008b). They found that ecosystem gross primary productivity (GPP) is more sensitive to summer drought than ecosystem respiration (Re) in subtropical forests, which is consistent with studies in Europe and the globe (Ciais et al., 2005; Schwalm et al., 2010; Shi et al., 2014). However, the responses of physiological processes (e.g. enzymatic activities and stomatal conductance) to seasonal drought in the humid subtropical zone and their relative contributions to the reduction in carbon fluxes have not been well quantified yet.

Atmospheric nitrogen (N) deposition has increased significantly in the subtropical region of China (Liu et al., 2013), and is expected to further increase in the coming decades (Galloway et al., 2004; Kanakidou et al., 2016). It has a positive effect on subtropical forest productivity (Chen et al., 2015; Lebauer and Treseder, 2008), and is considered to be a large contributor to the increasing terrestrial NEP in this region (Fu et al., 2015; Wei et al., 2012; Yu et al., 2014) and the whole country of China (Gu et al., 2015; Tian et al., 2011). Results from meta-analysis and modeling suggested that the response of plant production to N addition varies with precipitation or water availability (Hooper and Johnson, 1999; Yahdjian et al., 2011). Since the terrestrial C cycle is closely coupled with N and water cycles, understanding the interactions between N and water availability seems to be more crucial for the prediction of terrestrial C cycle and its feedback to climate change under the circumstance with increasing N deposition and drought events.

Ecosystem responses to multiple global change drivers might be additive (i.e. the combined effect is equal or not significantly different from the sum of individual effects) or non-additive (i.e. synergistic or antagonistic, which means that the combined effect is significantly greater or weaker than the sum of individual effects). Across all two-driver pairs of global change drivers among elevated CO₂ (eCO₂), warming, N addition, phosphorus addition, increased rainfall, and drought, unlike the common additive interactions, there were synergistic effects of eCO₂ × warming and eCO₂ × N addition, and antagonistic effects of N addition × drought on plant C pools as revealed in a global meta-analysis (Yue et al., 2017). Nevertheless, scarce studies focus on the interactive effects of drought and N deposition on ecosystem carbon fluxes (Meyer-Grünefeldt et al., 2013; Niu et al., 2009), especially in forest ecosystems subjected to drought (Drewniak and Gonzalez-Meler, 2017).

In this study, we applied the Community Land Model Version 4.5 (hereafter referred to as CLM4.5), which couples C, N, and water cycle explicitly, to analyze the changes in ecosystem carbon fluxes and related plant physiological processes under the summer drought conditions of 2003 and 2007 in a subtropical evergreen coniferous forest in southern China. The scientific questions addressed in this study included: (1) How do plant physiological processes respond to drought, and how do these contribute to decreased carbon fluxes during seasonal drought periods? (2) How do carbon fluxes respond to seasonal drought and N addition individually? (3) Are there interactive effects of seasonal drought and N addition on ecosystem carbon fluxes and whether they are additive or not? We hypothesized that the combined effects of N deposition and seasonal drought on terrestrial carbon fluxes in subtropical forests will be significantly different from the sum of individual effects (i.e. non-additive effects).

Table 1

The differences in air temperature (T), precipitation (P), soil water content (SWC) in July of drought years (2003 and 2007) and baseline years (2004–2006 and 2008).

Environmental variable	Differences between drought and baseline years		Baseline years (mean ± 1SE)
	2003	2007	
T (°C)	3.07*	1.58	28.83 ± 1.81
P (mm mon ⁻¹)	-88.81*	-90.01*	92.7 ± 27.59
SWC (m ³ m ⁻³)	-0.048*	-0.043*	0.369 ± 0.025

*represents significant differences (P < 0.05) in July between drought and baseline years.

2. Materials and methods

2.1. Site description

The Qianyanzhou (QYZ) subtropical coniferous forest site is part of the ChinaFlux network and is located in southeast China (26°44'29"N, 115°03'29"E, elevation 102 m). The forest site has a subtropical monsoon climate with warm and dry winters, and hot and wet summers. The mean annual air temperature and annual precipitation are 18 °C and 1505 mm, respectively, according to the meteorological records of 1989–2008. Precipitation during July–August has a high inter-annual variability influenced by the subtropical high over the western Pacific. Total precipitation in July of 2003 and 2007 was significantly lower than that in baseline years. At the same time, the mean monthly air temperature in July was also higher than baseline value. Consequently, the summer drought occurred when the soil water contents were significantly lower than baseline value (Table 1). The original vegetation of this site was evergreen broadleaf forest, which was harvested around 1950 (Huang et al., 2007). The current evergreen coniferous plantation was planted around 1985 on gently undulating terrain with slopes between 2.8 and 13.5 degrees. The dominant tree species now are Slash pine (*Pinus elliottii*), Masson pine (*Pinus massoniana*), and Chinese fir (*Cunninghamia lanceolata*), with a tree density of approximately 1460 stems ha⁻¹ and a mean canopy height of 13 m (Wen et al., 2006). The soil is weathered from red sand rock, and the soil texture is categorized as 2.0–0.05 mm (17%), 0.05–0.002 mm (68%) and < 0.002 mm (15%) (Yang, 2005).

2.2. Eddy-covariance and meteorological data

Eddy covariance instruments, which consist of open-path analyzer, infrared gas analyzers for CO₂ and water vapor, three-dimensional sonic anemometer, and a data acquisition system, were mounted at 39.6 m on a tower. The tower footprint has a length of 1915 m (Mi et al., 2006). A half-hourly NEP was estimated over the canopy by calculating CO₂ storage below the height of the flux measurement system. The data gaps of NEP were filled mainly by the nonlinear regressions method (Falge et al., 2001). Observed GPP and Re were estimated from half-hourly NEP following Zhang et al. (2006). Estimated NEP data provided by ChinaFLUX for this forest ecosystem was quite well consistent with those estimated by JapanFlux and KoFlux (Saigusa et al., 2013). These flux observations have been successfully used in the earlier studies on effects of seasonal drought on carbon and water fluxes, water use efficiency, and the Bowen ratio (Song et al., 2006; Sun et al., 2006; Tang et al., 2014a; Wen et al., 2010; Yu et al., 2008a). In this study, observed NEP, GPP, and Re were aggregated at a daily step to evaluate the performance of CLM4.5. Further details about the instruments and data quality evaluation technique are provided in Wen et al. (2010).

Meteorological variables and soil water content were also measured at the site (Wen et al., 2010). Half-hourly climate data (i.e. air

temperature, relative humidity, wind speed, incident short-wave radiation, incident long-wave radiation, atmospheric pressure, and precipitation) observed from 2003 to 2008 were used to run CLM4.5. These climate data were gap-filled following the methods applied in North American Carbon Cycle interim synthesis (Schwalm et al., 2011). Missing values were filled using the meteorological data observed at the same site within the Chinese Ecosystem Research Network (CERN) dataset (<http://ww.cnern.org.cn/>). Soil water contents measured with TDR probes at depth of 50 cm were used to evaluate the CLM4.5 simulated values.

2.3. Model description

The process-based terrestrial biosphere model CLM4.5, which is the land model component of the Community Earth System Model version 1.2 (CESM 1.2), includes biogeophysical, hydrological, and biogeochemical components and estimates carbon, water, and energy fluxes among the soil, plant, and atmosphere (Oleson et al., 2013). In CLM4.5, the Farquhar leaf photosynthesis model and the Ball-Berry stomatal conductance model are used to calculate the leaf photosynthesis rate (Collatz et al., 1992; Farquhar et al., 1980). Sun and shade leaves are considered separately in the photosynthesis model to scale up carbon fluxes from the leaf to canopy level. R_e is divided into plant autotrophic respiration (R_a), which includes maintenance respiration (R_m) and growth respiration (R_g), and heterotrophic respiration (R_h). NEP is the difference between GPP and R_e . A fully prognostic treatment of the terrestrial C and N cycles and interactions between these cycles are included in CLM4.5 to mediate biological mechanisms of plants and soil heterotrophs. Since we focused on the effects of water stress and N addition on carbon fluxes, the following section just describes the relevant processes in CLM4.5. A more detailed description of the full model can be found in Oleson et al. (2013).

The influences of soil water stress on leaf photosynthesis rate are modeled as the direct effects of this on stomatal conductance (g_s , $\mu\text{mol m}^{-2} \text{s}^{-1}$), maximum carboxylation rate (V_{cmax} , $\mu\text{mol m}^{-2} \text{s}^{-1}$), and leaf respiration (R_d , $\mu\text{mol m}^{-2} \text{s}^{-1}$), as follows:

$$g_s = m \frac{A_n}{C_s/P_{atm}} h_s + b\beta_t \quad (1)$$

$$V_{cmax} = V_{cmax}' \times \beta_t \quad (2)$$

$$R_d = R_d' \times \beta_t \quad (3)$$

where A_n ($\mu\text{mol m}^{-2} \text{s}^{-1}$) is the net leaf photosynthesis, C_s (Pa) is the CO_2 partial pressure at the leaf surface, P_{atm} (Pa) is the atmospheric pressure, h_s (unitless) is the relative humidity at the leaf surface, m (unitless) is a plant functional type-dependent parameter, and b (unitless) is the minimum stomatal conductance; V_{cmax}' ($\mu\text{mol m}^{-2} \text{s}^{-1}$) and R_d' ($\mu\text{mol m}^{-2} \text{s}^{-1}$) are the values of the maximum carboxylation rate and leaf respiration, respectively, without soil water stress. The soil water stress factor (β_t) is defined as:

$$\beta_t = \sum_{i=1}^{10} w_i r_i \quad (4)$$

where r_i is the root fraction at soil layer i and w_i is a corresponding plant wilting factor, calculated as a function of soil water potential and a

Table 2
A description of the key parameters used in CLM4.5.

Parameter	Definition	Default value	Adjusted value	Reference
CN_l	Leaf C:N ratio	35	40	Zhan et al. (2012)
τ_l	Leaf Longevity (year)	3	2.57	Zhang et al. (2010)
τ_r	Fine root Longevity (year)	3	0.95	Zhang et al. (2010)
$Q_{10\text{-fr}}$	Temperature Sensitivity Coefficient for maintenance respiration of fine root	1.5	2.0	Wang et al. (2009)
$Q_{10\text{-hr}}$	Temperature Sensitivity Coefficient for decomposition	1.5	2.3	Wang et al. (2009)

plant-dependent response to drought stress. β_t ranges from 0 (maximum drought stress) to 1 (no drought stress). In addition, soil water stress also downscales R_h ($\text{gC m}^{-2} \text{s}^{-1}$), as is directly expressed by multiplying the optimal rate with a soil decomposition rate scalar for soil water potential (r_{water} , ranging from 0 to 1), as follows:

$$R_h = R_h' \times r_{water} \quad (5)$$

where R_h' is the heterotrophic respiration without soil water stress, and r_{water} is calculated using soil water potential.

CLM4.5 calculates a down-regulation factor ($f(N)$, ranging from 0 to 1) at each time step to adjust photosynthesis and immobilization to match the rate determined by both soil N availability (N_{soil} , gN m^{-2}) and the total ecosystem N demand (NF_{demand} , $\text{gN m}^{-2} \text{s}^{-1}$), which consists of plant N demand (NF_{plant_demand} , $\text{gN m}^{-2} \text{s}^{-1}$) and microbial N demand (NF_{immb_demand} , $\text{gN m}^{-2} \text{s}^{-1}$), as shown below:

$$f(N) = NF_{demand} \times \Delta t / N_{soil} \quad (6)$$

$$NF_{plant_demand} = CF_{avail_alloc} \frac{N_{allom}}{C_{allom}} \quad (7)$$

$$NF_{immb_demand} = \sum \frac{CF_{pot,u} (1 - rf_u - \frac{CN_d}{CN_u})}{CN_d} \quad (8)$$

where CF_{avail_alloc} ($\text{gC m}^{-2} \text{s}^{-1}$) is the assimilated carbon available to be allocated for new growth and N_{allom}/C_{allom} is the plant-level nitrogen to carbon stoichiometry for new growth, which is calculated based on prescribed carbon to nitrogen ratios (C:N) of each plant organ for each plant functional type. $CF_{pot,u}$ ($\text{gC m}^{-2} \text{s}^{-1}$) is the potential carbon flux out of the upstream pool, rf_u is the respiration fraction for carbon flux leaving the upstream pool, and CN_u and CN_d are the C:N ratios of the upstream and downstream pools, respectively. Negative values of NF_{immb_demand} mean that microbes immobilize inorganic N from soil.

2.4. Model adjustment and simulations

We adjusted five key model parameters, as listed in Table 2, to improve the model's performance in simulating carbon fluxes at the QYZ site, which addressed the overestimation of R_e and thus underestimation of NEP at this site when using default parameters as reported in Zhang et al. (2016). The adjusted values of these parameters were derived from previous related studies (cited in Table 2). All of the following model simulations were run with these adjusted parameter values.

We first ran the model to equilibrium to obtain the initial values for the state variables (i.e. C and N pool sizes) using a two-stage spin-up method. Initial spin-up followed the accelerated decomposition approach for 600 simulation years, and then a normal decomposition spin-up was operated for 1000 years with a repeating 6 year (2003–2008) cycle of meteorological forcing, and with constant land-use (broadleaf evergreen trees, Sect. 2.1), N deposition ($0.5 \text{ gN m}^{-2} \text{ yr}^{-1}$), and CO_2 levels (284 ppmv) representing pre-industrial conditions. After reaching equilibrium, a transient run was performed from 1850 to 2008 with dynamic CO_2 , climate, N deposition, and land use. The dynamic CO_2 and N deposition data for this site were downloaded from the global dataset described in Thornton et al. (2007).

To explore the individual and interactive effects of seasonal drought

Table 3
Design of simulation experiments.

Simulation	Seasonal drought ^a	Effect of soil water stress on g_s	Effect of soil water stress on V_{cmax}	N addition ^b
S1	Yes	Yes	Yes	No
S2	No	Yes	Yes	No
S3	Yes	Yes	No	No
S4	Yes	No	Yes	No
S5	Yes	Yes	Yes	Yes
S6	No	Yes	Yes	Yes

^a We replaced driving data during July of 2003 and 2007 with the historical mean July precipitation (100 mm) to represent the normal conditions (i.e. no seasonal drought.).

^bThe background N deposition rate at QYZ is about 3 g N m⁻² yr⁻¹ (Zhu et al., 2015). The addition of N is 10 g N m⁻² yr⁻¹ based on the increased rate of N deposition at QYZ in recent decades (Jia et al., 2014).

and N addition on the carbon exchange of the QYZ forest ecosystem, we conducted six simulation experiments (Table 3). In the first experiment (S1), the model was driven by observed forcing data, which was a realistic simulation. The modeled monthly GPP, Re, and NEP from S1 during 2003–2008 were evaluated against eddy covariance measurements. The second experiment (S2) was treated as a baseline experiment by replacing the precipitation data in July of the years 2003 and 2007 with the long-term (1989–2008) average monthly precipitation. The changes in modeled carbon fluxes between S1 and S2 represented the individual effect of seasonal drought stress on carbon fluxes. To further explore the contribution of the two key physiological processes (i.e. V_{cmax} and g_s) to reducing GPP during seasonal drought periods, we conducted two additional experiments (S3 and S4), which were the same as S1 but excluding the water stress effect on V_{cmax} and g_s in S3 and S4, respectively. Experiments S5 and S6 kept the same driving conditions as experiments S1 and S2, but with an additional N deposition of 10 g N m⁻² yr⁻¹ to the ecosystem. The differences in modeled carbon fluxes between S2 and S5, and between S2 and S6, were defined as combined effects of seasonal drought and N addition and individual effects of N addition, respectively.

Only modeled data in July and August of the years 2003 and 2007 were used to quantify the individual and interactive effects of drought and N deposition to carbon fluxes. We classified the drought severity into three levels in terms of relative soil water content (RSWC): mild drought (0.40 ≤ RSWC < 0.47), moderate drought (0.33 ≤ RSWC < 0.40), and severe drought (RSWC < 0.33). Here, RSWC was defined as the ratio of soil water content to the saturated soil water content, which is calculated based on soil texture (Lawrence et al., 2011). From simulations, we used soil water content of the sixth soil layer in CLM4.5 (29–49 cm), with the aim to correspond with the observed values at depth of 50 cm. We used One-way ANOVAs to examine the statistical difference in average daily values for corresponding variables among the simulation experiments. Two-way ANOVAs were used to identify the effects of drought and N additions and their interactions on the daily values of ecosystem C fluxes. We also conducted a simple effect test to further examine the interaction of seasonal drought and N deposition on C fluxes. All statistical analyses were conducted with SPSS software (SPSS 13.0 for windows).

3. Results

3.1. Model evaluation

Comparisons between modeled and observed GPP, Re, and NEP at QYZ are shown in Fig. 1 and Table 4. Modeled carbon fluxes from the simulation using the adjusted parameter values (CLM4.5-a) were more consistent with observations than those from the simulation using the default parameter values (CLM4.5-o). Specifically, CLM4.5-a had lower

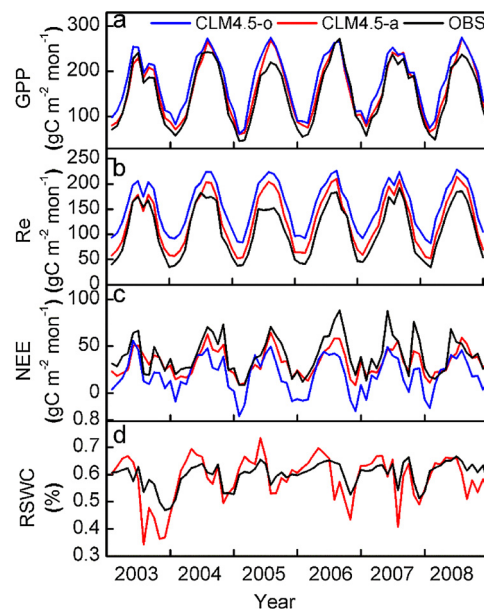


Fig. 1. Comparisons between observed (OBS) and simulated (CLM4.5-o and CLM4.5-a) monthly (a) GPP, (b) Re, (c) NEP, and (d) RSWC from 2003 to 2008 at the QYZ subtropical forest site. The seasonal drought occurred in the years 2003 and 2007.

mean bias errors (MBE) for monthly Re (19.4 gC m⁻² mon⁻¹) and NEP (-7.6 gC m⁻² mon⁻¹) than CLM4.5-o. The root mean square errors (RMSE) decreased by 60% and 56% for monthly Re and NEP, respectively. Furthermore, the model simulated the seasonal dynamics of RSWC and its response to seasonal drought well (R² = 0.61, Fig. 1d; Table 4). These results showed that adjustment of the model parameters improved the performance of CLM4.5 in simulating carbon fluxes at QYZ, and it is feasible and appropriate to apply CLM4.5 to analyze the responses of carbon fluxes and carbon cycling processes in the QYZ subtropical forest to seasonal drought and N deposition.

3.2. Effects of seasonal drought on ecosystem carbon fluxes

During the summer drought period in 2003, the precipitation deficit combined with high air temperature led to a rapid decrease in RSWC from 0.47 to 0.29 (Fig. 2a and c). Consequently, the soil water stress factor (βt) decreased from 1.00 to 0.35 (Fig. 2c). The soil water stress caused a sudden drop in the carbon exchange between the atmosphere and the QYZ forest ecosystem, such that the forest even became a net source of carbon for a time with a rate of 0.31 gC m⁻² d⁻¹ (Fig. 3e). Compared with carbon fluxes in the baseline years, average daily GPP, Re, and NEP during the seasonal drought period of 2003 decreased by 2.2, 0.6, and 1.6 gC m⁻² d⁻¹, respectively (Fig. 3a, c, and e). With a lighter degree of drought during July of 2007 (Fig. 2b and d), the average daily GPP, Re, and NEP decreased only by 0.94, 0.33 and 0.61 gC m⁻² d⁻¹, respectively (Fig. 3b, d, and f).

The decrease in GPP during seasonal drought was mainly attributable to the regulation of sunlit fractions of the vegetation canopy rather than shaded fractions. When SWC was sufficient, average daily GPP of the sunlit canopy was 4.4 gC m⁻² d⁻¹ during July–August in 2003 and 2007, which was larger than that of the shaded canopy (3.8 gC m⁻² d⁻¹) (Fig. 4a). Compared to the model output in experiment S2 with sufficient water supply, modeled daily GPP of the sunlit canopy in experiment S1 decreased by 37%, which was much larger than the reduction of 8% in the shaded canopy.

Compared to the slight decrease of 2% in modeled leaf area index (LAI) under seasonal drought stress (Fig. 4b), the large regulation of the maximum carboxylation rate (V_{cmax}) and stomatal conductance (g_s) was regarded as the main reason of GPP reduction (Fig. 4c and d). Modeled

Table 4
Performance of simulated GPP, Re, and NEP from the simulations with default parameter values (CLM4.5-o) and with adjusted parameter values (CLM4.5-a).

	MBE		RMSE		R ²	
	CLM4.5-o	CLM4.5-a	CLM4.5-o	CLM4.5-a	CLM4.5-o	CLM4.5-a
GPP (gC m ⁻² mon ⁻¹)	28.6	11.8	32.4	17.5	0.95	0.96
Re (gC m ⁻² mon ⁻¹)	48.7	19.4	49.9	22.3	0.97	0.97
NEP (gC m ⁻² mon ⁻¹)	-20.1	-7.6	23.4	12.9	0.65	0.74
RSWC	-0.08	-0.08	0.09	0.09	0.61	0.61

V_{cmax} of sunlit and shaded leaves had a similar response to soil water stress with the reduction of ca. 35%, while the g_s of sunlit leaves decreased by 37%, which was much larger than that of shaded leaves (Fig. 4c and d). By comparing the differences in modeled GPP among experiments S1–S4, we found that when RSWC was lower than 40%, non-stomatal limitation (i.e. downregulation of V_{cmax}) was the dominant cause of reduced photosynthesis, compared to the contribution of stomatal limitation. Modeled daily GPP was regulated by biochemical processes in experiment S3 and decreased to 3.1 gC m⁻² d⁻¹ when RSWC reached 28% during the summer drought period, while modeled daily GPP was regulated by stomatal limitation alone in experiment S4 and thus only decreased to 6.3 gC m⁻² d⁻¹ (Fig. 5).

As shown in Fig. 6, R_m was the largest fraction of Re in the QYZ forest ecosystem, which was 3.19 gC m⁻² d⁻¹ and accounted for 64% of Re. The second largest fraction was R_h , which accounted for 22% of Re. During seasonal drought periods, R_m , R_g , and R_h decreased by 17%, 34%, and 50%, respectively, indicating that R_h was most sensitive to soil water stress.

3.3. Effects of N addition on ecosystem carbon fluxes

Our modeled results showed that N addition stimulated GPP, Re, and NEP of the QYZ subtropical forest ecosystem. Under enhanced N deposition without seasonal drought in experiment S6, canopy LAI increased from 5.7 to 7.2 m² m⁻² (Fig. 7b). Accordingly, mean daily GPP and Re increased by 1.6 gC m⁻² d⁻¹ and 0.93 gC m⁻² d⁻¹, and thus led to carbon sink increasing from 1.7 to 2.4 gC m⁻² d⁻¹, with a carbon sink response of 25 gC per gN to N deposition (Fig. 7a). Furthermore, the increase in canopy GPP resulted from the increase in both sunlit leaf photosynthesis and shaded canopy LAI (Fig. 7c and d). The increase in vegetation respiration contributed the largest fraction to that of Re stimulated by enhanced N deposition. The combined total of R_m and growth respiration R_g increased by 0.84 gC m⁻² d⁻¹, while soil heterotrophic respiration was almost unchanged due to little change in soil organic carbon pool and environmental conditions (Fig. 6).

3.4. Interactive effects of seasonal drought and N addition on ecosystem carbon fluxes

The result of two-way ANOVAs showed that there was an interactive effect of seasonal drought and N addition on carbon fluxes (Table 5). The simple effect test also demonstrated that the effects of N addition on GPP, Re, and NEP varied with drought severity (Table 6). Specifically, modeled GPP, Re, and NEP significantly increased by more than 20%, 14%, and 40%, respectively, due to N addition at mild and moderate drought, but did not have significant change at severe drought level. Moreover, the combined effects of drought and N addition (referred to as N × D) was not significantly different from sum of the individual effects (referred to as N + D) at mild and moderate drought level, but was significantly weaker than the latter with severe drought (Fig. 8). For the severe drought level, the combination effects on GPP, Re, and NEP on average were -34%, -28%, and -56% respectively, which were significantly lower than the sum of individual effects of -20%, -21%, and -7% (Fig. 8c, f and i). These results suggested that the interactive effects of N addition and seasonal drought on carbon fluxes of the QYZ subtropical forest were additive at the mild and moderate drought levels but non-additive at the severe level. The regulation of drought on the effects of N on carbon fluxes was associated with the balance between ecosystem N supply and plant N demand. Although these processes were both reduced by drought, the plant N demand decreased faster than ecosystem N supply, which overrides N limitation on plant growth at severe drought level (Fig. 9).

4. Discussion

This study investigated the individual, combined and interactive effects of seasonal drought and nitrogen deposition on carbon fluxes of a subtropical forest in southern China. Although modeled results revealed the interactive effects of these two factors on carbon fluxes, unlike our hypothesis, we found that the interactive effects of nitrogen addition and seasonal drought on carbon fluxes of the subtropical forest were additive at the mild and moderate drought levels but non-additive

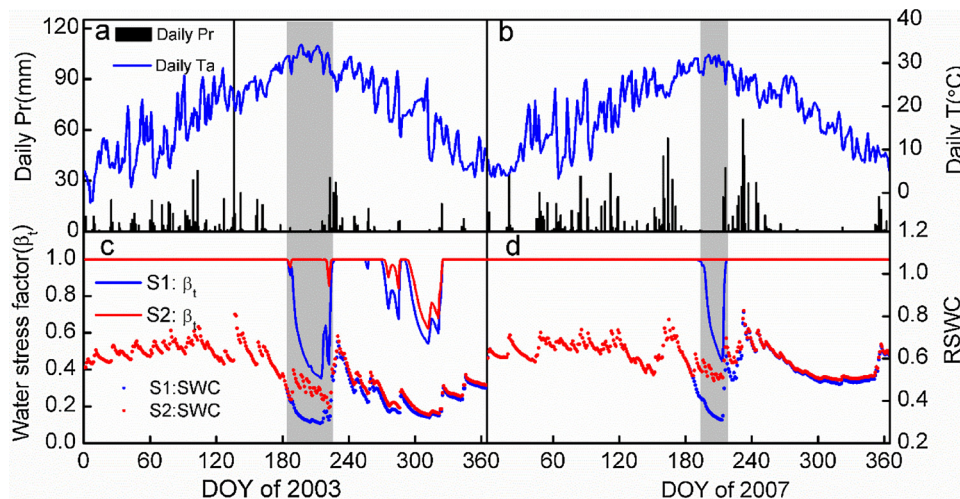


Fig. 2. Time series of daily mean (a, b) air temperature (T) and precipitation (Pr), and (c, d) soil water content (SWC) and soil water stress factor (β_t) in 2003 and 2007. Experiment S1 represents the simulation with observed climate data during 2003–2008. Experiment S2 represents the simulation as S1 but replacing the precipitation data in July of the years 2003 and 2007 with the long-term (1989–2008) average monthly precipitation. The shaded areas indicate the seasonal drought period of 2003 lasting from day of year (DOY) 182 to 227 and 2007 (DOY 191–216), defined by days with $\beta_t < 1$ (i.e. RSWC < 0.47) during July–August.

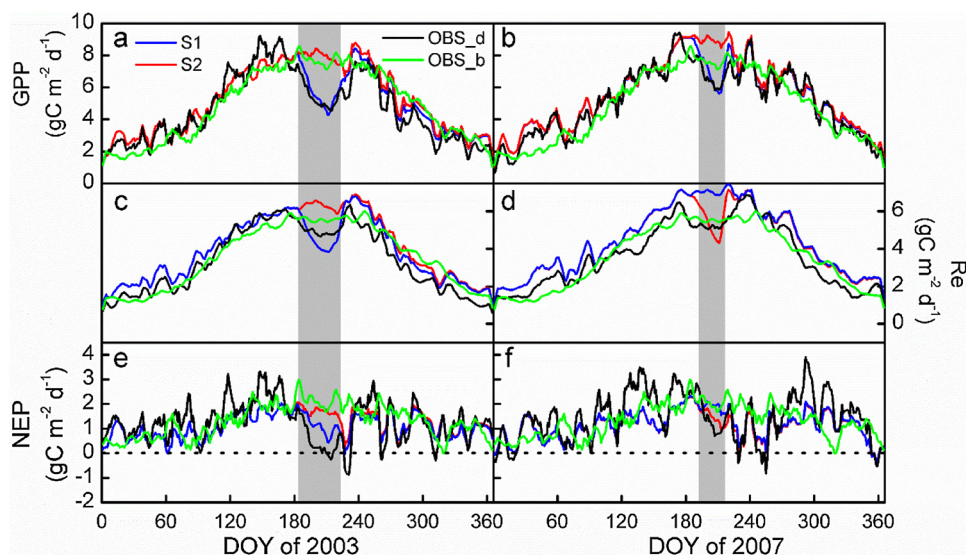


Fig. 3. Time series of 7-day running means of modeled and observed daily (a, b) GPP, (c, d) Re, and (e, f) NEP in 2003 and 2007. Experiment S1 represents the simulation with observed climate data during 2003–2008. Experiment S2 represents the simulation as S1 but replacing the precipitation data in July of the years 2003 and 2007 with the long-term (1989–2008) average monthly precipitation. The shaded areas indicate the seasonal drought period of 2003 (DOY 182–227) and 2007 (DOY 191–216), defined as days with $\beta t < 1$ during July–August. Green and black lines correspond to observed data from 2003 and 2007 (OBS_d) and average observed daily values for other years (i.e. baseline year, OBS_b) during the investigated period (2003–2008), respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

at the severe level. This could be explained by the regulation of soil water stress on the responses of carbon fluxes to N addition, because water availability fluctuates over shorter timescales than nitrogen availability. In line with our finding, Huang and Gerber (2016) found that N limitation is less severe in extreme drought events at a global scale, and Fariior et al. (2015) proposed that the main limiting resource limitation in carbon sinks of water limited forests can shift from water to N and back, because of variability in precipitation. The physiological mechanisms underlying the change of relative role of water and N in regulating carbon fluxes during seasonal drought was that plant physiology is more sensitive to water stress than that of ecosystem available N supply (Fig. 9). Although plant growth was suppressed under mild or moderate drought stress, plant demand was still larger than nitrogen availability. Thus, N addition could counteract the negative effects of drought stress on plant growth. However, Liebig’s law (i.e. only the most limiting factor has impact) appeared with intensified water stress.

Since drought stress severely limited plant growth, this led to plant demand being lower than ecosystem N supply, N limitation was almost completely prevented. Our study poses challenges to the extrapolation of ecosystem responses from single-factor studies to prediction of global change with concurrent multifactor changes in subtropical forest ecosystems, because the combined effects of seasonal drought and N deposition can differ from the simple sum of their individual effects. Since many climate change scenarios forecast that the East Asian monsoon region will experience more frequent and severe drought events (Dai, 2013; Wang and Chen, 2014), the enhanced ability of subtropical forest ecosystems to act as carbon sinks caused by N fertilization may diminish greatly. Our results highlight the importance of accurate prediction of severity and region of the seasonal drought, which will substantially influence the estimation of the gain of carbon uptake induced by increasing N deposition for subtropical forests in China and elsewhere.

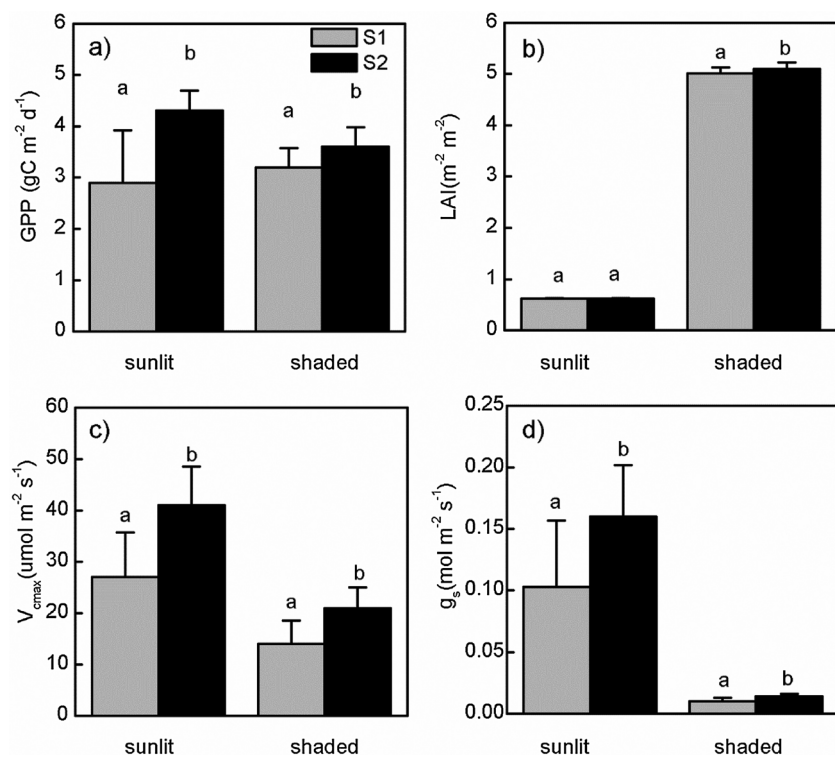


Fig. 4. Average daily (a) GPP, (b) leaf area index (LAI), (c) maximum rate of carboxylation (V_{max}) and (d) stomatal conductivity (g_s) of sunlit and shaded fractions of vegetation canopy during seasonal drought period in 2003 (DOY 182–227) and 2007 (DOY 191–216). Error bars correspond to one standard deviation. Different letters on the bar indicate significant differences ($P < 0.05$) in average daily values among different experiments.

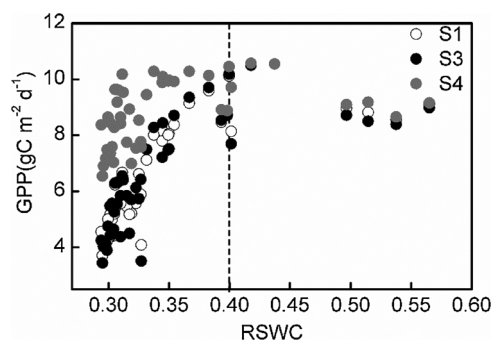


Fig. 5. Daily canopy GPP change with RSWC during seasonal drought periods in 2003 and 2007. Results from three simulations (S1, S3, and S4) are presented, among which S1 indicates both stomatal (i.e. g_s) and non-stomatal limitations (i.e. V_{cmax}) to photosynthesis, while S3 and S4 indicate non-stomatal and stomatal limitations only, respectively.

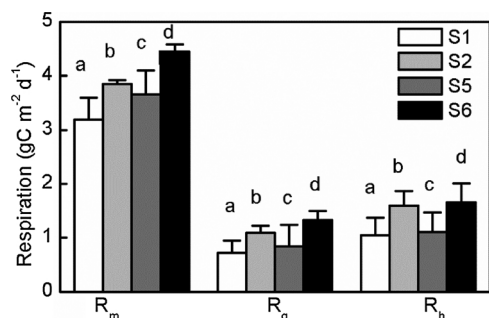


Fig. 6. Average daily maintenance respiration (R_m), growth respiration (R_g) and heterotrophic respiration (R_h) during seasonal drought periods in 2003 (DOY 182–227) and 2007 (DOY 191–216). Error bars correspond to one standard deviation. Different letters on the bar indicate significant differences ($P < 0.05$) in average daily values among different simulation experiments.

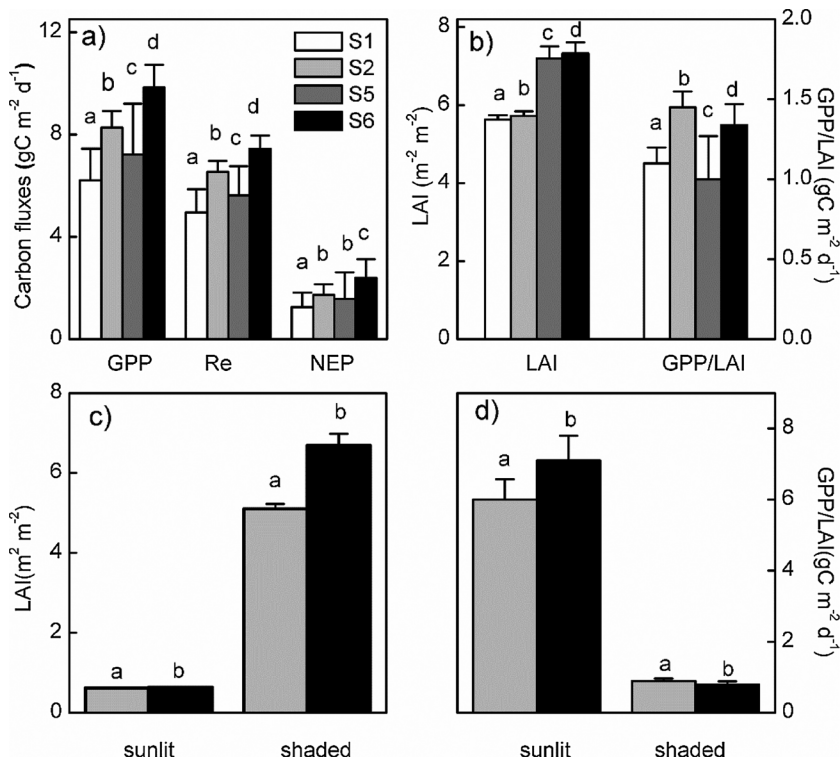


Fig. 7. Average daily (a) GPP, Re, and NEP, (b) LAI of the canopy and leaf photosynthesis (GPP/LAI), (c) LAI, and (d) GPP/LAI of the sunlit and shaded canopy during seasonal drought period in 2003 (DOY 182–227) and 2007 (DOY 191–216). Error bars correspond to one standard deviation. Different letters on the bar indicate significant difference ($P < 0.05$) in average daily values among different simulation experiments.

Table 5

Results (F-Values) of ANOVAs on the effects of seasonal drought (D), N, and their interactions on GPP ($gC\ m^{-2}\ d^{-1}$), Re ($gC\ m^{-2}\ d^{-1}$), NEP ($gC\ m^{-2}\ d^{-1}$).

	GPP	Re	NEP
N	139.8 [*]	164.7 [*]	39.9 [*]
D	352.7 [*]	582.9 [*]	61.9 [*]
N × D	12.6 [*]	5.1 [*]	9.6 [*]

*represents differences significant at $P < 0.005$.

Table 6

The effects of N addition on average daily values of GPP ($gC\ m^{-2}\ d^{-1}$), Re ($gC\ m^{-2}\ d^{-1}$), NEP ($gC\ m^{-2}\ d^{-1}$) at different drought levels.

Drought levels	GPP		Re		NEP	
	Control	N	Control	N	Control	N
mild	7.5 ^a	9.4 ^b	6.2 ^a	7.2 ^b	1.3 ^a	2.2 ^b
moderate	6.9 ^a	8.3 ^b	5.2 ^a	6.0 ^b	1.7 ^a	2.4 ^b
severe	5.1 ^a	5.4 ^a	4.2 ^a	4.61 ^a	0.97 ^a	0.79 ^a

Different letters represent differences significant at $P < 0.005$.

Numerous studies had documented that the reduction of plant primary productivity dominates the decreased carbon sinks in subtropical forest ecosystems during seasonal drought (Sun et al., 2006; Xie et al., 2016; Yuan et al., 2016). The degree to which GPP is reduced in forests during seasonal drought depends on the reduction in enzyme activity and stomatal conductance, but their relative contribution is still in debate (Keenan et al., 2009). Generally, non-stomatal limitations on photosynthesis come to predominate over stomatal limitation with increasing drought severity in C_3 plants (Flexas and Medrano, 2002; Grassi and Magnani, 2005). Our result showed that non-stomatal limitations play an important role in photosynthetic response to soil water stress, which is supported by a recent field experiment at the same site indicating that non-stomatal limitations explained 50% of the drought-induced limitation of photosynthesis (Zhou et al., 2015). The importance of non-stomatal limitations in reducing photosynthesis during

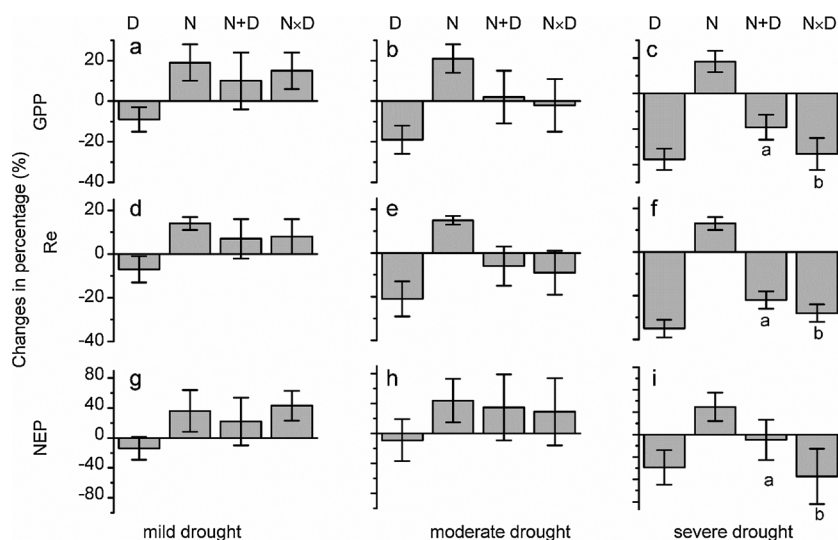


Fig. 8. Effects of drought and N addition on (a, d, g) GPP, (b, e, h) Re, and (c, f, i) NEP at different drought levels during seasonal drought period in 2003 (DOY 182–227) and 2007 (DOY 191–216). D = seasonal drought, indicating individual effects of drought; N = nitrogen addition, indicating individual effects of nitrogen addition; N + D indicates sum of individual effects of drought and nitrogen; D × N = nitrogen and drought added in combination, indicating combined effects of drought and N. Different letters on the error bars indicate significant differences ($P < 0.005$) between combined effects and sum of individual effects.

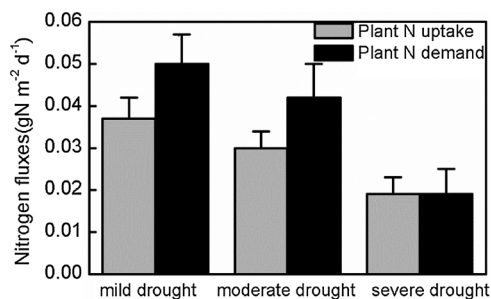


Fig. 9. Average daily plant N uptake and plant N demand from experiment S1 at different drought levels during seasonal drought period in 2003 (DOY 182–227) and 2007 (DOY 191–216). Error bars correspond to one standard deviation.

summer drought has also been observed in Mediterranean forests ecosystems, which usually experience summer drought (Flexas et al., 2014; Keenan et al., 2009, 2010; Niinemets, 2002). The characteristic rapid development and extreme intensity of summer drought in the East Asia Monsoon region (Li et al., 2010; Yuan et al., 2016) are similar conditions in typical drought/photosynthesis studies, in which well-watered plants were suddenly subjected to severe drought (Grassi and Magnani, 2005; Zhou et al., 2013). Thus, non-stomatal limitations must be considered for understanding the photosynthetic response of vegetation to seasonal drought in this region.

Nitrogen addition led to significant increases in the NEP of the evergreen coniferous forest, which was in line with the results of previous studies that found that after management subtropical forest is nitrogen limited (Wei et al., 2012; Wu et al., 2017). The enhanced NEP by fertilization in subtropical forest ecosystems is mainly caused by plant growth in N-rich ecosystems, and reduced soil decomposition in N-limited ecosystems (Chen et al., 2015). Our result showed that N addition significantly stimulated plant growth, which was largely explained by increase of leaf area with a slight decrease in leaf photosynthesis. Similar results have been reported in pine forests (Brix and Ebell, 1969; Lai et al., 2002; Teskey et al., 1994). For example, Lai et al. (2002) found that despite the two-fold increase in LAI with fertilization, net primary productivity of a loblolly pine forest was enhanced by only 25%. The increased LAI by N addition could affect light transmission within canopy and reduced the leaf photosynthesis at deeper canopy layer, which in turn limited the positive effects of N addition on the canopy carbon uptake.

As an effective tool to analyze the effects of nitrogen deposition and drought on C fluxes, CLM4.5 still faces challenges in comprehensively

understanding of the coupling processes among terrestrial C, N, and water cycles. For instance, mesophyll conductance (g_m) is treated as infinite in this model, while an increasing number of studies have recognized the importance of mesophyll conductance in regulating forest ecosystem productivity during drought periods (Campany et al., 2016; Keenan et al., 2010). The oversimplification of the influence of water stress on leaf photosynthesis and respiration processes (e.g. g_s , V_{cmax} , and R_d) in CLM4.5 has been shown to lead to overestimates of the negative effects of drought on respiration (Powell et al., 2013). Since CLM4.5 adopts a simplified scheme to represent plant N uptake and effects of N limitation on plant growth and soil decomposition (i.e. supply-demand relationships), several aspects of the effects of drought on the ecosystem N cycle cannot be simulated in this model. For example, it cannot simulate reducing N transport, as well as the redistribution in the soil, and the reduction of soil decomposition due to N fertilization in nutrient rich forest ecosystems, which is usually found in subtropical forest ecosystems. Nevertheless, our results provided insights beyond the specific settings of CLM4.5 and demonstrated that manipulative experiments examining combined drought and N effects are necessary for predicting the impacts of global change drivers on ecosystem functioning in this region.

5. Conclusions

This study used the CLM4.5 with adjusted key parameters to investigate the interactive effects of seasonal drought and nitrogen deposition on carbon fluxes of a subtropical evergreen coniferous forest ecosystem. We found that seasonal drought severity influenced the effect of N addition on carbon fluxes of subtropical forest ecosystems, which significantly stimulated GPP, Re, and NEP in well water supply, mild drought, and moderate drought conditions but had no impacts on them in the severe drought condition. Our results suggested that although increasing N deposition can stimulate carbon sink of East Asia monsoon subtropical forests, this stimulation depends on the drought severity, which may determine the interactive effects are additive or non-additive and the relative importance of water and N limitation. This variation in interactive effects of nitrogen and water on carbon exchanges requires additional evidence from systematic manipulative experiments. Nevertheless, our results imply the necessity of considering the interactive effects of seasonal drought and nitrogen deposition and accurate prediction of seasonal drought severity and region in forecasting the carbon sequestration of subtropical forest ecosystems in East Asian monsoon region and elsewhere.

Disclosure of potential conflict of interest

The authors declare that they have no conflict of interest.

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