

Quantifying the effects of elevated CO₂ on water budgets by combining FACE data with an ecohydrological model

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ABSTRACT

Response of leaf area index (LAI) is the key determinant for predicting impacts of the elevated CO₂ (eCO₂) on water budgets. Importance of the changes in functional attributes of vegetation associated with eCO₂ for predicting responses of LAI has rarely been addressed. In this study, the Water Vegetation Energy and Solute (WAVES) model was applied to simulate ecohydrological effects of the eCO₂ at two free-air CO₂ enrichment (FACE) experimental sites with contrasting vegetation. One was carried out by the Oak Ridge National Laboratory on the forest (ORNL FACE). The other one was conducted by the University of Minnesota on the grass (BioCON FACE). Results demonstrated that changes in functional attributes of vegetation (including reduction in specific leaf area, changes in carbon assimilation and allocation characteristics) and availability of nutrients are important for reproducing the responses of LAI, transpiration and soil moisture at both sites. Predicted LAI increased slightly at both sites because of fertilization effects of the eCO₂. Simulated transpiration decreased 10.5% at ORNL site and 13.8% at BioCON site because of reduction in the stomatal conductance. Predicted evaporation from interception and soil surface increased slightly (<1.0 mm year⁻¹) at both sites because of increased LAI and litter production, and increased soil moisture resulted from reduced transpiration. All components of run-off were predicted to increase because of significant decrease in transpiration. Simulated mean annual evapotranspiration decreased about 8.7% and 10.8%, and mean annual run-off increased about 11.1% (59.3 mm year⁻¹) and 9.5% (37.6 mm year⁻¹) at the ORNL and BioCON FACE sites, respectively. Copyright © 2014 John Wiley & Sons, Ltd.

KEY WORDS elevated atmospheric CO₂; water and carbon coupling; FACE experiments; hydrological impacts

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INTRODUCTION

The steady rise in atmospheric CO₂ concentration may alter terrestrial water budgets considerably because elevated CO₂ (eCO₂) has significant influences on the functioning of plant stomata (Medlyn *et al.*, 2001; Ainsworth and Rogers, 2007), which is the pathway of nearly 50% of the water transferred from land surface to the atmosphere (Dirmeyer *et al.*, 2006). At the leaf scale, eCO₂ can increase water use efficiency by suppressing stomatal transpiration and stimulating photosynthesis (Eamus, 1991; Wand *et al.*, 1999; Yu *et al.*, 2004). Experimental evidences indicated that stomatal conductance (g_s) reduced persistently by about 20% under eCO₂ condition (~550 ppm) (Medlyn *et al.*, 2001; Ainsworth and Long, 2005). If all other factors remain constant, eCO₂ will lower terrestrial evapotranspiration (ET) and result in increase in water availability. In fact, several studies have demonstrated that eCO₂ increased

run-off only on the basis of the reduction of g_s at leaf level to eCO₂ alone (e.g. Aston (1984), Gedney *et al.* (2006) and Cao *et al.* (2010)). However, the leaf-scale water-saving effects of eCO₂ by lowering g_s can be offset by the concurrent increase in leaf area index (LAI) at stand level (Betts *et al.*, 1997; Piao *et al.*, 2007), change in vegetation distribution at regional scale (Morgan *et al.*, 2007; Macinnis-Ng *et al.*, 2011) and other environmental factors including rising temperature (Dieleman *et al.*, 2012). These feedbacks are poorly understood and difficult to investigate in field experiments (Luo *et al.*, 1999; Körner, 2011; Leuzinger *et al.*, 2011; Luo *et al.*, 2011). Thus, whether eCO₂ will increase run-off and by how much are uncertain and subject of current debate.

Generally, much of our knowledge of impacts of eCO₂ on water budget in the future comes from numerical modelling. At the global scale, sophisticated land surface models were used with general circulation models to study the eCO₂ effects on water availability (e.g. Sellers *et al.* (1996), Betts *et al.* (1997), Gedney *et al.* (2006), Piao *et al.* (2007), Betts *et al.* (2007), Gerten *et al.* (2008), Cao *et al.* (2010)). However, predicted changes in water budgets were highly

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variable and inconclusive because of different stomatal responses (De Kauwe *et al.*, 2013), different vegetation structural feedbacks (LAI and/or distribution) (Gerten *et al.*, 2008; Bounoua *et al.*, 2010) and poor hydrological performance (Wood *et al.*, 2011; Wang and Dickinson, 2012; Zhou *et al.*, 2012). At the catchment and plot scales, several studies predicted that water yield increased from less than 3% to about 90% (Aston, 1984; Hatton *et al.*, 1992; Eckhardt and Ulbrich, 2003; Kruijt *et al.*, 2008; Leuzinger and Körner, 2010; Warren *et al.*, 2011a). However, carbon–water relationships were usually decoupled or loosely coupled in these studies (e.g. Eckhardt and Ulbrich (2003) and Leuzinger and Körner (2010)), and parameterization of hydrological and physiological processes were imbalanced (e.g. Kruijt *et al.* (2008)) in the models employed in these studies. As a result, physiological effects of the eCO₂ cannot be simulated dynamically, and interactions of water, carbon and energy between plant and soil as well as between plant and atmosphere cannot be captured systematically (Gerten *et al.*, 2004; Körner, 2006; De Kauwe *et al.*, 2013). Basically, previous modelling studies on the impacts of eCO₂ on water yield are poorly validated or constrained by field observations from free-air CO₂ enrichment (FACE) experiments, in which CO₂ was manipulated under natural condition. At present, many FACE experiments on different ecosystems have been conducted, and observations about the ecohydrological effects of eCO₂ are available for validating models.

The magnitude of change in LAI is a key determinant of whether eCO₂ will result in significant changes in water budgets because foliage is the primary interface of water and carbon and increase in LAI would enhance transpiration rate and canopy interception (Woodward, 1990; Piao *et al.*, 2007; Bounoua *et al.*, 2010). Observations from the FACE experiments on closed-canopy forest stand showed that LAI changed from –8% to 43% (Norby and Zak, 2011). Piao *et al.* (2007) indicated that allowing LAI to change with rising CO₂ will offset about 50% of the water saved by the effects of eCO₂ on g_s globally. The physiological processes associated with eCO₂ can stimulate plant growth and increase canopy LAI via two mechanisms. One is via direct CO₂ fertilization effects (Körner *et al.*, 2007); the other is indirectly via increased soil water availability resulting from reduced g_s and soil water uptake (Morgan *et al.*, 2004). It is reported that the direct fertilization effects of eCO₂ on LAI were likely to vary remarkably among functional groups (Nowak *et al.*, 2004; Körner, 2006) and the indirect effects via soil water were likely to be significant in water-limited regions (Wullschleger *et al.*, 2002a; Morgan *et al.*, 2004; Körner *et al.*, 2007). However, response of LAI to both direct and indirect effects of the eCO₂ are not well understood (Pritchard *et al.*, 1999; Ainsworth and Rogers, 2007), and validation of the simulated responses of LAI to eCO₂ is not a major focus of most studies (Cowling and Field, 2003) in spite of the fact that nearly all

models have parameterized LAI as the control of plant productivity and canopy transpiration. In addition, functional changes in intrinsic physiological traits of vegetation, such as specific leaf area (SLA) (Ainsworth and Long, 2005), photosynthetic capacity (Medlyn *et al.*, 1999; Ainsworth and Long, 2005), foliar nitrogen (Reich *et al.*, 2006) and adaption in the carbon allocation to meet larger resource demand (Rogers *et al.*, 1994; Iversen, 2010), may further modulate response of LAI greatly under the eCO₂ condition. Meanwhile, physiological effects of the eCO₂ as well as development of LAI may be further regulated by higher-order interactions (Leuzinger *et al.*, 2011), for instance, availability of nitrogen (Luo *et al.*, 2004; Reich *et al.*, 2006). However, influences of the changes in functional attributes of vegetation associated with the eCO₂ on responses of LAI have rarely been addressed.

In this study, a coupled water and carbon ecohydrological model (WAVES) was applied to reproduce both physiological and hydrological responses observed in the FACE experiments. In WAVES, water and carbon processes are coupled dynamically with appropriate feedbacks included at a daily time scale. The model strikes a good balance between complexity and accuracy of prediction in water, energy and carbon processes. Observations from two FACE experiments with contrasting vegetation were collected. One is a close-canopy forest FACE experiment carried out by the Oak Ridge National Laboratory (ORNL FACE), the other one is grass FACE experiment carried out by the University of Minnesota (BioCON FACE). After the WAVES model was calibrated using the control plots under ambient CO₂ concentration (aCO₂), two different modelling experiments were conducted to examine whether changes in functional attributes of vegetation are important for modelling responses of LAI and water budgets under the eCO₂ conditions. Three functional changes under eCO₂ condition, which are all changed in the field experiments and central to determine response of LAI and hydrological aspect of plant growth in WAVES model, were considered here, and they were maximum carbon assimilation rate, SLA and partitioning factor of daily assimilated carbon between above-ground and below-ground. In addition, the parameter reflecting availability of nutrients in the WAVES model was adjusted to mimic progressive nitrogen limitation on the growth under eCO₂ condition at both sites. This study aims to (1) examine whether an ecohydrological model with coupled water–carbon representation and a consistent level of complexity in both hydrological and physiological processes can reproduce observed effects of the eCO₂ on LAI and water budgets (including transpiration and soil water) in the FACE experiments, (2) examine whether changes of functional attributes of vegetation induced by eCO₂ are important for modelling responses of LAI and water use under the eCO₂ conditions and (3) investigate whether eCO₂ can exert noticeable changes in water budgets at two FACE

experimental sites and how the impacts vary among different components of water budgets.

METHOD

The WAVES model

In WAVES, net radiation is partitioned between canopy and soil available energy using the Beer's law. Daily transpiration is calculated by a 'big-leaf' application of the Penman–Monteith formula. Leaf g_s is calculated by the equation developed by Ball (1987) and Leuning (1995), and this is then scaled up to canopy scale using the method proposed by Sellers *et al.* (1992). The micrometeorological feedback between canopy and atmosphere is regulated by the omega coefficient proposed by Jarvis and McNaughton (1986). The daily carbon assimilation rate is estimated by the maximum carbon assimilation rate and relative growth rate multiplicatively. The relative growth rate varies between 0 and 1 to represent the availability of different resources for growth using an integrated rate method (IRM) developed by Wu *et al.* (1994) on the basis of saturation rate kinetics. The WAVES model use in this study coded CO_2 as a variable within the canopy conductance (g_c) module as in Equation (1) and daily assimilation (A_i) module using IRM approach as in Equation (2).

$$g_c = g_0 \text{LAI} + \frac{g_1 A_i}{(C_{si} - \Gamma)(1 + D_{ci}/D_{co})} \frac{1 - \exp(-k \text{LAI})}{k} \quad (1)$$

where g_0 is the residual stomatal conductance, g_1 is an empirical coefficient, A_i is the daily carbon assimilation rate, C_{si} is the CO_2 mole fraction of the air at the canopy surface, Γ is the CO_2 compensation point, D_{ci} is the vapour pressure deficit at the canopy surface, D_{co} is an empirical coefficient, LAI is the canopy LAI and k is the attenuation coefficient for light. g_0 , C_{si} , D_{co} and Γ were constant and the same for both sites, while k was estimated from observed data, and g_1 was fixed as 0.8 for both sites.

$$A_i = A_{\max} \frac{1 + W_2 + W_3 + W_4}{\frac{1}{m_1 x_1} + \frac{W_2}{x_2} + \frac{W_3}{x_3} + \frac{1}{m_4 x_4}} \quad (2)$$

where A_{\max} is the maximum carbon assimilation rate; W_2 , W_3 and W_4 are the weighting factor for water, nutrients and CO_2 relative to light, respectively; x_1 , x_2 , x_3 and x_4 are normalized availability of photosynthesis active radiation, water, nutrients and CO_2 , respectively, and m_1 is the temperature modifier and m_4 is the vapour pressure modifier. All the weighting factors and normalized availabilities were empirical parameters and calibrated within the ranges as recommended by Zhang and Dawes (1998). The availability of water that can be extracted by roots for transportation is estimated according to

the distributions of both roots density and soil water content as in Ritchie *et al.* (1986).

Three carbon pools (or compartments) of leaves, roots and stems are set for respiration and allocation as in Running and Coughlan (1988). Assimilation is allocated according to the priorities as in Running and Gower (1991): (1) maintenance respiration, (2) growth respiration, (3) leaf and root growth and (4) stem growth. The ratio of leaf/root allocation reflects growth stress, and smaller ratio indicates that more carbon is allocated to roots to acquire nutrients or water for growth. Carbon allocated to leaves is assumed to increase leaf area by an amount determined by the SLA, and the carbon allocated to roots is distributed amongst soil nodes weighted by the availability of soil water and nutrients. So, the physiological responses of canopy conductance and assimilation rate in WAVES are fully coupled with climatic regulation on stomata and both water and nutrients availability to roots, which allows LAI to vary with different environmental conditions.

The infiltration of net rainfall and soil water movement along the soil profile are simulated using a fully finite difference numerical solution of the Richards equation (Ross, 1990; Dawes and Short, 1993). For each soil type, an analytical soil model proposed by Broadbridge and White (1988) is employed to describe the relationships amongst water potential, volumetric water content and hydraulic conductivity. Overland flow (i.e. surface flow) can be generated from the infiltration excess rainfall and rainfall over saturated area. Lateral flow (i.e. subsurface flow) can be generated via the saturated water table and is simulated by Darcy's law if non-zero slope is specified. Water can leak out of soil column if it is set in the model. A more detailed modelling strategy and descriptions of WAVES are provided in the works of Zhang *et al.* (1996) and Zhang and Dawes (1998).

The capability of WAVE model for simulating coupled water and carbon processes has been demonstrated against a number of experimental datasets including Zhang *et al.* (1996), Zhang *et al.* (1999a, 1999b, 1999c) and (Wang *et al.*, 2001). Comparing with other models for investigating the physiological and hydrological impacts of eCO_2 , such as models use in the studies of Cramer *et al.* (2001), Eckhardt and Ulbrich (2003), Luo *et al.* (2008), Kruijt *et al.* (2008) and De Kauwe *et al.* (2013), the advantages of the WAVES model used in this study are: (1) dynamically linking hydrological processes with vegetation growth so that it can accurately simulate development of LAI, canopy transpiration, rooting dynamics and soil water stress on both transpiration and growth; (2) accurate representation of soil moisture dynamics in saturated and unsaturated zones using the Richards equation; (3) consistent level of complexity in representing hydrological and physiological processes with appropriate feedbacks incorporated; (4) integrated

representation of multiple limiting factors on vegetation growth, retaining complex mechanism of chemical and mechanical controls.

Experiments and data

The ORNL FACE experiment and data. The ORNL FACE experiment research site is a planted sweetgum (*Liquidambar styraciflua*) monoculture located in eastern Tennessee. Mean annual precipitation was about 1371 mm, and the mean annual temperature was 13.9 °C. Trees were about 12–21 years old with an average height of 12 m and average LAI of 5.5 m² m⁻². Six 25-m diameter plots were laid out in 1997, and construction of the FACE facility began thereafter. The FACE experiments span from 1998 to 2008. The experimental design comprised two plots with eCO₂ treatment and three plots with aCO₂ treatment. Atmospheric CO₂ in the elevated plots was maintained at a target daytime concentration of 525 ~ 555 ppm during the growing season, ca 40% higher than CO₂ levels in the ambient plots. More detailed information about experimental design can be found at <http://face.ornl.gov/>.

The observational daily meteorological data (including temperature, precipitation, humidity and radiation), LAI and soil moisture content (SWC) to a depth of 20 cm were accessed from the FACE Data Management System maintained by the Carbon Dioxide Information and Analysis Centre (<http://public.ornl.gov/face/index.shtml>). The canopy transpiration (E_c) was derived from measurement of sap flux and averaged over the two eCO₂ plots (ring 1 and ring 2) and two aCO₂ plots (ring 4 and ring 5) in the growing season of 1999, 2004 and 2008. The E_c data used in this study are the same as that of Warren *et al.* (2011a). For consistency, observations of SWC and LAI were also averaged over ring 1 and ring 2 to present the eCO₂ conditions and over ring 4 and ring 5 to represent aCO₂ conditions during the modelling.

The BioCON experiment and data. The BioCON FACE is an ecological experiment that started in 1997 at the University of Minnesota's Cedar Creek Ecosystem Science Reserve. Mean annual precipitation was 660 mm with mean monthly temperatures of -11 °C in January and 22 °C in July. The BioCON consists of 371 plots (2 m × 2 m), established on secondary successional grassland on a sandy outwash soil. The experimental treatments were arranged in complete factorial combination of CO₂ (ambient or 560 ppm), species number (1, 4, 9 and 16) and N level (control and fertilized). The grass species were planted in 1998, including C3, C4, forbs and legumes across four functional types. More detailed information about experimental design can be referred to Reich *et al.* (2001) or can be found at <http://www.biocon.umn.edu/>. In this study, plots having a monoculture *Agropyron repens* (C3 grass) were chosen for modelling study. Both aCO₂ and eCO₂ treatments have two

replicas. The aCO₂ plots are plot number 111 in ring 2 and plot number 235 in ring 4, and the eCO₂ plots are plot 24 in ring 1 and plot 145 in ring 3. The short height of *A. repens* is less than 1.0 m, and maximum root depth is about 1.0 m (Craine *et al.*, 2003). The modelling period was from January of 1998 to October of 2005 (about 8 years).

Daily observed meteorological forcing data, including precipitation and maximum and minimum air temperature, and radiation were obtained from the Cedar Creek weather station. The LAI data were estimated from the observed photosynthetically active radiation data approximately at monthly interval during the growing season of each year. The LAI was averaged over the replicated plots with the same CO₂ treatments. About 21 records of LAI from 2002 to 2005 were used to calibrate model. Soil moisture data observed to a depth of 20 cm were collected, but only about 24 records measured in the first 2 years were available. Soil moisture data were also averaged over the two replicated plots with the same CO₂ treatment.

Parameter estimation

There are 26 vegetation parameters in the WAVES model, which control growth, carbon allocation and physiological and phenological responses of vegetation to different environmental conditions. The key physiological parameters are listed in Table I. Most of these parameters can be measured directly or taken from plant physiological literature, with only a few remaining for fitting or adapting to local conditions. Some of the vegetation parameters in both experimental sites were adopted from publications or estimated from available data including maximum carbon assimilation rate (A_{max}), light extinction coefficient, SLA and above-ground partition factor (C_f). A_{max} and C_f are two hypothetical physiological parameters in the WAVES model. A_{max} represents maximum carbon assimilation rate under optimum conditions. C_f represents the ratio of newly assimilated carbon allocated to above-ground under no water stress condition. In this study, light-saturated carbon assimilation rates at current CO₂ conditions observed in gas exchange experiments (Wullschlegel *et al.*, 2002b; Ellsworth *et al.*, 2004) were adopted as A_{max} at both sites. C_f was estimated from the ratio of observed increase in above-ground biomass to increase in total biomass during the modelling periods. Some of the hypothetical parameters, such as weight of water availability, optimum temperature, degree-daylight hours for growth and so on, were adopted from source references or calibrated against observed LAI, canopy transpiration and soil water content observations.

The soil properties were identified from the National Cooperative Soil Survey (NCSS) of USA (<https://soilseries.sc.egov.usda.gov>) on the basis of the site-specific classification, which was found from the published literature on both sites. Soils were classed as Aquic Hapludult soil at the ORNL

Table I. Names, units, source references and parameter values of the key physiological parameters of WAVES model.

No.	Parameter name (unit)	Source references	ORNL FACE		BioCON FACE	
			aCO ₂	Expt2 of eCO ₂	aCO ₂	Expt2 of eCO ₂
1	1 minus albedo of the canopy (-)	Brutsaert (1982)	0.878	←	0.848	←
2	1 minus albedo of the soil (-)	Brutsaert (1982)	0.862	←	0.818	←
3	Rainfall interception coefficient (m day LAI ⁻¹)	Vertessy <i>et al.</i> (1996)	0.00021 (d)	←	0.0004	←
4	Light extinction coefficient (-)	Monteith and Unsworth (2008)	0.54 (a)	←	0.636 (A)	←
5	Maximum carbon assimilation rate (kgC m ² day ⁻¹)	Collatz <i>et al.</i> (1991)	0.0135 (c)	0.0126 (c)	0.0070 (B)	0.0062 (B)
6	Slope parameter for the conductance model (-)	Leuning (1995)	0.8	←	0.8	←
7	Max plant available soil water potential (m)	Hillel (1980)	-200	←	-100	←
8	IRM weight for water (-)	Wu <i>et al.</i> (1994)	1.42	←	1.62	←
9	IRM weight for nutrients (-)	Wu <i>et al.</i> (1994)	0.62	←	0.2	←
10	Temperature when growth is 1/2 optimum (°C)	Farquhar <i>et al.</i> (1980)	7.4	←	9.8	←
11	Temperature when growth is optimum (°C)	Farquhar <i>et al.</i> (1980)	21.8	←	17.6	←
12	Year/day of germination (-)		118 (b)	←	-1	←
13	Degree-daylight hours for growth (°C h ⁻¹)	Charles-Edwards (1982)	41234	←	-1	←
14	Saturation light intensity (μmoles m ² day ⁻¹)	Wu <i>et al.</i> (1994)	1025	←	1251	←
15	Maximum rooting depth (m)	Hatton <i>et al.</i> (1992)	3.5	←	1.0 (C)	←
16	Specific leaf area (LAI kgC ⁻¹)	Charles-Edwards (1982)	25.0 (a)	23.6 (a)	34.9 (A)	33.3 (A)
17	Leaf respiration coefficient (kgC kgC ⁻¹)	Running and Coughlan (1988)	0.00065	←	0.0011	←
18	Stem respiration coefficient (kgC kgC ⁻¹)	Running and Coughlan (1988)	0.00014	←	-1	←
19	Root respiration coefficient (kgC kgC ⁻¹)	Running and Coughlan (1988)	0.0023	←	0.0012	←
20	Leaf mortality rate (fraction of C/day)	Running and Coughlan (1988)	0.0016	←	0.0068	←
21	Above-ground partitioning factor (-)	Running and Gower (1991)	0.788 (a,b)	0.761 (a,b)	0.23 (A)	0.21 (A)
22	Aerodynamic resistance (s day ⁻¹)	Brutsaert (1982)	8.2	←	25.9	←
23	Nutrient availability (-)	Hatton <i>et al.</i> (1992)	1.0	0.9	1.0	0.9

eCO₂, elevated CO₂; aCO₂, ambient CO₂; IRM, integrated rate method; LAI, leaf area index. Parameter values in bold were adopted from publications or estimated from published data for two experimental sites. Sources of ORNL FACE site were (a) Warren *et al.* (2011a), (b) published data from the ORNL FACE site: <http://public.ornl.gov/face/ORNL/omldata.shtml>, (c) Sholtis *et al.* (2004) and (d) Wullschlegel *et al.* (2002b). Sources of BioCON FACE site were (A) estimated from accessed observed data, (B) Ellsworth *et al.* (2004) and (C) Craime *et al.* (2003). Parameter values in *italic* were determined from source references or calibrated within their physical meaning (Dawes *et al.* (1998) and Zhang and Dawes (1998)) against observed LAI, transpiration and/or soil water content data. Parameter values in normal font style were adopted from source references without calibration. The left arrows indicate that parameter value of experiment 2 for eCO₂ condition is kept the same as that under aCO₂ condition. ‘-1’ means that parameter was not specified in the model.

FACE site (van Miegroet *et al.*, 1994; Wullschlegler *et al.*, 2002b; Warren *et al.*, 2011a) and Lamellic Udipsammets (i.e. Argic Udipsammets) soil at the BioCON site (Lee *et al.*, 2001; Dijkstra *et al.*, 2006; Dijkstra *et al.*, 2007). Soil properties were inferred from the Wolfvever soil series and Zimmerman series for ORNL and BioCON FACE sites, respectively. Soil types derived from NCSS were used to establish soil layers and initial soil parameters for the soil model. Depth of modelled soil profile was set to 3.5 m according to the depth of typical soil column from the surveyed data at the ORNL FACE site. It was set as 1.25 m at the BioCON site considering the maximum depth of the root (Craine *et al.*, 2003), although depth of the Zimmerman soil series is much deeper than 1.25 m. In addition, more than 20 unequally spaced nodes were set along the soil profile at both sites, on which soil water content and root growth were estimated. The soil hydraulic parameters of different layers were also calibrated under the aCO₂ condition.

Both vegetation and soil parameters were optimized against observed data under the aCO₂ condition using the shuffled complex evolution (SCE-UA) method (Duan *et al.*, 1992). All parameters were calibrated within their feasible ranges, which were given by Dawes *et al.* (1998) on the basis of extensive literature survey. The objective functions of LAI, canopy transpiration and soil water content were optimized simultaneously and given equal weights to form the total objective function of SCE-UA method. Both bias (*B*) and Nash–Sutcliffe coefficient (*Ens*) (Nash and Sutcliffe, 1970) were considered to quantify the dynamic and systematic differences between simulated and observed values as in Viney *et al.* (2009) as follows:

$$Ens = 1 - \frac{\sum_{i=1}^n (y_{sim,i} - y_{obs,i})^2}{\sum_{i=1}^n (y_{obs,i} - \bar{y}_{obs})^2} \quad (3-1)$$

$$B = \frac{\sum_{i=1}^n y_{sim,i} - \sum_{i=1}^n y_{obs,i}}{\sum_{i=1}^n y_{obs,i}} \quad (3-2)$$

$$f_{obj} = Ens - 5|\ln(1 + B)|^{2.5} \quad (3-3)$$

where *n* is the number of days of simulated or observed period, *y_{obs}* is the observed data, *y_{sim}* is simulated data, subscript *i* is the index of the data and *f_{obj}* is the objective function for assessing the goodness of a given parameter set.

At the ORNL FACE site, available daily LAI, canopy transpiration and soil water content data were used to calibrate the vegetation and soil parameters. While at the BioCON FACE site, infrequent daily LAI and soil water content data were used. The purpose of calibration was to obtain a set of parameter values that represent site-specific plant and soil conditions.

Modelling experiments under eCO₂ condition

Two modelling experiments were conducted to estimate the ecohydrological responses to eCO₂ at both sites. In the first experiment (Expt1), all vegetation and soil parameters were kept the same as those under the aCO₂ condition, and only the CO₂ concentration was elevated to 550 ppm. Expt1 was designed to examine whether a water–carbon coupled model can capture the physiological and hydrological effects of eCO₂ assuming that functioning of vegetation were not changed under the eCO₂ conditions. In the second experiment (Expt2), changes in vegetation functional attributes associated with the eCO₂ were considered with eCO₂ concentration. Three vegetation parameters in the WAVES model, which are critical to water use efficiency and LAI simulation and also observed to change at both sites, are changed under the eCO₂ condition, while the rest of the vegetation and soil parameters were kept the same as those under the aCO₂ condition. These three functional parameters are maximum carbon assimilation rate (*A_{max}*), SLA and the above-ground partitioning factor of newly assimilated carbon (*C_f*). *A_{max}* and *C_f* are considered as surrogates to represent observed photosynthetic down-regulation and changes in carbon allocation under eCO₂ condition in the field. Values of these three parameters under eCO₂ conditions were all adopted from published literature or estimated from observed data. In Expt2, nutrient availability was also changed from 1.0 to 0.9 to represent progressive nitrogen limitation under the eCO₂ treatment. Expt2 was designed to examine whether functional changes in vegetation attributes are important for simulating the ecohydrological effects of eCO₂ on LAI and water budgets.

RESULTS

Modelling results under the aCO₂ condition

Optimized vegetation parameters under the aCO₂ condition at both sites are listed in Table I. On the basis of the optimized vegetation and soil parameters, simulated LAI, canopy transpiration and soil water content at the ORNL FACE site are compared with observations in Figure 1, and results of the BioCON FACE site are shown in Figure 2.

At the ORNL FACE site, the biases were about −0.2%, 0.1% and −2.1%, and the Nash–Sutcliffe efficiencies were 0.72, 0.72 and 0.69 for LAI, canopy transpiration and SWC, respectively. At the BioCON FACE site, the biases were about −2.8% and 0.7% for LAI and SWC, and the Nash–Sutcliffe efficiencies were 0.74 and 0.44, respectively. The WAVES model captured the daily and seasonal variations of LAI, canopy transpiration and soil water content well at both sites. At the ORNL FACE site, the WAVES model captured the inter-annual variations in LAI, except for 2008, where LAI was overestimated by the WAVES model [Figure 1(a)]. The slopes between

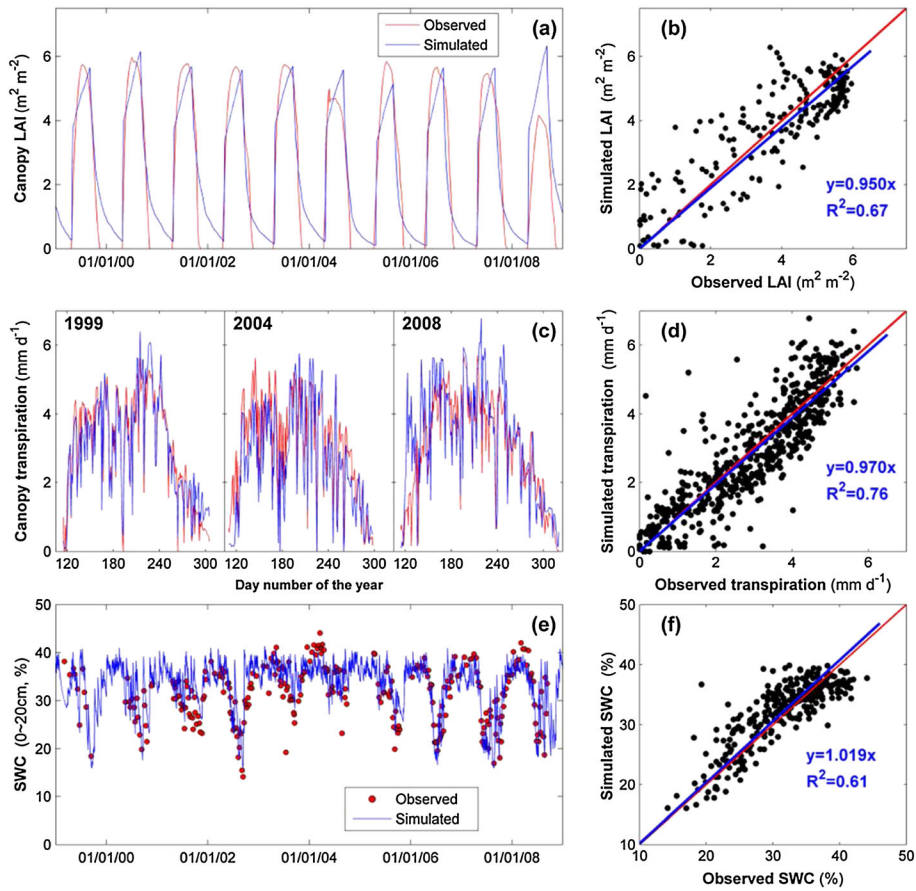


Figure 1. Comparison between simulated and observed leaf area index (LAI), (a) and (b); canopy transpiration in 1999, 2004 and 2008, (c) and (d); and soil water content of the ORNL FACE site under ambient CO₂ conditions, (e) and (f). In subplot (b), the LAI of 5th, 15th and 25th of the months during growing season were compared.

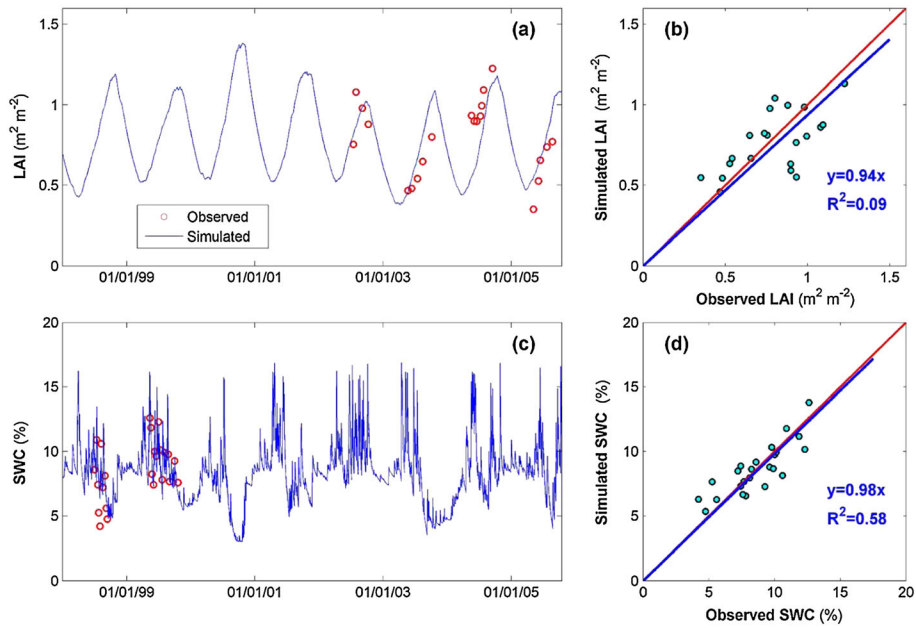


Figure 2. Comparison between simulated and observed leaf area index, (a) and (b); and soil water content of the BioCON FACE site under ambient CO₂ conditions, (c) and (d).

simulated and observed daily transpiration [Figure 1(d)] and soil water content [Figure 1(f)] are very close to 1.0 at the ORNL FACE site. The coefficients of determination (R^2) are 0.67, 0.76 and 0.61 for LAI, transpiration and SWC, respectively. At the BioCON FACE site, the WAVES model slightly underestimated LAI with a slope of 0.94 [Figure 2(b)], while the slope between simulated and observed soil water content is close to 1.0 [Figure 2(d)].

Simulated ecohydrological responses under the eCO₂ condition

The simulated impacts of eCO₂ on LAI, transpiration and soil water content in Expt1 and Expt2 were compared with observed changes as shown in Figure 3. The WAVES model significantly overestimated responses of LAI and underestimated response of transpiration and soil water content in Expt1 (i.e. without considering changes of functional parameters and reduction in availability of nutrients) at both sites. However, simulated responses are much closer to observed responses when the maximum carbon assimilation rate, SLA, above-ground partitioning factor and availability of nutrient were estimated on the basis of the measurements (Figure 3). This implies that functional changes of vegetation are important for the WAVES model to capture the responses of LAI and shift in water budget caused by eCO₂.

At the ORNL FACE site, observed responses of LAI, canopy transpiration and soil moisture (0–20 cm) to eCO₂ are 1.1%, –14.2% and 0.9%, respectively. The annual variation of observed LAI response is quite large with one standard deviation of about 6.8% across year. When only CO₂ was elevated to 550 ppm and all parameters were fixed as under the aCO₂ conditions (i.e. Expt1), WAVES produced a much larger increase (14.8%) in LAI, a smaller increase (3.6%) in transpiration and a smaller decrease (0.6%) in soil moisture. Under Expt2 condition, responses of LAI, transpiration and soil water content were 2.6%, –10.5% and 0.9% at the ORNL FACE site [Figure 3(a)], respectively. Predicted responses of LAI and transpiration to eCO₂ are significantly improved at the ORNL FACE site when both CO₂ and few functional parameters were changed according to observations in the fields under the eCO₂ treatment. At the BioCON site, the observed responses of LAI and soil water content (0–20 cm) to eCO₂ are 1.32% and 10.96% [Figure 3(b)]. When CO₂ was increased from 370 to 550 ppm (i.e. Expt1), the WAVES model predicted a significant increase in LAI by about 36.1% and decrease in soil moisture by about 9.9%. Similarly, when both CO₂ and a few parameters were changed, predicted responses under Expt2 were much closer to the observed responses. The WAVES model estimated a 0.8% increase in LAI and 5.1% increase in soil moisture at the BioCON site under Expt2 condition [Figure 3(b)]. According to the observed changes, the effects of eCO₂ on LAI were small (~1%) at both sites (Figure 3), but responses of soil water content at (0–20 cm) were quite different. The soil water content was increased by about 1% at the ORNL FACE site but increased about 11% at the BioCON FACE site.

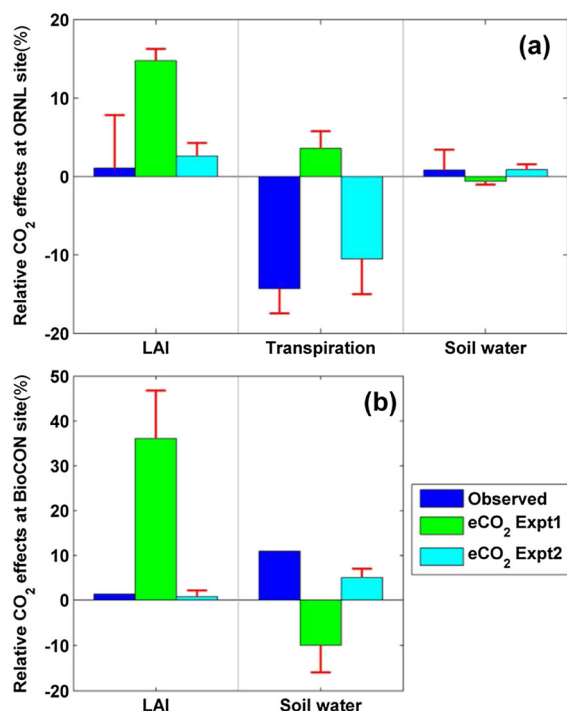


Figure 3. Comparison of simulated and observed responses of leaf area index (LAI), soil water content or canopy transpiration to elevated CO₂ at ORNL FACE site (a) and BioCON FACE site (b). The error bar represents one standard deviation across year.

Changes in water budgets at the two FACE sites

Simulated mean annual water balance components, i.e. ET and run-off (Q), under aCO₂ and eCO₂ (considering both eCO₂ and vegetation functional changes, i.e. Expt2) conditions at both sites are compared in Figure 4. Note that the results of 2005 were not included for estimating changes in water budgets in the BioCON FACE site because only part of 2005 was simulated. Changes in different components of ET and Q were also investigated, including evaporation from interception (E_i, including both canopy and litter layer), canopy transpiration (E_c), evaporation from soil (E_s), surface flow (Q_s, i.e. overland flow), subsurface flow (Q_{ss}, i.e. saturated lateral flow) and deep drainage (Q_d, i.e. percolated soil water from the bottom of soil column to deeper layer).

Total ET decreased and run-off increased at both sites, and these results suggest that eCO₂ suppressed ET and increased run-off. For different components of ET, only canopy transpiration significantly decreased, but evaporation from interception and soil surface increased slightly

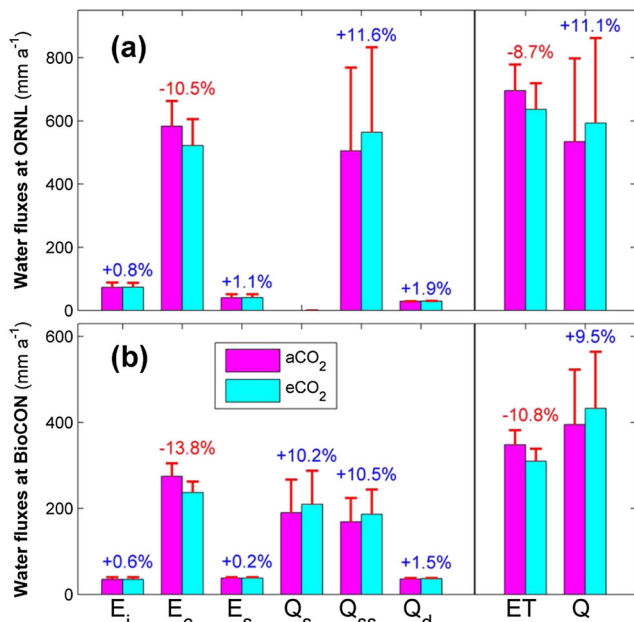


Figure 4. Water fluxes under both ambient CO₂ (aCO₂) and elevated CO₂ (eCO₂) conditions at ORNL FACE site (a) and BioCON FACE site (b). Change in water fluxes induced by eCO₂ was shown as percentage. The error bar represents one standard deviation across year.

(<1.0 mm year⁻¹). All three components of the simulated runoff increased at both sites (Figure 4). Under the eCO₂ condition, ET from the forest at the ORNL FACE site decreased about 8.7% (60.3 mm year⁻¹), and runoff increased about 11.1% (59.3 mm year⁻¹). For different components of ET, E_c decreased 10.5% (61.3 mm year⁻¹), while E_i and E_s increased about 0.8% (0.6 mm year⁻¹) and 1.1% (0.4 mm year⁻¹) at the ORNL FACE site, respectively. For different components of Q, no overland flow was generated under either the aCO₂ or eCO₂ conditions at the ORNL FACE site, while both Q_{ss} and Q_d were increased. The Q_{ss} increased 11.6% (58.7 mm year⁻¹), while Q_d increased about 1.9% (0.6 mm year⁻¹). At the BioCON site [Figure 4(b)], total ET decreased about 10.8% (37.7 mm year⁻¹) and runoff increased about 9.5% (37.6 mm year⁻¹). Evaporation from interception increased about 0.6% (0.2 mm year⁻¹), and evaporation from soil surface increased 0.2% (0.08 mm year⁻¹), while transpiration reduced about 13.8% (38.0 mm year⁻¹) under the eCO₂ condition. All three components of the simulated runoff increased at the BioCON FACE site, and the increases in Q_s, Q_{ss} and Q_d were about 10.2% (19.3 mm year⁻¹), 10.5% (17.7 mm year⁻¹) and 1.5% (0.5 mm year⁻¹), respectively.

DISCUSSION

Performance of the WAVES model

Leaf phenology remains one of the most challenging processes to parameterize (Arora and Boer, 2005), and this

is no exception for the WAVES model. The inter-annual variability of leaf onset and offset were not captured accurately at ORNL FACE site because germination date, carbon gain of leaf onset and total degree-daylight hours for growth were fixed in the WAVE model. A large bias in the peak LAI of 2005 and 2008 was predicted, possibly due to the WAVES model failed to consider the windstorm in 2004 and serious drought in 2007, which were believed to have introduced significant legacy into the following year (Warren *et al.*, 2011b; Warren *et al.*, 2011a). In spite of discrepancies in the leaf phenology, the WAVES model captured seasonal and daily variations of LAI at ORNL FACE site satisfactorily with very small bias (-0.2%) and high Nash-Sutcliffe coefficient (0.72). The predicted LAI for the BioCON site agrees reasonably well with the measurements.

The canopy transpiration and soil water content were accurately simulated at both sites under aCO₂ conditions, which demonstrated the robustness of the WAVES model in simulating water fluxes through soil-plant-atmosphere continuum. For the predicted canopy transpiration at the ORNL FACE site, the WAVES model captured daily and seasonal variations well, and the bias in the simulated transpiration was principally introduced by error in the simulated LAI time series. Previously, the WAVES model was tested against field data of ET (Zhang *et al.*, 1996), LAI (Wang *et al.*, 2001), soil water and groundwater (Zhang and Dawes, 1998) and isotope concentrations (Zhang *et al.*, 1999c; Zhang *et al.*, 1999b; Wang *et al.*, 2001), and these studies have demonstrated the ability of WAVES to satisfactorily simulate ecohydrological processes. Recently, the WAVES model was applied in studies of the impact of climate change on groundwater recharge (e.g. Green *et al.* (2007), McCallum *et al.* (2010), Crosbie *et al.* (2011), and Post *et al.* (2012)). The WAVES model can accurately simulate both plant growth and water yield because of two advantages. One is the coupled water, energy and carbon processes representations in the WAVES model. This coupled modelling structure enabled WAVES model to capture the daily, seasonal and annual variations in plant growth and canopy transpiration. The other one is balanced complexity and accuracy in both hydrological and physiological processes. Coupled interactions between plant and atmosphere as well as between plant and soil are complex, and their responses to environmental changes (including rising CO₂) are not well understood (Luo *et al.*, 1999; Hetherington and Woodward, 2003; Bonan, 2008). They are likely to manifest nonlinearly across different spatio-temporal scales (Körner *et al.*, 2007; Leuzinger *et al.*, 2011). Thus, it is important for models to address the coupling processes of soil-plant-atmosphere continuum with an appropriate scale-dependent parameterization and balanced complexity (Blöschl and Sivapalan, 1995; Luo *et al.*, 2011; Beven and Cloke, 2012). The WAVES model strikes a good balance

among generality, realism and accuracy (Zhang *et al.*, 1996; Zhang and Dawes, 1998) and thus provides satisfactory predictions of the water, energy and carbon balances with readily available inputs.

Importance of the changes in functional attributes for predicting ecohydrological responses under the eCO₂ condition

This study considered changes in the functional attributes and emphasized the feedbacks of canopy LAI caused by eCO₂. Gas exchange observation showed that light-saturated photosynthetic rate at same CO₂ concentration of sweetgum forest at the ORNL FACE site decreased about 7% (Sholtis *et al.*, 2004) and about 10% for *A. repens* at the BioCON FACE site (Ellsworth *et al.*, 2004). Photosynthetic down-regulation was generally related to reduction in leaf nitrogen concentration under eCO₂ condition (Medlyn *et al.*, 1999; Ellsworth *et al.*, 2004). Although photosynthetic down-regulation effects may offset the positive response of photosynthesis to eCO₂, it rarely completely eliminates it. LAI at both sites was increased, indicating increase of net photosynthesis. This agrees with field studies that net primary production increased about 23% at ORNL FACE site (Norby *et al.*, 2005) and biomass increased 8–12% at BioCON FACE site (Reich *et al.*, 2006) caused by eCO₂. In the WAVES model, SLA determines conversion of leaf carbon allocation to leaf area, and it is a key determinant of how much carbon a plant can assimilate for a given time. Thus, response of the LAI is sensitive to change in the SLA. SLA decreased about 5% at both sites. Ainsworth and Long (2005) also reported that SLA decreased about 8.4% for trees and 7.5% for C3 grass across several FACE experiments. Previous studies indicated that decrease in SLA under eCO₂ condition was induced by accumulation of non-structural carbohydrates (Pritchard *et al.*, 1999) as a result of increased photosynthesis under eCO₂ conditions. Change in above-ground partitioning factor was also considered in this study because it is an important factor controlling carbon allocation for the development of LAI in the WAVES model. Estimation of decrease in the ratio of above-ground biomass to total biomass indicated that more new assimilated carbon was allocated to roots under eCO₂ condition at both sites. At the ORNL FACE site, Norby *et al.* (2004) and Iversen (2010) reported that root production was increased and more carbon was preferentially allocated to roots rather than stem. At the BioCON FACE site, Reich *et al.* (2001) showed that eCO₂ induced increase in the below-ground biomass was larger than increase in the above-ground biomass. Increased carbon allocated to roots was considered to develop a deeper rooting profile to acquire more resources (Rogers *et al.*, 1994; Iversen, 2010), because photosynthesis was significantly stimulated, and nutrient demand was increased

consequently (Medlyn *et al.*, 1999). Responses of these three intrinsic attributes all directly or indirectly related to the unsatisfied nutrient availability under eCO₂ condition, especially for nitrogen. Thus, nutrient availability was also changed in this study to reflect progressive nitrogen limitation on growth under eCO₂ condition (Luo *et al.*, 2004).

Two modelling experiments for eCO₂ treatment showed that feedbacks in canopy LAI were critical for predicting the hydrological impacts (i.e. canopy transpiration and soil water content) of eCO₂ and changes in functional attributes were important for modelling the feedbacks of canopy LAI under eCO₂ condition. At the ORNL FACE site, experiment without any changes in functional attributes in vegetation (i.e. Expt1 for eCO₂ treatment) consumed more water and depleted soil water because of significant increase in LAI caused by increase in CO₂. It implies that feedbacks of LAI at plot scale may offset the water-saving effects through suppressed stomatal conductance by eCO₂. Experiment with functional changes (i.e. Expt2 for eCO₂ treatment) predicted a little higher increase in LAI, smaller decrease in canopy transpiration and almost equivalent response of soil water content. Larger increase in LAI is possibly the reason for smaller decrease in canopy transpiration, because LAI is an important factor for determining water use. Expt2 of eCO₂ treatment predicted about a reduction of 10.5% in transpiration, which is slightly smaller than the observed changes in the 3 years with available data but is close to estimate of Wullschlegel *et al.* (2002b) at the ORNL FACE site. At the BioCON site, Expt1 for eCO₂ predicted a large increase in LAI, which intercepted and transpired more water and resulted in decrease in soil water content. At both sites, simulated and observed increases in LAI due to eCO₂ are small. It infers that future rising CO₂ will not increase LAI noticeably in energy-limited (annual rainfall is larger than annual potential ET) ecosystems. Norby and Zak (2011) reported that changes in LAI are small in the forest FACE experiments with high canopy LAI (>5.0), which are all in wet environments. LAI of ecosystems in energy-limited climatic regime is insensitive to eCO₂ possibly because CO₂ and water are not the first-order constraints on the growth of vegetation (Field *et al.*, 1995; Wullschlegel *et al.*, 2002a). Regarding the changes in soil water content, increase in BioCON FACE site is much greater than that in the ORNL FACE site, and the large difference is possibly caused by the different rooting profiles in forest and grass ecosystems. The differences in soil moisture response between the two sites may be explained by the fact that grasses have most of the roots in the top soil layer while trees have much deeper roots. The study by Duursma *et al.* (2011) showed that blue gum forest (*Eucalyptus saligna*) can extract less water from deep soil layer (~3.5 m) under eCO₂ condition. Thus, both observed and simulated

responses of soil water content in surface layer to eCO₂ are larger at the BioCON site than those at the ORNL FACE site.

Modelling experiments in this study suggest that feedbacks in canopy LAI are important for quantifying the potential effects of eCO₂ on water budgets. Failure to account for this feedback can significantly overestimate the water-saving effects [e.g. Aston (1984), Gedney *et al.* (2006) and Cao *et al.* (2010)]. This study also highlights that changes in functional attributes are important for capturing the feedbacks of LAI to eCO₂. Not including these changes can overestimate the response in LAI and underestimate the water-saving effects or even offset water-saving effects completely. Previous studies indicated that changes in functional attributes were closely related to availability of nitrogen under eCO₂ conditions, which implies that coupling between soil cycling of nitrogen and vegetation functioning under eCO₂ condition are necessary for models to predict the impacts of eCO₂ on water budgets adequately.

Impacts of the eCO₂ on water budgets

The WAVES model predicted decrease in ET and increase in run-off (Q) due to eCO₂ at both sites. Evaporation from interception (E_i , including canopy and litter layer) were predicted to increase slightly ($<1.0 \text{ mm year}^{-1}$) because of increase in LAI and consequent increase in litter production, which intercepted more water. Simulated decrease in canopy transpiration resulted from decreased canopy conductance under eCO₂ condition as described in Equation (1). Evaporation from soil surface (E_s) at both FACE sites increased slightly because of the increase in soil water content at surface layer due to eCO₂ and more water available for evaporation. All the three components of the simulated run-off were predicted to increase under eCO₂ condition, and they all resulted from decrease in canopy transpiration. Decreased transpiration under eCO₂ conditions result in more water in the soil comparing with that under aCO₂ conditions. Increased soil water content can facilitate generation of overland flow, lateral flow and seepage. Modelling results showed that run-off had larger inter-annual variability than ET (Figure 4) because of the buffering effects of the soil water storage and dynamic responses of vegetation growth to climate variability (Zhang *et al.*, 2001; Huxman *et al.*, 2004; Cheng *et al.*, 2011; Duursma *et al.*, 2011). Estimated changes in ET and total run-off at the ORNL FACE site in this study are close to changes predicted by Warren *et al.* (2011a) using Biome BGC model, who estimated that transpiration reduced about 10~16% and run-off increased about 16%.

The FACE experiments were principally designed to investigate the societal and scientific interests in potential capacity of CO₂ uptake by plants under eCO₂ condition and its potential mitigation of climate change (Hendrey and Miglietta, 2006). However, to some extent, results from

past two decades indicated that the effects of eCO₂ on water budgets may be of more overall significance than effects on carbon storages (Holtum and Winter, 2010) because initial enhancement of productivity by eCO₂ diminished quickly over time (Norby *et al.*, 2010; Norby and Zak, 2011), but reduction in stomatal conductance (g_s) is significant and persistent (Medlyn *et al.*, 2001). Ainsworth and Long (2005) reported that g_s was reduced by 20% averaged over 12 investigated FACE experiments. If all other factors remain unchanged, 20% reduction in g_s due to eCO₂ can lead to noticeable increase in water yield. Potential increase in water availability under eCO₂ may be particularly important for water-limited regions (Wullschleger *et al.*, 2002a). However, leaf-level water-saving effects tend to decline over time and larger spatial scales because of higher-level interactions (Leakey *et al.*, 2009; Leuzinger *et al.*, 2011; Warren *et al.*, 2011a) or offset by increase in LAI (or vegetation expansion) induced by either direct CO₂ fertilization effects or indirect water effects (Morgan *et al.*, 2004; Donohue *et al.*, 2009; Macinnis-Ng *et al.*, 2011), especially in water-limited regions. In this study, LAI increased slightly and run-off increased significantly at both ecosystems, which are likely to be typical responses for ecosystems in the energy-limited regions (i.e. wet regions). In energy-limited regions, water is already more than the ecosystem can evaporate, and ecosystem functioning might be mainly constrained by temperature and nutrients rather than water availability or CO₂. Thus, increase in LAI is small, and increase in soil water content did not stimulate growth. As a result, run-off was increased significantly at both sites. In the water-limited regions, impacts of the eCO₂ on water budgets and subsequent indirect effects via water availability on the response of LAI may be quite different (Wullschleger *et al.*, 2002a; Morgan *et al.*, 2004; Morgan *et al.*, 2007; Macinnis-Ng *et al.*, 2011; Morgan *et al.*, 2011).

CONCLUSIONS

Net effect of rising atmospheric CO₂ on water availability is uncertain and depends on responses of both stomatal conductance and LAI. In this study, a coupled water and carbon ecohydrological model (WAVES) was applied to examine physiological and hydrological responses at the two FACE experiments established on different ecosystems, i.e. one forest (ORNL FACE) and one grass (BioCON FACE). Our results showed that changes in vegetation functional attributes are important for reproducing responses of LAI, canopy transpiration and soil moisture under the eCO₂ condition. The WAVES model captured the changes in LAI and water budgets to eCO₂ very well at both sites when functional vegetation changes were considered. The LAI was predicted to increase slightly, and run-off increased

significantly at both forest and grass FACE sites. Predicted mean annual ET decreased about 8.7% and 10.8%, and mean annual run-off increased about 11.1% (59.3 mm year⁻¹) and 9.5% (37.6 mm year⁻¹) at the ORNL and BioCON FACE sites, respectively. This study highlights that functional vegetation changes are important for predicting changes in coupled water and carbon relationship under the eCO₂ conditions, and more experimental evidences are needed for further improvements of ecohydrological models to capture such changes.

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