Ecohydrologic impact of reduced stomatal conductance in forests exposed to elevated CO_2*

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ABSTRACT

Plants influence ecosystem water balance through their physiological, phenological, and biophysical responses to environmental conditions, and their sensitivity to climate change could alter the ecohydrology of future forests. Here we use a combination of measurements, synthesis of existing literature, and modelling to address the consequences of climate change on ecohydrologic processes in forests, especially response to elevated CO_2 (eCO_2). Data assessed from five free-air CO_2 enrichment (FACE) sites reveal that eCO_2-reduced stomatal conductance led to declines in canopy transpiration and stand water use in three closed-canopy forest sites. The other two sites were in the early stages of stand development, where a strong eCO_2-stimulation of canopy leaf area led to enhanced stand water use. In the sweetgum FACE experiment in Oak Ridge, Tennessee (USA), eCO_2 reduced seasonal transpiration by 10–16%. Intra-annual peak measured fluxes in transpiration ranged from 4·0–5·5 mm day^{-1}, depending on year. The Biome-BGC model simulated similar rates of transpiration at this site, including the relative reductions in response to eCO_2. As a result, simulations predict ~75 mm average annual increase in potential water yield in response to eCO_2. The direct effect of eCO_2 on forest water balance through reductions in transpiration could be considerable, especially following canopy closure and development of maximal leaf area index. Complementary, indirect effects of eCO_2 include potential increases in root or leaf litter and soil organic matter, shifts in root distribution, and altered patterns of water extraction. Copyright © 2010 John Wiley & Sons, Ltd.

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INTRODUCTION

The terrestrial water cycle functions across multiple spatial and temporal scales, simultaneously driven by dynamics of water transport vertically through the soil–plant–atmosphere continuum and horizontally across the landscape (Chahine, 1992; Loaiciga *et al.*, 1996; Rodriguez-Iturbe, 2000). Ecosystems, in turn, respond to the resulting soil and topographic conditions created by the vertical and horizontal flux of water and exert an influence on the hydrologic cycle through feedbacks that are driven by the distribution, structure, function, and dynamics of plant communities (Newman *et al.*, 2006). In addition, water use within and movement from ecosystems is strongly regulated by component interactions between soils and plants in response to climatic and edaphic factors (Jackson *et al.*, 2001; Newman *et al.*,

2006). Local, regional, and global water cycles are therefore likely to be sensitive to current and projected changes in climate including warmer temperatures, altered precipitation patterns, and rising CO_2 concentrations in the atmosphere (Cramer *et al.*, 2001; Thornton *et al.*, 2002; Gerten *et al.*, 2004; Meehl *et al.*, 2007).

Research conducted on the response of woody vegetation to climate change, in particular, to atmospheric CO_2 enrichment, has revealed the sensitivity of several key plant processes to elevated CO_2 (eCO_2). The most prominent of these has been that the eCO_2 can lead to higher leaf photosynthesis, a general stimulation of net canopy carbon uptake, and enhanced rates of net primary production (NPP)—with the potential for increased carbon storage in terrestrial ecosystems (Norby *et al.*, 2005; Leakey *et al.*, 2009). There is an equally strong expectation that the CO_2-induced reductions in stomatal conductance and leaf-level transpiration may have important consequences for forest water dynamics (Betts *et al.*, 2007; Leuzinger and Körner, 2010) and, in turn, for ecosystem-scale processes that depend on soil water availability.

Although the leaf-level responses of stomatal conductance to eCO_2 are important, they are by themselves insufficient to draw conclusions about ecohydrological processes that operate at longer and larger temporal and spatial scales (Wullschleger *et al.*, 2002b). eCO_2 can

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increase carbon allocation below ground, thereby increasing root biomass, shifting root distribution within the soil profile, and potentially increasing build-up of soil organic matter (SOM) through root turnover and exudation (Jastrow *et al*., 2005; Iversen *et al*., 2008). Root distribution, production, and turnover can affect water infiltration dynamics because of the influence of root channels and preferential pathways of water transport within the profile. Additional organic matter inputs to the soil can increase the soil water–holding capacity and buffer water release and flows within the vadose zone. Interactions among root distribution, SOM, and soil water content will impact seasonal timing and depth of water extraction, and thereby apparent water stress (and carbon uptake) during the growing season. Integrated consideration of soil–root and leaf–atmosphere responses to changes in CO_2 availability (Wullschleger *et al*., 2002a) must be scaled to impacts realized at canopy and landscape levels to ultimately address higher-order questions about forest water use and potential water conservation on ecosystem-scale processes.

A larger-scale, longer-term consideration of shifts in vegetation structure may then be linked to species-specific competitive interactions within ecosystems in response to the changing environment, such as woody plant expansion or contraction from specific landscapes.

Achieving an integrated understanding of how climate change will impact hydrologic cycles in forests will require a concerted effort. It is, however, an important goal and one that can best be addressed through an approach that engages experimentalist and modeller. There have been a variety of modelling efforts to assess the impacts of changing environmental conditions on ecosystem water use (Law *et al*., 2000; Hanson *et al*., 2005; Siqueira *et al*., 2006; Luo *et al*., 2008) that vary widely in their spatial scale and temporal time step. Ecosystem water flux is often linked to individual environmental constraints to stomatal conductance (e.g. radiation and vapour pressure deficit (VPD); Ewers *et al*., 2005), maintenance of hydraulic conductance through the soil–plant–atmosphere continuum (Sperry *et al*., 1998), and various measures and estimates of site water balance (Wilson *et al*., 2001; Schäfer *et al*., 2002; Warren *et al*., 2005; Granier *et al*., 2007; Leuzinger and Körner, 2010). As issues that surround the response of forests to climate change become more complex, additional studies that integrate across temporal and spatial scales will be required.

In this study, we use a combination of analysis of experimental data, synthesis of existing literature, and modelling to address the mechanisms and implications of climate change on ecohydrologic processes in forests. Research conducted over the last 12 years at the Oak Ridge National Laboratory (ORNL) free-air CO_2 enrichment (FACE) facility highlights the role of leaf- and canopy-scale processes in determining the hydrologic response of forests to climate change. Information from these investigations coupled with published results from other forest FACE experiments are used to parameterize the Biome-BGC model (Thornton *et al*., 2002), an ecosystem process model that simulates water, energy, and biogeochemical fluxes on a daily time step. Model mechanisms controlling site water balance are evaluated against long-term measurements, and predictive ecohydrological responses to atmospheric CO_2 enrichment are explored at the landscape scale.

MATERIALS AND METHODS

Comparative CO₂ enrichment studies

Ecohydrological impacts of woody plant response to eCO_2 have long been inferred from measurements conducted on single leaves, seedlings, or individual saplings grown in growth chambers, greenhouses, or open-top outdoor chambers (Norby *et al*., 1999). While they are useful for the recognition of potential physiological responses to eCO_2 like photosynthesis (Wullschleger *et al*., 1992), the size and longevity of forests generally precluded investigations of stand-level responses. In addition, the artificial nature of these enclosed systems can easily confound results of CO_2 treatments, driven by concurrent alterations in the localized plant environment and interactive feedbacks; e.g. spectral quality, thermal gradients, wind, moisture availability, soil characteristics, or rooting depth. Accurate measurement and modelling of eCO_2-dependent water flux dynamics under natural conditions and at larger spatial and temporal scales has thus required a substantial shift in the experimental systems (Norby *et al*., 2001). As such, FACE technology has been employed, void of chamber walls and permitting plots that were large enough such that the experiments were not limited to seedlings, single trees, or clusters of small-stature individuals. FACE studies in woody ecosystems began in earnest in the 1990s, with some studies continued for a decade or longer, exposing maturing stands to inter-annual climate variations in conjunction with regulated CO_2 concentrations. Here, we consider five long-term FACE studies that have been conducted in temperate forest ecosystems, with plantations of young poplar (treatments applied as trees aged 0–6 years, coppiced at year 3; POP/EuroFACE), aspen/birch/maple (0–12 years; Aspen-FACE), pine (14–27 years; Duke), sweetgum (12–21 years; ORNL), and mature mixed hardwood (~100 years; Web-FACE). Ecohydrological data from these five sites comprised the comparative literature review (Table I), with measurement and modelling of the sweetgum plantation at ORNL used as a case study (described below).

ORNL site description and experimental facilities

The research reported here, much of which spans the period 1998–2008, took place in a 12- to 21-year-old sweetgum (*Liquidambar styraciflua* L.) tree plantation established in Oak Ridge National Environmental Research Park in eastern Tennessee (35°54′N;

Table I. Physiological and hydrological responses of trees and forests to atmospheric CO_2 enrichment.

Parameter	Web-FACE	Duke	ORNL	Aspen-FACE	POP/EuroFACE
Stomatal conductance	−4 to −21	−5	−14 to −44	0 to −44/+19	−16 to −39
Stand water use	−14	−7	−13	+25	+12 to +23
Evapotranspiration	−10	na	−7	na	na
Runoff	na	+	na	na	na
Drainage	na	+	na	na	na
Upper soil moisture	0/+	+	0/+	+	na
Root production	na	+	+	0/+	+
Root standing crop	0/−	+	+	+	+
LAI	0	0/+	0/+	+	+
Species	*Carpinus betulus*	*Pinus taeda*	*Liquidambar styraciflua*	*Populus tremuloides*	*Populus x euramericana*
	Fagus sylvatica	—	—	*Betula papyrifera*	—
	Quercus petraea	—	—	*Acer saccharum*	—
References	Cech *et al.* (2003)	Ellsworth *et al.* (1995)	Gunderson *et al.* (2002)	Noormets *et al.* (2001)	Liberloo *et al.* (2005)
	Keel *et al.* (2007)	Ellsworth (1999)	Norby *et al.* (2003)	Uddling *et al.* (2008, 2009)	Lukac *et al.* (2003)
	Leuzinger *et al.* (2005)	McCarthy *et al.* (2007)	Wullschleger and Norby (2001)		Tricker *et al.* (2005)
	Leuzinger and Körner (2007)	Pritchard *et al.* (2008)	Wullschleger *et al.* (2002b)	King *et al.* (2005)	Tricker *et al.* (2009)
	Bader *et al.* (2009)	Schäfer *et al.* (2002)	Iversen *et al.* (2008)	Pregitzer *et al.* (2008)	—

Quantitative and qualitative estimates were derived from the published literature for long-term studies where trees were exposed to ambient and *ca* 550 ppm CO_2 concentrations. Values represent the percentage change in a variable in response to eCO_2. Non-measured values are represented by 'na'.

84°20′W), at an elevation of 227 m. One-year-old sweetgum seedlings were planted in 1988 at $2\cdot3 \times 1\cdot2$ m spacing on previously cultivated alluvial land along the Clinch River. The soil is an Aquic Hapludult with a silty–clay–loam texture (21 : 55 : 24; sand : silt : clay). Rooting depth was ~$1\cdot2$–$2\cdot2$ m for individual sweetgum trees destructively extracted from the site after conclusion of the study (Warren *et al.*, unpublished). A survey of the site in 1998 indicated that the 10-year-old plantation had a basal area of about 29 m^2 ha^{-1} with an average height of 12 m and an average leaf area index (LAI) of $5\cdot5$ m^2 m^{-2}.

A FACE system was installed in four of the five 25-m diameter plots in 1997. The FACE system regulates the release of CO_2 from the vertical PVC vent pipes located around each plot on the basis of wind speed, wind direction, and *in situ* measurements of current CO_2 concentration within the canopy (Hendrey *et al.*, 1999). Since 1998, eCO_2 has been released into the two treatment plots during each growing season, while the tree stands in the other three plots were in air with the current ambient CO_2 (aCO_2) concentration. Atmospheric CO_2 in the elevated plots was maintained at a target daytime concentration of 525–555 ppm during the growing season, *ca* 40% higher than CO_2 levels in the ambient plots (380–400 ppm).

Mean annual temperature (1962–1993) at the study site is $13\cdot9$ °C and the annual precipitation averages 1371 mm. Precipitation is generally distributed throughout the year at the site; however, there are often 3- to 5-week periods of significant water deficit during late summer. Volumetric soil water content in the upper

soil (0–20 cm) was measured at six locations per plot throughout the growing season using time-domain reflectometry (Soil Moisture Equipment Corporation, Santa Barbara, CA, USA). Climate data were collected in all years with micrometeorological equipment including measurement of precipitation, wind, photosynthetically active radiation (PAR), and air temperature and relative humidity above and beneath the canopy. All micrometeorological data are documented and archived for public use at http://public.ornl.gov/face/ORNL/ornl_data.shtml.

Measured sap flow and canopy transpiration

The compensated heat-pulse technique (Greenspan Technology Pty. Ltd, Warwick, Queensland, Australia) was used in 1999 and 2004 to measure the sap flow for four trees in each of two aCO_2 and eCO_2 plots (16 trees in total). These trees were located near the centre of each plot and ranged in diameter from $12\cdot4$ to $14\cdot7$ cm in 1999 and $11\cdot4$ to $19\cdot8$ cm in 2004. A single heat-pulse probe was positioned in each tree so that the sensing thermistor was located at a sapwood depth of 19 mm. The control module and data logger were programmed to provide a heat pulse for $1\cdot8$ s and measurements were recorded every 60 min. Sap velocity was calculated from the corrected heat-pulse velocity based on Equation 3 of Barrett *et al.* (1995). All other aspects of data analysis are described in Wullschleger and Norby (2001).

Sap flow in 2008 was quantified using thermal dissipation probes (Dynamax Inc., Houston, TX, USA) installed at multiple depths in five trees in each of the two aCO_2 and two eCO_2 treatment plots. These trees were located across each plot and ranged in diameter (DBH) from $13\cdot2$

to 22·4 cm. As described by Granier (1987), the temperature difference between the heated and unheated probe is proportional to the voltage differential between the probes and can be related to sap velocity based on the empirical relationship between the voltage differential and the heat dissipation attributable to sap flow near the heated probe. Probes were insulated with polystyrene foam and reflective bubble insulation to minimize errors due to natural thermal gradients. Voltage differences between probes were sampled every 15 min during the growing season and stored on a data logger (model CR10X, Campbell Scientific). Radial patterns of sap flow were established using measurements of sap velocity at 1·5, 2·5, and 7·0 cm within dominant trees. Tree sap flow was calculated by linear interpolation of radial patterns of sap velocity through each consecutive annulus of sapwood area bound by sensors installed at different depths.

Hourly rates of stand transpiration (mm h^{-1}) for each of the two aCO$_2$ and two eCO$_2$ plots were estimated as a function of measured sap velocity, total stand sapwood area, and the fraction of sapwood functional in water transport. Sapwood area averaged across all plots was 23·7 m^2 ha^{-1} in 1999 (Wullschleger and Norby, 2001), 30·5 m^2 ha^{-1} in 2004, and 36·3 m^2 ha^{-1} in 2008. Treatment differences in sapwood area were not observed over the course of the experiment. Daily rates of stand transpiration (mm day^{-1}) in both the years were calculated via a simple summation of hourly rates.

Model description

We used the terrestrial ecosystem process model Biome-BGC, version 4.1.1 (Thornton *et al.*, 2002), incorporating an extension on the model self-initialization that uses a dynamic mortality routine (Pietsch and Hasenauer, 2006). The Biome-BGC model simulates states and fluxes of water, carbon, and nitrogen in a forest ecosystem, using a daily time step. The model is forced by daily weather data: minimum and maximum near-surface air temperature, incident shortwave radiation, atmospheric VPD, and precipitation. These were calculated from hourly observations made at the site from 1998 to 2008 (Riggs *et al.*, 2009). Other required model inputs include ecophysiological parameters, disturbance history, soil physical properties, atmospheric CO$_2$, and atmospheric nitrogen deposition.

The plant canopy LAI controls canopy radiation absorption and light transmission to the ground, water interception in the canopy, photosynthesis, and litter inputs to the detrital pools. Timing of the canopy development and senescence is dependent on temperature and day length following the approach of White *et al.* (1999), and ultimately constrains seasonal patterns of photosynthesis and transpiration. Photosynthesis is calculated with the Farquhar photosynthesis routine using kinetic constants as per Woodrow and Berry (1988); and de Pury and Farquhar (1997), as well as parameters defined by Kuehn and McFadden (1969); and Wullschleger (1993), and a V$_{max}$–J$_{max}$ relationship specifically described for ORNL

FACE (Sholtis *et al.*, 2004). The model is sensitive to feedbacks from mineralization processes and thus site nutrient availability. The model also depends heavily on water inputs and cycling through the ecosystem. Precipitation is partially intercepted by the canopy, depending on the LAI, an interception coefficient, and the precipitation intensity; and the residual is input directly to the soil water pool. The canopy water either evaporates on the same day or, if not all the intercepted water can be evaporated, is added to the soil water pool, to represent canopy dripping. Evaporation is calculated independently from the leaf and the soil surfaces with the Penman–Monteith equation as a function of air temperature, air pressure, VPD, incident solar radiation, and the transport resistance of water vapour and sensible heat. The model assumes a single canopy layer, and does not assess the potential contribution from the relatively sparse understorey. Precipitation inputs to the soil water pool can drain as outflow (water yield) or be stored and available for evaporative or transpirational loss from the system. The total soil water–holding capacity at saturation is determined from the total 'effective soil depth' and texture based on empirical pedotransfer functions (Clapp and Hornberger, 1978; Cosby *et al.*, 1984; Saxton *et al.*, 1986). Effective soil depth for both treatments was defined as 2 m, derived from the maximum observed rooting depth and reduced by the estimated stone fraction >2 mm. Subsequent model estimation of soil water potential was modified to fit the soil water retention curve previously developed for the Oak Ridge FACE site (Warren *et al.*, unpublished).

Potential water yield from the system requires knowledge of volumetric water content at field capacity, defined here as −0·033 MPa on the basis of field data collected at the Oak Ridge FACE site. The model assumes that water above saturation is lost immediately as outflow and that water between saturation and field capacity is lost at a rate of 50% per day. Remaining soil water is then available for evapotranspiration. Plant water uptake is driven by the demand of water for transpiration, where transpiration is regulated by stomatal conductance and, as evaporation, calculated with the Penman–Monteith equation. Maximum stomatal conductance is limited by reduction factors, dependent on solar radiation, VPD, water potential gradients, and temperature. The stomata response to solar radiation is described as a hyperbolic function, with the half saturation value generally set to 75 μmol m^{-2} s^{-1} after Körner (1995) who gives a range of values between 50 and 100 μmol m^{-2} s^{-1}. The other reduction factors are linear functions of the VPD, the soil water potential (a surrogate for the predawn leaf water potential), and the daily minimum temperature. Beyond certain threshold values, stomatal conductance is at its maximum or is zero (Table II). Total canopy conductance follows the electrical circuit analogy, with stomatal and cuticular conductance in parallel and leaf boundary layer conductance in series.

The model theory and its assumptions and methods of parameterization have been fully described elsewhere

Table II. Ecophysiological constants used in the Biome-BGC model of *Liquidambar styraciflua* as simulated under ambient (a) or elevated (e) atmospheric CO_2 as parameterized for the ORNL FACE research facility.

Parameter estimate		Unit	Parameter description	
eCO$_2$	aCO$_2$			
1	1	flag	1 = woody	0 = non-woody
0	0	flag	1 = evergreen	0 = deciduous
1	1	flag	1 = C3 photosynthesis	0 = C4 photosynthesis
1	1	flag	1 = model the phenology	0 = user-specified phenology
0	0	yday	Yearday to start new growth (when phenology flag = 0)	
0	0	yday	Yearday to end litter fall (when phenology flag = 0)	
0·2	0·2	—	Transfer growth period as fraction of growing season[a]	
0·3	0·3	—	Litter fall as fraction of growing season[a]	
1	1	yr^{-1}	Annual leaf and fine-root turnover fraction[b]	
0·7	0·7	yr^{-1}	Annual live wood turnover fraction[b]	
0·005	0·005	yr^{-1}	Annual whole-plant minimum mortality fraction[a]	
0·02	0·02	yr^{-1}	Annual whole-plant maximum mortality fraction[a]	
225	225	yr	Length for (low) elliptic mortality[a]	
75	75	yr	Length for (high) elliptic mortality[a]	
0	0	yr^{-1}	Annual fire mortality fraction[c]	
0·72	**0·38**	—	(allocation) new fine root C : new leaf C[c]	
2·49	**2·44**	—	(allocation) new stem C : new leaf C[c]	
0·16	0·16	—	(allocation) new live wood C : new total wood C[b]	
0·07	**0·08**	—	(allocation) new coarse root C : new stem C[c]	
0·1	0·1	—	(allocation) current growth : storage growth[c]	
33	**30**	kg C kg^{-1} N	C : N of leaves[c]	
67	**58**	kg C kg^{-1} N	C : N of leaf litter[c]	
44	44	kg C kg^{-1} N	C : N of fine roots[c]	
50	50	kg C kg^{-1} N	C : N of live wood[b]	
434	**430**	kg C kg^{-1} N	C : N of dead wood[c]	
0·38	0·38	—	Leaf litter labile proportion[b]	
0·44	0·44	—	Leaf litter cellulose proportion[b]	
0·18	0·18	—	Leaf litter lignin proportion[b]	
0·34	0·34	—	Fine-root labile proportion[b]	
0·44	0·44	—	Fine-root cellulose proportion[b]	
0·22	0·22	—	Fine-root lignin proportion[b]	
0·77	0·77	—	Dead wood cellulose proportion[b]	
0·23	0·23	—	Dead wood lignin proportion[b]	
0·005	0·005	LAI^{-1} d^{-1}	Canopy water interception coefficient[a]	
0·54	0·54	—	Canopy light extinction coefficient[b]	
2	2	—	All sided : projected leaf area[b]	
23·6	**25**	m^2 kg^{-1} C	Canopy average specific leaf area (projected area basis)[c]	
1·26	1·26	—	Shaded : sunlit specific leaf area[c]	
0·12	0·12	—	Fraction of leaf N in Rubisco[a]	
0·0045	**0·005**	m s^{-1}	Maximum stomatal conductance (projected area basis)[d]	
0·00006	0·00006	m s^{-1}	Cuticular conductance (projected area basis)[b]	
0·01	0·01	m s^{-1}	Boundary layer conductance (projected area basis)[b]	
−0·334	−0·334	MPa	Leaf water potential: start of conductance reduction[b]	
−2·2	−2·2	MPa	Leaf water potential: complete conductance reduction[b]	
500	500	Pa	VPD: start of conductance reduction[d]	
3600	3600	Pa	VPD: complete conductance reduction[b]	
0	0	°C	Night temperature: start of conductance reduction[b]	
−8	−8	°C	Night temperature: complete of conductance reduction[b]	

Parameter differences between CO_2 treatments are in bold.
[a] E. Pötzelsberger, personal assessment.
[b] White *et al.* (2000).
[c] Published data from the ORNL FACE site: http://public.ornl.gov/face/ORNL/ornl_data.shtml.
[d] Wullschleger *et al.* (2002b).

(White *et al.*, 2000; Thornton *et al.*, 2002; Thornton and Rosenbloom, 2005; Pietsch and Hasenauer, 2006).

Application of Biome-BGC to the ORNL FACE site

In this study, our aim was to (1) represent observed growth and water use of the ORNL FACE plots from 1998 to 2008 using the mechanistic ecosystem model Biome-BGC, (2) quantify non-measured ecosystem water fluxes, and (3) determine treatment-specific ecosystem water budgets. The model was informed by measurements within two eCO$_2$ plots or three aCO$_2$ plots, scaled to one simulation per treatment. Parameters were based

on site measurements, previous values used at similar sites, or informed estimates (Table II). Daily weather data were assumed to be constant across treatments, and included daily minimum and maximum temperatures, precipitation, relative humidity and total incident radiation, and albedo (assumed at 0·2). Differences between the two simulated ecosystems lay in some of the ecophysiological constants derived from measurements at the site, and, of course, the atmospheric CO_2 content.

A total of 42 ecophysiological parameters were required for the vegetation-specific parameterization (Table II), many of which were available from previous measurements at the ORNL FACE site. Parameters associated with carbon (C) and nitrogen (N) allocation within the various plant compartments were based on allometric relationships (Norby *et al.*, 2002). C allocation has shifted through time at the site, such that fine root : leaf, coarse root : stem, and stem : leaf allocation ratios declined over the years of the experiment; however, the model does not allow dynamic allocation parameters. Similarly, plant tissue C : N ratios that regulate respiration, and determine, for leaves, the maximum rate of carboxylation (V_{cmax}), show a positive trend over the years. In addition, the canopy-averaged specific leaf area declined through time. While there were multiple processes and components of the system that were dynamic, the limitations in this version of the model required some parameters to be based on mean values over the entire observation period.

Maximum stomatal conductance is a particularly important ecophysiological parameter for the water budget, and is greatly reduced by eCO_2 treatments. As described earlier, the model can reduce stomatal conductance based on the reduction factors associated with several environmental variables. The model assumes a linear relationship between stomatal conductance (g_s) and VPD between a lower (where g_s reduction begins) and an upper boundary (where stomata closure is complete). The lower boundary (0·5 kPa) could be estimated from canopy conductance—VPD data obtained in 1999 (Wullschleger *et al.*, 2002b). Stomatal response to atmospheric CO_2 concentration, however, has not yet been explicitly addressed in the model. In order to account for reduced stomata aperture under eCO_2, a lower maximum value for stomatal conductance was set—equal to 0·0045 m s^{-1} (eCO_2) as compared to 0·005 m s^{-1} (aCO_2)—based on canopy conductance estimates derived from sap flow measurements using an inverted Penman–Monteith equation (Wullschleger *et al.*, 2002b).

The Biome-BGC model was first parameterized to fit the average stand situation between 1999 and 2008, and then run for the whole time period to assess its applicability for prediction of canopy transpiration and site water fluxes until 2008. Several problems arose with the parameterization. First, simulated spring initiation of the canopy occurred several weeks earlier than observed leaf out. The sweetgum trees were established from a more northerly seed source (Missouri) and have always displayed bud-burst later than native vegetation. Thus, the seasonal development of simulated LAI for the model had to be adjusted by altering the empirical formulation of White *et al.* (1999) and hence shifting the day of leaf flushing by more than two weeks. Second, the soil water retention properties modelled using the empirical pedotransfer formulations of Clapp and Hornberger (1978); Saxton *et al.* (1986), and Cosby *et al.* (1984) did not match field observations. At a given volumetric water content, the soil water potential was underestimated (more negative) and thus drought stress and accordant reductions in stomatal conductance appeared too early in the simulations. Slight modifications of the original formulations significantly improved the model performance with regard to the transpiration predictions, especially during periods of limited water supply. Thus, premature complete stomatal closure (which was not observed) due to low soil water potential could be avoided in the model. Modifications included adjustment of the modelled water retention curve to better reflect field measurements and adjustment of relative maximum stomatal conductance between treatments—differences in field measurements (Wullschleger *et al.*, 2002b) varied from 0−20+%, a value of 10% was settled on for the simulations which provided the best fit to the data. Variability in the tree size and structure can also affect the ability of the model to derive outflow from tree-level transpiration scaled to the stand. These include specifically variation in tree size, canopy position, stand-level, and microsite topography (including subsurface clay 'lenses'), and seasonal dynamics of the coarse and fine litter layers. Each of these components is not directly included in the model, but may impact interception, evaporation, infiltration, and surface or subsurface flow dynamics.

RESULTS

Overview of FACE studies

eCO_2 consistently reduced the stomatal conductance by up to 44% across the five FACE studies (Table I), although in later years at Aspen-FACE eCO2 had little effect or stimulated stomatal conductance (Uddling *et al.* 2009). Reduced stomatal conductance led to a decline in stand water use for sites that did not have a strong stimulation of LAI. Response of LAI within the pine FACE site was linked to soil nutrient availability, although interannual environmental conditions, especially drought, limited this response (McCarthy *et al.*, 2007). Similarly at ORNL, eCO_2 tended to transiently increase sweetgum LAI during non-drought years, but not during drought and post-drought years (Norby *et al.*, 2003; Warren *et al.*, in review). In contrast, LAI and aboveground production were greatly enhanced by eCO_2 for *Populus* sp. in the Aspen-FACE and POP/EuroFACE studies, which resulted in substantial increases in stand water use. Despite some differences in LAI and stand water use among the FACE studies, eCO_2 increased water content in the upper 20 cm of the soil profile within the four non-irrigated FACE studies (Table I).
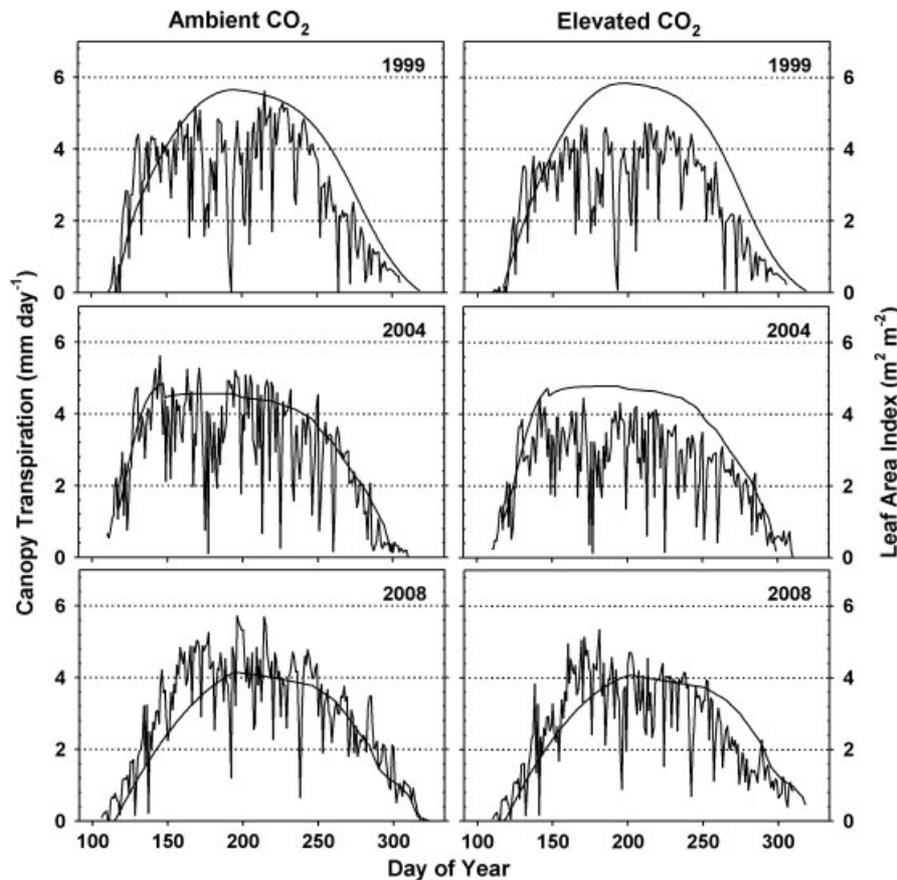
Figure 1. Daily canopy transpiration as scaled tree sap flow in a sweetgum forest plantation exposed to ambient or elevated atmospheric CO_2 across multiple years. Seasonal patterns of leaf area index (LAI) were based on three aCO_2 plots or two eCO_2 plots (smooth lines), derived from Norby *et al.* (2003); Norby and Tharp (2008).

Root production and root standing crop were enhanced in response to eCO_2 for the young tree plantations (although not for older trees at the Web-FACE site) (Table I). There were large seasonal and inter-annual shifts in the magnitude of root responses to eCO_2; however, increased carbon allocation to the eCO_2 roots has been maintained through time across the four young FACE studies. In addition, there was substantial evidence of fine or coarse root distribution shifting deeper (>15 cm) with the soil profile at three of the FACE sites (Lukac *et al.*, 2003; Iversen *et al.*, 2008; Pritchard *et al.*, 2008); rocky subsoil limited depth of measurements at Web-FACE, and there are no reports of distribution shifts at Aspen-FACE.

Transpiration at ORNL FACE

Canopy transpiration of sweetgum trees in the ORNL case study was sampled in years 2, 6, and 10. Inter-annual transpiration remained fairly constant through time, with intra-annual peak fluxes reaching $4 \cdot 0 - 5 \cdot 5$ mm day^{-1} (Figure 1). The average response of plots exposed to eCO_2 during mid summer (June, July, and August) was a 7–16% reduction in transpiration, depending on year. eCO_2 reduced annual canopy transpiration by 10–16% (Table III). Variation in annual transpiration and $eCO_2 : aCO_2$ (E : A) response was attributable to wind storms, drought, and other environmental stressors.

Canopy development and duration can provide some insight into the dynamics of plant water use; however, the magnitude of regulation may be overshadowed by other processes. In 1999, maximum LAI reached $5 \cdot 7 - 5 \cdot 8$ (Figure 1), similar to other non-drought years. In 2004, a windstorm damaged the canopies of trees in both treatments, as illustrated by the abrupt stabilization in LAI by late May, one month earlier than other years (Figure 1). In 2008, LAI was the lowest as the study was initiated, driven by interactions between the 2007 drought and N limitations. Inter-annual peak LAI for aCO_2 was highly conserved during eight of the ten years without extreme events ($5 \cdot 60 \pm 0 \cdot 04$), while peak LAI for eCO_2 plots remained much more variable ($5 \cdot 85 \pm 0 \cdot 17$). Despite the differences in external environmental conditions and their effect on LAI, canopy transpiration was relatively constant over the lifetime of the experiment; inter-annual variation in both treatments was <10%.

eCO_2 treatments consistently reduced canopy transpiration by 10–15%, with the greatest effects on site water balance occurring when water use was greatest (Figure 2). For example, as transpiration in aCO_2 plots reached 4 mm day^{-1}, eCO_2 plots used only ~3·5 mm day^{-1}. Similarly, there was little difference in absolute transpiration between treatments as water use declined below 1 mm day^{-1}. The linear relationship between eCO_2 and aCO_2 treatments was not significantly

Table III. Seasonal and inter-annual patterns of measured and simulated canopy transpiration in a sweetgum forest exposed to long-term CO$_2$ treatments.

| Year | CO$_2$ treatment | Canopy Transpiration (mm d^{-1}) (mm yr^{-1}) | | | | | | | E : A | E : A |
		May	June	July	August	September	October	Annual	Annual	Janurary–August
Measured values										
1999	Ambient	3·4	3·7	3·5	4·4	2·6	1·0	568	0·90	0·93
	Elevated	2·8	3·4	3·2	3·9	2·5	0·8	511	—	—
2004	Ambient	3·6	3·6	3·9	3·5	2·8	0·9	576	0·85	0·84
	Elevated	2·9	3·0	3·2	3·0	2·3	1·2	487	—	—
2008	Ambient	2·2	4·3	4·1	4·0	3·3	1·9	622	0·84	0·88
	Elevated	2·0	4·0	3·5	3·4	2·5	1·2	522	—	—
Modeled values										
1999	Ambient	3·7	3·7	3·4	4·0	3·3	1·4	614	0·85	0·85
	Elevated	3·1	3·2	2·9	3·4	2·8	1·1	521	—	—
2004	Ambient	2·7	3·1	3·4	3·2	2·8	1·2	507	0·84	0·85
	Elevated	2·3	2·7	2·9	2·7	2·3	1·0	428	—	—
2008	Ambient	2·5	4·2	3·9	3·7	3·2	1·6	589	0·87	0·87
	Elevated	2·1	3·7	3·4	3·2	2·8	1·4	511	—	—

Annual fluxes include values from April to November during leaf development and leaf abscission. Transpiration ratio of eCO$_2$ to aCO$_2$ (E : A) is calculated annually and for mid-season fully developed canopies.

different through time. A linear regression across years suggests a consistent 14·6% reduction in transpiration from eCO$_2$ plots ($R^2 = 0.93$, $n = 596$).

Modelling ORNL FACE

Simulated inter-annual LAI peaked at ~4 for eCO$_2$ and between ~4 and 4·5 for aCO$_2$. In contrast, measured maximum LAI ranged from 4 to 6 for eCO$_2$ and from 4 to 5·8 for aCO$_2$. The shape of the simulated LAI curve differed from observations, increasing throughout the summer to a peak in mid-September (Figure 3), two months later than the observed peak (Figure 1).

As expected, once the model was parameterized, the simulated canopy transpiration tracked measured transpiration quite well (Figure 4). Seasonal initiation of transpiration, peak values, and response to environmental conditions were similar for measured and modelled values. There was a two week delay in the simulated seasonal decline in transpiration; measured transpiration declined by day of year (DOY) 245, while simulated transpiration declined by DOY 260 (Figure 5). Even so, the model (driven by day length) accurately terminated transpiration in early November.

As the model was projected forward through time, simulated canopy transpiration was tightly grouped around actual measured values (Figures 4 and 5). The correlation between simulated and measured values was maintained through 2008, especially from June to August (DOY 152–243) when simulated transpiration was 96 and 98% (eCO$_2$ and aCO$_2$, respectively; s. e. ± 1%) of measured transpiration. In May, 2008, the simulations overestimated transpiration by 8% (eCO$_2$) and 13% (aCO$_2$). In 2008, from September to October, the simulations underestimated transpiration for aCO$_2$ by 5%, and overestimated transpiration for eCO$_2$ by 16% (Figure 5).

Biome-BGC was able to partition fluxes among different ecohydrological components on the basis of site water balance equations linked to simulated estimates of water flux. Precipitation inputs were balanced by evapotranspiration and soil water flow outputs. Water lost from the system via transpiration was a large component of simulated site water flux (Figure 6). The significant, long-term reduction in simulated eCO$_2$ transpiration agreed with the measured values through time. As a result, simulated water yield (surface runoff for saturated conditions and subsurface flow and drainage for unsaturated conditions) was significantly enhanced (~16%; s. e. ± 3%) by eCO$_2$. Potential water yield was 42 and 48% (aCO$_2$ and eCO$_2$) of annual precipitation at the site. The simulated eCO$_2$ ecosystem increased potential water yield by ~75 mm annually (s. e. ± 10 mm), released during the growing season. Treatment differences in inter-annual values of outflow (eCO$_2$–aCO$_2$) ranged from 58 to 137 mm, except for the year 2007 in which there was no difference in modelled outflow. This was an extraordinarily dry and hot year, which led to premature leaf senescence across the stand (Warren *et al.*, In Review), and Biome-BGC was not able to accurately model transpiration—values were overestimated by 20–40%.

DISCUSSION

Regulation of stand water use

Our studies show, both experimentally and through the use of a model, that reductions in the stomatal conductance due to eCO$_2$ can affect leaf, plant, and ecosystem water use. The ecohydrologic consequences are manifested in increased site water yield. In addition, reduced ecosystem transpiration under eCO$_2$ will reduce regional-scale atmospheric humidity and thereby enhance the VPD (and driving force for water loss) between
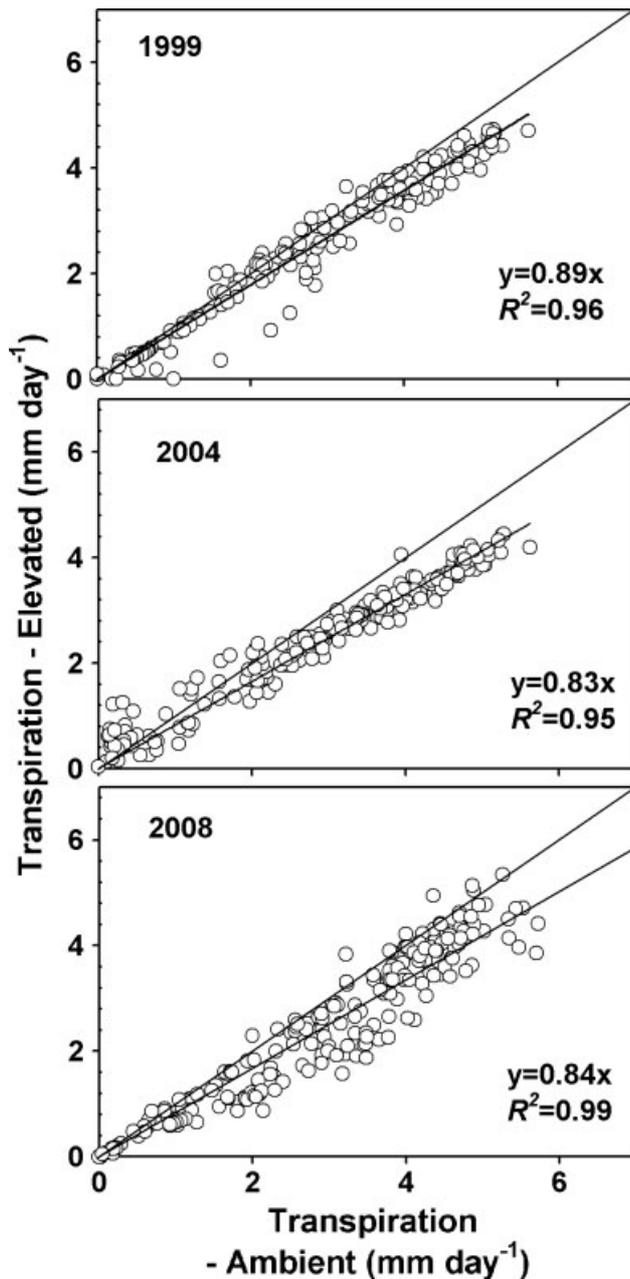
Figure 2. Measured canopy transpiration of sweetgum forest plantation FACE plots exposed to ambient or elevated atmospheric CO_2 across multiple years. Values below the solid 1:1 line represent greater transpiration in aCO_2 plots than in eCO_2 plots.

leaves and the atmosphere. Projected increases in air temperature will further increase VPDs. These feedback processes could increase transpiration and reduce water use efficiency (as grams of C uptake per gram of H_2O release), although under persistent drought and heat, stomatal conductance and stand water use slowly decline. In addition, there is an evidence of much greater reduction in water use in eCO_2 plots at ORNL FACE during extreme heat and drought events, especially for dominant trees whose measured sap flow declined by 60% relative to aCO_2 trees (Warren *et al.*, In review). Under such extreme events, the Biome-BGC model used in this study was not able to simulate measured values

of transpiration (overestimation; data not shown), which necessitates further model refinement and sensitivity to extreme climate conditions.

Water use through trees is further regulated by soil–root–leaf conductances associated with the characteristic forest structures—root deployment, xylem anatomy, tree height, branching patterns, and leaf area (Waring and Running, 1998). These structural features can change during stand development and can be altered by eCO_2, so it is important that assessments of the effects of eCO_2 on forest water use recognize the importance of stand structure, including its plasticity and temporal dynamics. Across the FACE sites compiled here, stage of stand development appeared to have the greatest influence on the response of canopy transpiration to eCO_2, where eCO_2 increased LAI and stand water use in the young rapidly growing plantations, while eCO_2 resulted in little change to LAI and substantial reductions in stand water use in the older, nutrient-limited stands.

As trees age and grow taller, structural and physiological changes can occur that affect water use. Stomatal conductance, photosynthesis, specific leaf area, and leaf-specific hydraulic conductance often are lower in taller trees, and hydraulic limitations can increase with tree height (Ryan *et al.*, 2006; Domec *et al.*, 2008). The C:N ratio of trees often increases during stand development as wood volume increases and labile N is incrementally sequestered into longer-lived pools (e.g. wood), which can reduce productivity and leaf area (Ryan *et al.*, 1997; Johnson, 2006). These factors can lead to a decline in overstory transpiration during stand development, but a decline in total ecosystem evaporation may be offset by enhanced evapotranspiration from the soil and understorey vegetation (Delzon and Loustau, 2005). At the ORNL FACE site, there was little evidence for enhanced understorey LAI over the course of the study across treatments; however, there was an increase in the woody biomass in eCO_2 plots, which could change soil–plant evapotranspiration due to altered understorey vertical structure (Souza *et al.*, 2010).

LAI and canopy development

LAI increases rapidly as tree seedlings are established on a site until crown closure occurs, after which LAI peaks and may slowly decline. The time required to attain peak LAI during stand development depends on the availability of environmental resources and stand density. In the ORNL sweetgum plantation, LAI had already peaked when the CO_2 treatments were initiated 10 years after plantation establishment. eCO_2 can accelerate canopy development of young trees prior to canopy closure and thereby alter other processes, including water use, that depend on leaf area. Indeed, eCO_2-stimulated canopy development and LAI at the two young rapidly growing stands at Aspen-FACE and POP/EuroFACE, suggesting that the resources other than CO_2 were not limiting, and resulted in greater stand water use in eCO_2 plots. However, such observations are confined to young stands
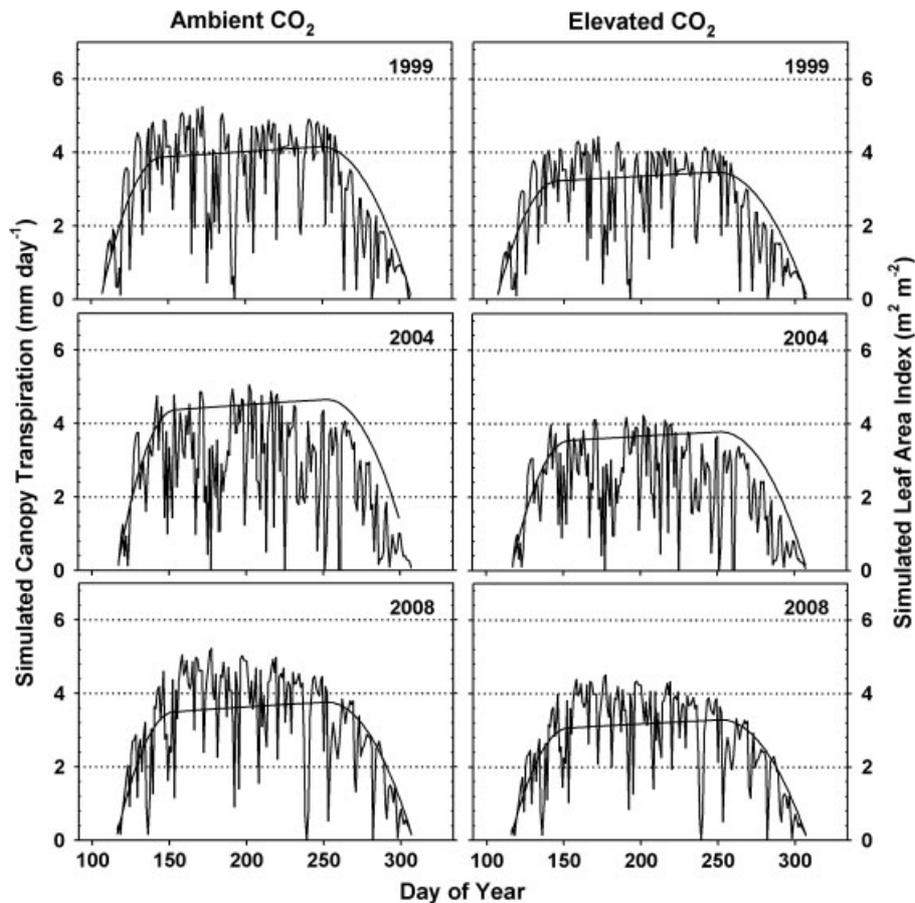
Figure 3. Simulated daily canopy transpiration in a sweetgum forest plantation exposed to ambient or elevated atmospheric CO$_2$ across multiple years based on an ecosystem process model (Biome-BGC), and seasonal patterns of stimulated leaf area index (LAI) (smooth lines).

and are not overly informative in terms of water use by fully developed forest stands (Norby *et al.*, 1999).

Even with a closed canopy, the ORNL sweetgum trees displayed large inter-annual variation in LAI, which was differentially affected by the CO$_2$ treatments. Year–year variation in LAI of CO$_2$-enriched plots may increase sensitivity to other site resources, suggesting that the eCO$_2$ may create transient imbalances in resources or push the stand towards thresholds in resource availability. Recent evidence from the ORNL site does indeed reveal reduced eCO$_2$ stimulation of NPP through time, attributable to reduced soil N availability that is linked to enhanced N sequestration in NPP biomass and soil pools (Norby *et al.*, 2010). Despite transient or persistent shifts in eCO$_2$: aCO$_2$ of NPP or LAI, there has not been a substantial change in the E : A transpiration rates (0·84–0·90), which is likely owing to the plasticity of stomatal response.

Roots and soil water extraction

Woody ecosystems exposed to the eCO$_2$ often increase root production and root standing crop (Table I) and shift root distribution deeper into the soil profile (Iversen, 2010), both processes that could alter water extraction dynamics. Access to deep water is important in many water-limited ecosystems, but the relationship between fine-root distribution and water uptake is not clear

and remains an important need for models (Jackson *et al.*, 2000). Root distribution was not well correlated to patterns of water extraction in several coniferous forests under drying conditions, as a minor fraction of roots at deeper depths seasonally provided the major fraction of water uptake (Warren *et al.*, 2005). Thus, knowledge of vertical patterns of water extraction across the season may be more important than knowledge of root distribution.

Quantification of water content in only the upper soil (~0–20 cm) at the five forest FACE studies thus may not necessarily reflect root water extraction dynamics as affected by CO$_2$ treatments, and may further be confounded by spatial variation in water content due to lateral water movement across the landscape (Schäfer *et al.*, 2002). Under moderate drought, there was reduced sap flow in mature deciduous trees exposed to eCO$_2$, which led to a slower decline in upper soil moisture than in aCO$_2$ plots; however, treatment differences in water content at 10 cm were not apparent during a more severe drought (Leuzinger and Körner, 2007), suggesting differences in deeper root water extraction patterns. In addition, eCO$_2$ significantly increased tree growth and sap flow in the mixed *Populus tremuloides, Betula papyrifera*, and *Acer saccharum* Aspen-FACE study, yet there was no decline, or even an increase in upper soil water content (Uddling *et al.*, 2008).
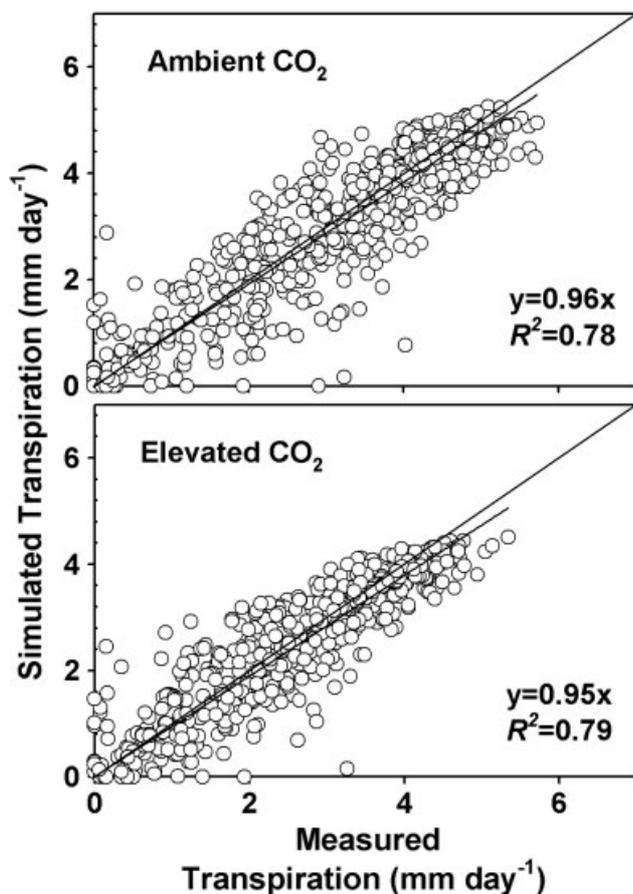
Figure 4. Canopy transpiration from ambient and elevated CO_2 plots through time as scaled from sap flow analysis (measured) and from parameterized modeling using Biome-BGC (simulated).

SOM and soil water availability

Soil water availability might also be increased by eCO_2 treatments due to the increased SOM or surface litter inputs that reduce evaporation (Schäfer *et al*., 2002; Uddling *et al*., 2008). There is an evidence for increased litter build-up in the forest floor under eCO_2 at Duke FACE (Lichter *et al*., 2005) and POP/EuroFACE (Hoosbeek and Scarascia-Mugnozza, 2009), and there is evidence for increased SOM under eCO_2 in the uppermost soil layer (0–5 cm) at ORNL FACE (Jastrow *et al*., 2005). Analyses of deeper layers (e.g. 0–15 cm) have not been able to show significant increases in SOM (Jastrow *et al*., 2005; Lichter *et al*., 2005), despite measured increases in root production and turnover at depth at these two sites (Iversen *et al*., 2008; Pritchard *et al*., 2008). If at a longer timescale, eCO_2 treatments resulted in a doubling of SOM in upper soil at the ORNL FACE, Duke FACE, or Aspen-FACE sites (e.g. 1·5–3·0% SOM), field capacity (water content at −0·033 MPa) could potentially increase by up to 12% based on equations in Rawls *et al*. (2003) using upper soil C and textural data (Dickson *et al*., 2000; Jastrow *et al*., 2005; D. Todd, unpublished; Oh and Richter, 2005). At the ORNL FACE site, eCO_2 has increased SOM in the 0–5 cm soil layer by ~10% over five years compared with aCO2 (Jastrow *et al*., 2005), correlating to ~1% increase in modelled

field capacity for this site (i.e. 0·341 and 0·345 m^3 m^{-3}, for aCO_2 and eCO_2). As SOM accumulation is relatively slow and declines with depth in the soil profile, the resulting impact on soil water retention during the course of these FACE studies is ecologically minor for forest species that rely on water extraction throughout the soil profile, although, across multi-decadal timescales, eCO_2-enhanced litter production may accelerate soil C accrual and reduce surface soil evaporation, and thus improve inherent water retention as forest soils develop, especially for previously cultivated and degraded soils low in SOM.

Simulations and model performance

Simulated LAI was up to 20% (aCO_2) to 45% (eCO_2) lower than the measured values and quite stable through time. Measured LAI was dramatically reduced during two extreme years (2004 windstorm, 2008 post-drought); however, simulated LAI was not able to model these events, resulting in simulated LAI actually much closer to measured LAI in these years (within 1% aCO_2 or 5–15% eCO_2). Even though the simulations failed to accurately model seasonal or inter-annual dynamics of LAI, they were able to predict the relative magnitudes of transpiration as affected by CO_2. These results reveal both the relative importance of LAI to the model, as well as the potential for improvement in other model processes linked to transpiration. Indeed, because of the dampened peak LAI, the model is less sensitive to LAI than other process-based models (Siqueira *et al*., 2006).

Simulated transpiration was strongly correlated to measured transpiration during the peak summer months, but overestimated in spring, and either underestimated (aCO_2) or overestimated (eCO_2) in autumn. These deviations could have significant impacts on seasonal patterns of water availability and net carbon uptake by initially accelerating seasonal water use that could induce seasonal drought earlier than might be expected. For the eCO_2 stands, this effect would be increased in autumn, potentially offsetting the benefits of eCO_2-reduced transpiration to net water balance. Failure to properly simulate timing of leaf out in the spring and senescence in the fall, and a lack of sensitivity to stress events can have a large impact on seasonal water use. Future studies should focus on these areas of uncertainty.

The C : N ratios, C and N allocation parameters, and specific leaf area were not dynamic parameters in the model, therefore the general mechanisms and dependencies causing shifts in these parameters over time are still not clear. Although the trends in these parameters appear linear over the course of this 12-year observation period, a continuation of the same trends into older developmental stages cannot be anticipated. Previous studies applying this model across forest chronosequences have concluded that the introduction of explicit age-class dynamics would improve model performance (Law *et al*., 2001, 2003),
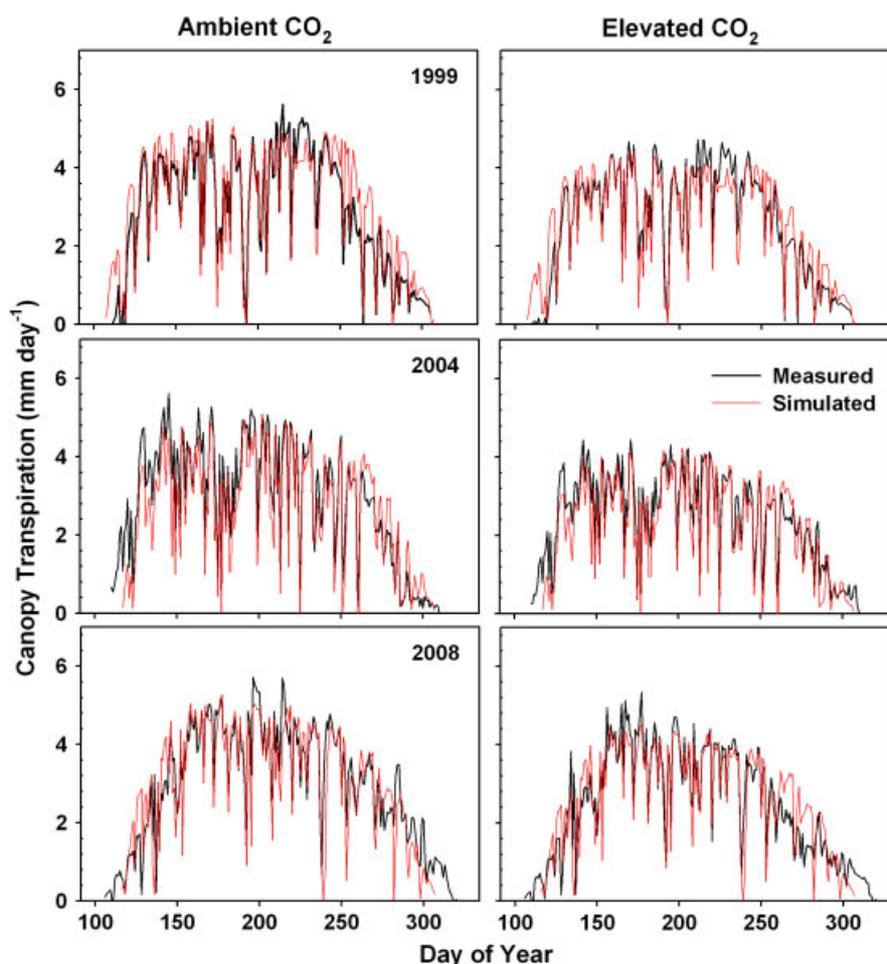
Figure 5. Comparison between measured and simulated daily canopy transpiration in a sweetgum forest plantation exposed to ambient or elevated atmospheric CO$_2$ across multiple years (1999, 2004, and 2008).
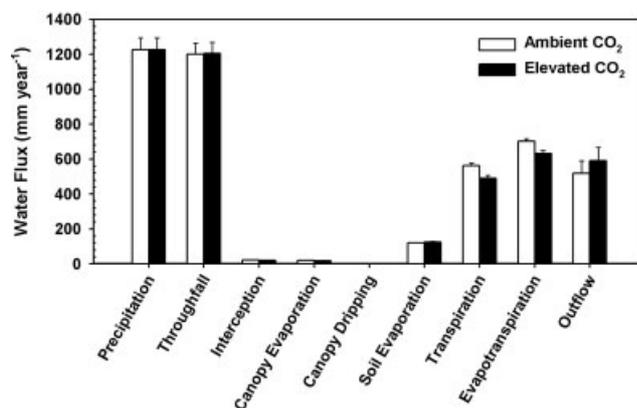

Figure 6. Simulated annual water flux components for the sweetgum forest plantation FACE plots exposed to ambient (a) or elevated (e) atmospheric CO$_2$. Values represent mean ecosystem response from 1998 to 2008 ($\pm$ s. e. across years), based on parameterization to 1999 measured values and a 10 000 year spin-up cycle.

high level, the water budget is not strongly influenced by shifts in these ecophysiological parameters.

In this regard, it should also be mentioned that additional allocation of biomass to the root system as stipulated by model parameters, and as observed for the eCO$_2$ treatment, does not provide any benefit for the simulated forest as neither nitrogen availability nor water uptake depend on the root biomass. Biome-BGC does not explicitly include root distribution within the vertical soil profile or rooting depth. Rather, the model uses the user-parameterized effective soil depth to describe total water availability from the system. The model logic is based on the assumption that tree roots will exploit the entire soil profile as necessary to provide a minimal water supply during dry periods. Maximum rooting depth is not assessed in many studies, but can be effectively modelled on the basis of potential evapotranspiration and knowledge of soil water distribution (Schenk, 2008). However, it should be kept in mind that modelling soil and rooting depth may be limited to individual species. In a mixed Douglas-fir–western hemlock forest, there is species specificity of the depth of active rooting and water extraction (Meinzer *et al.*, 2007) that would complicate model assumptions.

and our results support that finding. To assess the water budget during the ORNL FACE experiment, it was most feasible to use mean values for the measured ecophysiological parameters for two reasons. First, we were only interested in the 12 years of the experiment—a relatively short application time for the ecosystem model Biome-BGC. Second, as long as LAI remains at a reasonably

CONCLUSIONS

The measurement, modelling, and synthesis activities conducted in this study reveal that several important aspects of site water balance and ecosystem function are likely to be impacted by rising atmospheric CO_2 in the coming decades. Ecohydrological implications of ecosystem response to rising CO_2 will be site specific and temporally dynamic, dependent on stand development and successionary state. In the case of temperate deciduous forests, and barring effects of eCO_2 on LAI, reductions in canopy transpiration and stand water use due to direct effects of CO_2 on stomatal conductance will be reflected in increased soil water content and potential water yield. Our results support the expectation that large-scale regional soil and climate limitations to eCO_2 enhancement of forest productivity may lead to increased surface runoff directly through reduction in stomatal conductance (Betts *et al.*, 2007). Increased availability of water within a mixed species forest will have consequences for how individual trees and tree species respond to low soil water potentials during periods of water-deficit stress and for patterns of plant–plant competition for available water resources. To date, such observations have been beyond the scope of our experiments, although next-generation gap or biogeography models could be used to explore possible implications. Future simulations might also be extended to shifts in temperature and precipitation associated with climate change, including extreme events that are projected to increase in frequency. However, empirical multivariate studies necessary for validating and parameterizing more complex simulations (Luo *et al.*, 2008) are largely lacking, and may be difficult to assess due to interactive responses.

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