Ecohydrologic impact of reduced stomatal conductance in forests exposed to elevated CO₂*

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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 CO₂ (eCO₂). Data assessed from five free-air CO₂ enrichment (FACE) sites reveal that eCO₂-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 eCO₂-stimulation of canopy leaf area led to enhanced stand water use. In the sweetgum FACE experiment in Oak Ridge, Tennessee (USA), eCO₂ reduced seasonal transpiration by 10–16%. Intra-annual peak measured fluxes in transpiration ranged from 4–75 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 eCO₂. As a result, simulations predict ~75 mm average annual increase in potential water yield in response to eCO₂. The direct effect of eCO₂ 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 eCO₂ 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.

KEY WORDS climate change; FACE; global change; sap flow; streamflow; transpiration

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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 CO₂ 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 CO₂ enrichment, has revealed the sensitivity of several key plant processes to elevated CO₂ (eCO₂). The most prominent of these has been that the eCO₂ 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 CO₂-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 eCO₂ 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). eCO₂ can
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 CO2 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 ecophysiologic processes in forests. Research conducted over the last 12 years at the Oak Ridge National Laboratory (ORNL) free-air CO2 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 ecophysiologic responses to atmospheric CO2 enrichment are explored at the landscape scale.

**MATERIALS AND METHODS**

**Comparative CO2 enrichment studies**

Ecophysiologic impacts of woody plant response to eCO2 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 eCO2 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 CO2 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 eCO2-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 CO2 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). Ecophysiologic 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; 84°20′W).
Table I. Physiological and hydrological responses of trees and forests to atmospheric CO₂ enrichment.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Web-FACE</th>
<th>Duke</th>
<th>ORNL</th>
<th>Aspen-FACE</th>
<th>POP/EuroFACE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stomatal conductance</td>
<td>−4 to −21</td>
<td>−5</td>
<td>−14 to −44</td>
<td>0 to −44/19</td>
<td>−16 to −39</td>
</tr>
<tr>
<td>Stand water use</td>
<td>−14</td>
<td>−7</td>
<td>−13</td>
<td>+25</td>
<td>+12 to +23</td>
</tr>
<tr>
<td>Evapotranspiration</td>
<td>−10</td>
<td>na</td>
<td>−7</td>
<td>na</td>
<td>na</td>
</tr>
<tr>
<td>Runoff</td>
<td>na</td>
<td>+</td>
<td>na</td>
<td>+</td>
<td>na</td>
</tr>
<tr>
<td>Drainage</td>
<td>na</td>
<td>+</td>
<td>na</td>
<td>+</td>
<td>na</td>
</tr>
<tr>
<td>Upper soil moisture</td>
<td>0/+</td>
<td>+</td>
<td>0/+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Root production</td>
<td>na</td>
<td>+</td>
<td>na</td>
<td>0/+</td>
<td>+</td>
</tr>
<tr>
<td>Root standing crop</td>
<td>0/−</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>LAI</td>
<td>0</td>
<td>0/+</td>
<td>0/+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Species</td>
<td>Fagus sylvatica</td>
<td>Liquidambar styraciflua</td>
<td>Populus tremuloides</td>
<td>Populus x euramericana</td>
<td></td>
</tr>
<tr>
<td>Carya betulus</td>
<td>Pinus taeda</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

References


Quantitative and qualitative estimates were derived from the published literature for long-term studies where trees were exposed to ambient and ca 550 ppm CO₂ concentrations. Values represent the percentage change in a variable in response to eCO₂. 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 2.3 × 1.2 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 ~1.2–2.2 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 m² ha⁻¹ with an average height of 12 m and an average leaf area index (LAI) of 5.5 m² 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 CO₂ from the vertical PVC vent pipes located around each plot on the basis of wind speed, wind direction, and in situ measurements of current CO₂ concentration within the canopy (Hendrey et al., 1999). Since 1998, eCO₂ 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 CO₂ (aCO₂) concentration. 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 (380–400 ppm).

Mean annual temperature (1962–1993) at the study site is 13.9°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 aCO₂ and eCO₂ plots (16 trees in total). These trees were located near the centre of each plot and ranged in diameter from 12.4 to 14.7 cm in 1999 and 11.4 to 19.8 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 1.8 s and measurements were recorded every 60 min. Sap velocity was calculated from the corrected heat-pulse velocity based on Equation 3 of 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 aCO₂ and two eCO₂ treatment plots. These trees were located across each plot and ranged in diameter (DBH) from 13.2
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 237 m\(^2\) ha\(^{-1}\) in 1999 (Wullschleger and Norby, 2001), 305 m\(^2\) ha\(^{-1}\) in 2004, and 363 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\(_{\text{max}}\)–J\(_{\text{max}}\) 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\textsubscript{2} as parameterized for the ORNL FACE research facility.

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

Parameter differences between CO\textsubscript{2} treatments are in bold.

\textsuperscript{a} E. Pötzelsberger, personal assessment.

\textsuperscript{b} White et al. (2000).

\textsuperscript{c} Published data from the ORNL FACE site: http://public.ornl.gov/face/ORNL/ornl_data.shtml.

\textsuperscript{d} Wallsgreger 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\textsubscript{2} plots or three aCO\textsubscript{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 CO₂ 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 (V̇max), 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 eCO₂ 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 (gₛ) and VPD between a lower (where gₛ 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 CO₂ concentration, however, has not yet been explicitly addressed in the model. In order to account for reduced stomata aperture under eCO₂, a lower maximum value for stomatal conductance was set—equal to 0.0045 m s⁻¹ (eCO₂) as compared to 0.005 m s⁻¹ (aCO₂)—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
eCO₂ 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, eCO₂ 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 eCO₂ 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, eCO₂ increased water content in the upper 20 cm of the soil profile within the four non-irrigated FACE studies (Table I).
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 4.0–5.5 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 5.7–5.8 (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 (5.60 ± 0.04), while peak LAI for eCO$_2$ plots remained much more variable (5.85 ± 0.17). 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 CO₂ treatments.

<table>
<thead>
<tr>
<th>Year CO₂ treatment</th>
<th>Measured values</th>
<th>Canopy Transpiration (mm d⁻¹) (mm yr⁻¹)</th>
<th>E : A</th>
<th>E : A</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>May</td>
<td>June</td>
<td>July</td>
<td>August</td>
</tr>
<tr>
<td>1999 Ambient</td>
<td>3.4</td>
<td>3.7</td>
<td>3.5</td>
<td>4.4</td>
</tr>
<tr>
<td>2004 Ambient</td>
<td>2.8</td>
<td>3.4</td>
<td>3.2</td>
<td>3.9</td>
</tr>
<tr>
<td></td>
<td>3.6</td>
<td>3.6</td>
<td>3.9</td>
<td>3.5</td>
</tr>
<tr>
<td></td>
<td>3.0</td>
<td>3.2</td>
<td>3.0</td>
<td>2.3</td>
</tr>
<tr>
<td>2008 Ambient</td>
<td>2.2</td>
<td>4.3</td>
<td>4.1</td>
<td>4.0</td>
</tr>
<tr>
<td></td>
<td>2.0</td>
<td>4.0</td>
<td>3.5</td>
<td>3.4</td>
</tr>
<tr>
<td>Modeled values</td>
<td>1999 Ambient</td>
<td>3.7</td>
<td>3.7</td>
<td>3.4</td>
</tr>
<tr>
<td></td>
<td>3.1</td>
<td>3.2</td>
<td>2.9</td>
<td>3.4</td>
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<td></td>
<td>2.1</td>
<td>3.7</td>
<td>3.4</td>
<td>3.2</td>
</tr>
</tbody>
</table>

Annual fluxes include values from April to November during leaf development and leaf abscission. Transpiration ratio of eCO₂ to aCO₂ (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 eCO₂ plots ($R^2 = 0.93$, $n = 596$).

**Modelling ORNL FACE**

Simulated inter-annual LAI peaked at ~4 for eCO₂ and between ~4 and 4.5 for aCO₂. In contrast, measured maximum LAI ranged from 4 to 6 for eCO₂ and from 4 to 5.8 for aCO₂. 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% (eCO₂ and aCO₂, respectively; s. e. ± 1%) of measured transpiration. In May, 2008, the simulations overestimated transpiration by 8% (eCO₂) and 13% (aCO₂). In 2008, from September to October, the simulations underestimated transpiration for aCO₂ by 5%, and overestimated transpiration for eCO₂ 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 eCO₂ 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 eCO₂. Potential water yield was 42 and 48% (aCO₂ and eCO₂) of annual precipitation at the site. The simulated eCO₂ 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 (eCO₂–aCO₂) 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 eCO₂ can affect leaf, plant, and ecosystem water use. The ecohydrologic consequences are manifested in increased site water yield. In addition, reduced ecosystem transpiration under eCO₂ will reduce regional-scale atmospheric humidity and thereby enhance the VPD (and driving force for water loss) between...
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 H₂O 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 eCO₂ plots at ORNL FACE during extreme heat and drought events, especially for dominant trees whose measured sap flow declined by 60% relative to aCO₂ 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 eCO₂, so it is important that assessments of the effects of eCO₂ 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 eCO₂, where eCO₂ increased LAI and stand water use in the young rapidly growing plantations, while eCO₂ 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 understory vegetation (Delzon and Loustau, 2005). At the ORNL FACE site, there was little evidence for enhanced understory LAI over the course of the study across treatments; however, there was an increase in the woody biomass in eCO₂ plots, which could change soil–plant evapotranspiration due to altered understory 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 CO₂ treatments were initiated 10 years after plantation establishment. eCO₂ 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, eCO₂-stimulated canopy development and LAI at the two young rapidly growing stands at Aspen-FACE and POP/EuroFACE, suggesting that the resources other than CO₂ were not limiting, and resulted in greater stand water use in eCO₂ plots. However, such observations are confined to young stands.
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).
SOM and soil water availability

Soil water availability might also be increased by eCO₂ treatments due to the increased SOM or surface litter inputs that reduce evaporation (Schäfer et al., 2002; Uddling et al., 2008). There is evidence for increased litter build-up in the forest floor under eCO₂ at Duke FACE (Lichter et al., 2005) and POP/EuroFACE (Hoosbeek and Scarascia-Mugnozza, 2009), and there is evidence for increased SOM under eCO₂ 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, eCO₂ 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, eCO₂ 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 m³ m⁻³, for aCO₂ and eCO₂). 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, eCO₂-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% (aCO₂) to 45% (eCO₂) 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% aCO₂ or 5–15% eCO₂). 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 CO₂. 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 (aCO₂) or overestimated (eCO₂) 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 eCO₂ stands, this effect would be increased in autumn, potentially offsetting the benefits of eCO₂-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),
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 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 eCO2 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.
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 CO2 in the coming decades. Ecohydrological implications of ecosystem response to rising CO2 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 eCO2 on LAI, reductions in canopy transpiration and stand water use due to direct effects of CO2 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 eCO2 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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