

Importance of changing CO₂, temperature, precipitation, and ozone on carbon and water cycles of an upland-oak forest: incorporating experimental results into model simulations

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Abstract

Observed responses of upland-oak vegetation of the eastern deciduous hardwood forest to changing CO₂, temperature, precipitation and tropospheric ozone (O₃) were derived from field studies and interpreted with a stand-level model for an 11-year range of environmental variation upon which scenarios of future environmental change were imposed. Scenarios for the year 2100 included elevated [CO₂] and [O₃] (+ 385 ppm and + 20 ppb, respectively), warming (+ 4 °C), and increased winter precipitation (+ 20% November–March). Simulations were run with and without adjustments for experimentally observed physiological and biomass adjustments.

Initial simplistic model runs for single-factor changes in CO₂ and temperature predicted substantial increases (+ 191% or 508 g C m⁻² yr⁻¹) or decreases (–206% or –549 g C m⁻² yr⁻¹), respectively, in mean annual net ecosystem carbon exchange (NEE_a ≈ 266 ± 23 g C m⁻² yr⁻¹ from 1993 to 2003). Conversely, single-factor changes in precipitation or O₃ had comparatively small effects on NEE_a (0% and –35%, respectively). The combined influence of all four environmental changes yielded a 29% reduction in mean annual NEE_a. These results suggested that future CO₂-induced enhancements of gross photosynthesis would be largely offset by temperature-induced increases in respiration, exacerbation of water deficits, and O₃-induced reductions in photosynthesis. However, when experimentally observed physiological adjustments were included in the simulations (e.g. acclimation of leaf respiration to warming), the combined influence of the year 2100 scenario resulted in a 20% increase in NEE_a not a decrease. Consistent with the annual model's predictions, simulations with a forest succession model run for gradually changing conditions from 2000 to 2100 indicated an 11% increase in stand wood biomass in the future compared with current conditions.

These model-based analyses identify critical areas of uncertainty for multivariate predictions of future ecosystem response, and underscore the importance of long term field experiments for the evaluation of acclimation and growth under complex environmental scenarios.

Keywords: *Acer*, climatic change, evapotranspiration, net ecosystem exchange, nitrogen limitation, *Quercus*, respiration, succession

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Introduction

Increasing concentrations of atmospheric CO₂ and other trace gases including tropospheric ozone (O₃) have been observed over the past several decades. These concentrations are certain to continue to increase

in the future coincident with increasing human population and the expansion of population centers (IPCC, 1992; NAST, 2000). Increasing temperature means and changing precipitation patterns are also expected (Houghton *et al.*, 2001). All of these environmental variables have been the focus of considerable research for a wide range of ecosystems, but detailed experimental research on their combined influence in even single ecosystems has not been attempted.

Single and multifactor controlled experiments on deciduous hardwood forests or forest species of the eastern United States provide an important resource that can be used to elucidate short- and long-term effects of key variables (e.g. Samuelson *et al.*, 1996; Norby *et al.*, 1997, 2002; Melillo *et al.*, 2002; Hanson & O'Hara, 2003; Karnosky *et al.*, 2003). Such studies are conducted at point locations, and extrapolation of their results to broad regions must be done with caution. In addition, difficulties in predicting multiple interacting responses stem from potential interactions that exist between environmental factors. Such interactions can have either positive or negative effects on many of the ecosystem properties and services important to human society (Winnett, 1998; Fowler *et al.*, 1999).

Models represent the primary means by which short-term impacts of single or multiple interacting environmental drivers can be evaluated over time and across space (Winnett, 1998; Aber *et al.*, 2001; Rastetter *et al.*, 2003). Ollinger *et al.* (2002) conducted an analysis of the interacting effects of nitrogen deposition, O₃, elevated CO₂ plus land use history on northern hardwood forests in North America, and Cramer *et al.* (2001) have published a global-scale analysis of the influence of elevated CO₂ and climate change drivers. Unfortunately, predictions from such broad-scale modeling cannot be adequately tested because of a lack of experimental measurements.

This paper uses models that performed well in a multiyear simulation of current C and water budgets of an upland-oak forest (Hanson *et al.*, 2004) to evaluate the influence of single and multifactor environmental change scenarios projected for 2100. Model outputs for scenarios of altered CO₂, O₃, temperature and precipitation and their combination were executed with and without modifications to account for physiological and growth responses 'learned' from long-term field experimental studies (Winnett, 1998). Two key goals of this work were to evaluate the relative importance of the individual environmental drivers and to estimate their combined influence under future environmental change scenarios. In addition, we hoped to gain an appreciation of the magnitude of the homeostatic response of upland-oak forests by contrasting differences in model outputs for key ecosystem processes

(e.g. gross production, transpiration, respiration) predicted by simplistic model runs vs. those including estimates of experimentally derived vegetation acclimation and adjustment. The results of these simulations are evaluated against published model outputs, and the extent to which they are 'reasonable' is discussed in the context of nonmodeled, yet important, ecosystem limitations associated with nitrogen availability. Analyses and conclusions presented in this paper are specific to the composition and characteristics of the upland-oak forest type of Walker Branch watershed in Oak Ridge, TN (Johnson & Van Hook, 1989), but they should be applicable to analogous oak forests with deep soils located in the eastern United States.

Methods

The Walker Branch upland-oak forest

The Walker Branch watershed (35°57'N; 84°17'W; 250–330 m elevation) is located on the US Department of Energy's National Environmental Research Park in Oak Ridge, TN (Johnson & Van Hook, 1989). Long-term (50 years) mean annual precipitation was 1352 mm and mean annual temperature is 14.2 °C. The acidic forest soils (pH 3.5–4.6) are primarily typic Paleudults. Plant extractable water (water held between 0 and –2.5 MPa) for the upper meter of soil is approximately 183 mm. A large fraction of this water (44%) is held in the upper 0.35 m of the soil profile. This surface layer is the location of 60% of all fine roots in the 0–0.90 m soil profile (Joslin & Wolfe, 1998). Depth to bedrock is approximately 30 m and deep rooting may be a source of some water. Walker Branch is a good example of oak-dominated forests occupying approximately 617 000 km² or 42% of the total forested area in the eastern United States (Powell *et al.*, 1992) which are important to society as a source of forest products, recreational opportunities, and clean water (Hanson & O'Hara, 2003).

Environmental change scenarios

The Intergovernmental Panel on Climate Change's (IPCC) Third Assessment report on climate change science (Houghton *et al.*, 2001) and the United States' National Assessment Synthesis Team's report on climate-change impacts (NAST, 2000) provide the basis for the year 2100 scenarios of increasing atmospheric CO₂, temperature, precipitation and O₃ change scenarios evaluated in this paper (Table 1).

Projections for [CO₂] follow the IS92a emission scenario (IPCC, 1992) and yield a value of ~760 ppm by 2100. This represents an increase of +385 ppm since 2000 when contrasted with typical ground level [CO₂]

Table 1 Scenarios for future environmental conditions impacting upland oak eastern forests 50–100 years from today using the Walker Branch forest as a typical example

Variable	Change relative to 2000
Atmospheric CO ₂	+ 385 $\mu\text{mol mol}^{-1}$ = approximately 760 ppm
Temperature	+ 4 °C
Precipitation	+ 20% winter, 0% summer
Ground-level O ₃	+ 20 ppb growing season

for the eastern United States. Available data from free-air CO₂ enrichment (FACE) and open-top chamber studies do not typically provide experimental results for such high [CO₂]. Therefore, extrapolations of responses from intermediate [CO₂]-exposure experiments to simulations for 760 ppm [CO₂] were required as described below.

IPCC estimates for global temperature increases range from 0.9 to 4.5 °C, but the eastern United States is expected to exhibit greater-than-average warming (Houghton *et al.*, 2001; Johns *et al.*, 2003; Dai *et al.*, 2004). This paper uses a warming scenario of +4 °C that is within the likely range for the southeastern United States, and is also a good match to ongoing or completed experimental manipulations. Decreases in the diurnal temperature range (i.e. asymmetric warming) have been observed in the climate record and are predicted outputs from current climate models (Dai *et al.*, 2001; Houghton *et al.*, 2001), but the magnitude of such change is small (−0.2 to −0.5 °C per century Dai *et al.*, 2001; Stone & Weaver, 2002) and is therefore not simulated here.

Estimates of changing precipitation patterns in the eastern United States cover a broad range from decreases to increases (NAST, 2000). For this paper, the IPCC scenarios for eastern North America showed small increases in winter rainfall (+20% from November to March), and no change in summer precipitation. This does not imply that future climates will have no variation in summer drought, however, as temperature increases by themselves will drive additional soil water deficits.

IPCC scenarios for increasing future O₃ concentrations are highly uncertain because of the regional nature of precursor emissions and the potential influence of alternate future climates (Prather *et al.*, 2001). They also contrast with the recent national patterns observed from the United States Environmental Protection Agency air trends analysis that show declining O₃ from 1980 to 2003 coincident with reductions in NO_x and volatile organic carbon emissions over that time period (<http://www.epa.gov/>

[airtrends/ozone.html](#)). Nevertheless, to evaluate the relative impact of possible future O₃ increases coincident with changes in other environmental variables, this paper assumes a mean 20 ppb increase in O₃ in the eastern United States driven largely by increases in anticipated anthropogenic O₃ precursors (Stevenson *et al.*, 1998; Fowler *et al.*, 1999; Prather *et al.*, 2003).

Alternative choices for expected changes in [CO₂], temperature, precipitation, and [O₃] could have been justified for this analysis, but those listed in Table 1 are based on published IPCC expectations, and represent levels of change that experimentation has shown would have significant impacts on forest tree physiology or growth. Changes in atmospheric element deposition (e.g. nitrogen, sulfur, base cations) were not included as a primary variable in this analysis, but the potential for ecosystem element inputs (e.g. N) to limit predicted responses is discussed. The importance of insect infestations, wind damage, fire, ice storms, and invasive species are acknowledged as important variables associated with future environmental change, but are beyond the scope of this paper.

Experimental observations

Observations of short- and long-term plant responses to elevated CO₂, precipitation change, warming, and O₃ were derived primarily from field experimental studies on deciduous trees and forest systems. This paper focuses on data for species common to Walker Branch, but experimental results from other species or forest types were included as necessary to provide complete information in support of the model evaluations. Key conclusions from available experiments on single or multifactor manipulations of deciduous forests species or stands are summarized for organ-level physiological responses in Table 2 and for plant or ecosystem-level responses in Table 3, and justified in the following sections.

Elevated CO₂. Tree responses to elevated CO₂ were derived from observations in a FACE experiment in a sweetgum (*Liquidambar styraciflua* L.) plantation approximately 12 km from the Walker Branch watershed (Norby *et al.*, 2002). During 6 years of exposure to elevated CO₂ (~550 ppm) this closed-canopy forest stand has exhibited higher rates of photosynthesis and increased net primary production (NPP) compared with current-condition controls. The additional C assimilated by these trees is allocated primarily to fine root production (Norby *et al.*, 2004), and to small increases in wood production. However, these latter effects were not statistically significant. Foliar and litter N concentrations are lower in elevated

Table 2 Experimentally observed acclimation or adjustment of plant physiological and plant organ responses

Physiological response variables	Environmental variable		
	CO ₂ (+ 385 ppm)	Temperature (+ 4 °C)	Precipitation (+ 20% November–March)
Photosynthesis ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Increases consistent with the Farquhar model at $[\text{CO}_2] = 385$ is + 83%	Possible acclimation of Farquhar temperature functions	Reduced proportionate with cumulative uptake approximately –5% annually
Stomatal conductance ($\text{mmol m}^{-2} \text{s}^{-1}$)	Decreased Ball–Berry slope reduced by 9%	Ball–Berry predictions	Reductions with cumulative uptake
Leaf mass/area (LMA; g m^{-2})	Increased 9%	No change	No change
Leaves – upper canopy	Reduced 2%	No change	No change
Leaves – middle canopy	Increased 7%	No change	No change
Leaves – lower canopy			
Organ [N] (g g^{-1})			
Leaves – upper canopy	Reduced 15%	No change	No change
Leaves – middle canopy	Reduced 13%	No change	No change
Leaves – lower canopy	Reduced 10 %	No change	No change
Wood	No change	No change	No change
Fine roots	No change	No change	No change
Maintenance respiration			
Leaf ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	No direct effect	Base rate –33% at 0 °C	No change
Wood ($\mu\text{mol m}^{-3} \text{s}^{-1}$)	Base rate + 17% at 0 °C	No change	No change
Fine root ($\mu\text{mol g}^{-1} \text{s}^{-1}$)	No direct effect	No change	No change
Respiration Q_{10}	No change	No change	No change
Growth respiration ($\text{g C g dry matter}^{-1}$)	f [tissue chemistry]	f [tissue chemistry]	f [tissue chemistry]

CO₂, but total N uptake is higher (Johnson *et al.*, 2004). Total leaf mass production is higher, but leaf area index (LAI) has not been affected (Norby *et al.*, 2003). The responses of *L. styraciflua* are qualitatively similar to those observed in previous experiments with *Quercus alba* L. and *Liriodendron tulipifera* L. seedlings and saplings (Norby *et al.*, 1999). All those species are appropriate for application to simulations of the Walker Branch forest, and the FACE experiment with sweetgum provides longer-term data for a closed-canopy forest in which the trees are in a linear growth phase. LAI and NPP of the sweetgum stand are similar to that of the upland-oak forest on the Walker Branch watershed, although stand structure is different.

Photosynthetic enhancement in elevated CO₂, which averaged 46% in the upper canopy for a 200 ppm increase, has shown no indication of downregulation after long-term exposure to elevated CO₂, despite lower foliar N concentration (Gunderson *et al.*, 2002; Sholtis *et al.*, 2004). For the calculated intercomparisons in this paper the Farquhar model of photosynthesis (Farquhar *et al.*, 1980; Farquhar & von Caemmerer, 1982) was assumed to provide an adequate characterization of the short-term response of leaves to atmospheric CO₂ predicting an 80–90% increase in light-saturated assimilation at 760 ppm CO₂. Long-term changes in assimilation were driven by changes in leaf nitrogen concentration and leaf mass per unit area. Reductions in stomatal conductance, as observed for sweetgum and other hardwoods (Gunderson *et al.*, 1993; Gunderson *et al.*, 2002), are appropriately predicted by the Ball-Berry model (Ball *et al.*, 1987) modified based on experimental data with a slightly reduced slope (Gunderson *et al.*, 2002).

Foliar respiration rates in the sweetgum stand were the same in current and elevated CO₂ (Amthor, 2000; Tissue *et al.*, 2002). Total annual wood respiration was 50.4% higher (DeLucia *et al.*, 2005) based on 21.9% higher growth respiration and 48.1% higher volume-specific maintenance respiration (equivalent to a 17% increase in maintenance respiration at 0 °C; Edwards *et al.*, 2002). Specific respiration of fine roots was not affected by CO₂ enrichment (George *et al.*, 2003), but observed enhancements of soil respiration resulting from long-term CO₂ exposures (King *et al.*, 2004) were expected to result from changing root biomass and soil labile carbon pools.

NPP increased 22% in response to 6 years of CO₂ enrichment, with no indication of a decline in response over those years (Norby *et al.*, 2002, 2004). This rate of NPP increase is consistent with the mean response for forests reported by Nowak *et al.* (2004). Extrapolating responses at 550 ppm CO₂ to the 760 ppm level for 2100 required us to exceed the available experimental data. It

is unlikely that the response above 550 ppm is linear or that it has already saturated. Therefore, the β function (Amthor & Koch, 1995) was used to provide an appropriate translation from 550 to 760 as follows:

$$P_e/P_a = 1 + \beta \ln(C_e/C_a), \quad (1)$$

where P_a and P_e are NPP in current and elevated CO₂ and C_a and C_e are the respective CO₂ concentrations. The 22% increase in NPP in the FACE experiment corresponded to a β of 0.55, which yields a 40% increase in total NPP at 760 ppm CO₂. Based on organ-specific β responses observed in the FACE experiment at 550 ppm, analogous increases for 760 ppm would yield a 14% increase in leaf mass production, 17.1% increase in woody stem plus coarse root increment, and 282% increase in fine root production. At 550 ppm the large increase in fine root production was associated with an equivalent increase in fine root mortality but no difference in turnover rate (Norby *et al.*, 2004), and we make the same assumption for the 760 ppm simulations presented here. Seasonal differences in root production and mortality do result in significant increases in fine root standing crop in midsummer, which is captured in these model simulations by the balance observed between patterns of root production and mortality. Although Norby *et al.* (2004) reported that elevated CO₂ had increased root distribution with depth, such a dramatic response is not expected for the simulated upland-oak forest discussed in this paper where high bulk density and limited nutrient supplies in deep soils would probably preclude such a response.

Studies addressing the response of deciduous forests to elevated CO₂ at ~ 550 ppm show modest changes in stomatal conductance, small reductions in canopy transpiration, and no change in LAI (Wullschlegel & Norby, 2001; Gunderson *et al.*, 2002; Wullschlegel *et al.*, 2002). Elevated CO₂ treatments have produced no significant change in canopy phenology (Norby *et al.*, 2003).

Warming. Tree responses to warming were derived primarily from observations of two multiyear open-top chamber experiments using assemblages of saplings within temperature-controlled chambers at a field site within 15 km of the Walker Branch watershed. The first experiment with red maple (*Acer rubrum* L.) and sugar maple (*A. saccharum* Marsh.) combined current condition and warming (+4 °C) treatments with elevated CO₂ (Norby & Luo, 2004). The second, ongoing experiment exposed sweetgum, northern red oak (*Q. rubra* L.), yellow birch (*Betula allegheniensis* Britton), and big-tooth aspen (*Populus grandidentata* Michx.) to three temperature treatments (+0, +2 and +4 °C). The first two species are common to

Walker Branch watershed, whereas birch and aspen were chosen to represent trees from more northerly, cooler climates.

Photosynthesis and stomatal conductance in maples were reduced by atmospheric warming (and the concurrent changes in water balance), except during the cooler months of spring and early autumn (Gunderson *et al.*, 2000). Responses in the ongoing study are similar, despite observed shifts in the temperature optima for photosynthesis.

After 4 years of experimental warming manipulations, aboveground woody biomass was 35% lower in the warmed chambers (only 9% lower in combination with elevated CO₂). Annual growth increment, however, was reduced by elevated temperatures only in the second year, when an unusually hot summer depressed relative growth rate (Norby & Luo, 2004). Although estimated from integrated multiyear observations on developing saplings in eastern Tennessee, the 'expected' effects of warming on growth of mature forest trees (Table 3) contains a fair amount of uncertainty. To make the sapling growth observations appropriate for simulations of large forest trees, the 4-year growth responses were normalized to constant leaf area (Norby, 1996) and scaled accordingly.

Temperature responses of photosynthesis and respiration are incorporated into many models, but there remains substantial uncertainty as to the degree and nature of acclimation under field conditions (Berry & Björkman, 1980; Atkin & Tjoelker, 2003; Bernacchi *et al.*, 2003). Observations of sugar and red maple, sweetgum, northern red oak, yellow birch, and big-tooth aspen, have repeatedly demonstrated temperature acclimation of both foliar respiration and photosynthesis (Gunderson *et al.*, 2000; C. A. Gunderson, unpublished data). For example, respiration at the reference temperature of 0 °C, averaged 33% lower in leaves for the +4 °C treatment plants. Rates observed for the +2 °C treatments were intermediate between the other treatments. Changes in Q_{10} have been small and are not included in these simulations. For comparison with current conditions, base respiration rates at 0 °C were simulated to be reduced by 33% to account for temperature acclimation. A constantly changing base rate adjustment driven by a running mean temperature would be a more accurate way to model temperature acclimation, but appropriate integration times for such acclimation have not been determined. Dewar *et al.* (1999) proposed feedback controls on respiration based on carbohydrate supplies that might be used in a predictive model of temperature-induced acclimation. Photosynthetic acclimation has been observed consistently in lab and field-grown trees as a shift of temperature optimum toward the prevailing tempera-

tures. Incorporating these observations into mechanistic models using the Farquhar & von Caemmerer (1982) parameters for temperature responsiveness (e.g. Bernacchi *et al.*, 2001, 2003) is not straightforward, however, and no change in the model functioning has been proposed at this time. Reports of changes in leaf nitrogen and carbohydrate status have been reported in warming experiments, but at present the results are too inconsistent to warrant modifying the model parameterization for the current simulations.

Increasing air temperature also drives changes in forest water use in keeping with known relationships between transpiration and vapor pressure deficit (Wullschleger *et al.*, 2000) and temperature effects on leaf area phenology (Table 3).

Experimental manipulations, ground-based observations of natural phenomena, and global satellite imaging all indicate that warmer temperatures will change the timing of bud release, flowering, and leaf senescence, lengthening the growing season and potentially increasing NPP (Sparks & Menzel, 2002; White *et al.*, 2002; White & Nemani, 2003; Zhao & Schwartz, 2003). In the 4-year maple experiment of Norby *et al.* (2003), bud expansion was usually advanced by 4–12 days with a 4 °C warming. In the ongoing warming experiment with multiple tree species, budbreak and leaf emergence have been accelerated in all species by 4–16 days with a +4 °C elevation (C. A. Gunderson, unpublished data). Autumnal senescence under current conditions is typically considered to be a function of photoperiod (White *et al.*, 1997). However, warming from urban heat islands (Zhang *et al.*, 2004) and observations from temperature manipulations (Norby *et al.*, 2000, 2003; C. A. Gunderson, unpublished data) have consistently shown delayed leaf chlorophyll loss and abscission by anywhere from 2 to 23 days for a +4 °C increase in temperature. Combining early bud break with delayed leaf senescence, growing seasons in warming experiments for trees have been extended by as much as 15–40 days. An 8-day spring advance and a 15-day fall extension are simulated in this paper (Table 3).

Precipitation change. Results for upland-oak forest responses to increasing precipitation are derived from the multiyear Walker Branch Throughfall Displacement Experiment (TDE; Hanson *et al.*, 1998, 2003c). In that study, interannual variations in precipitation were shown to lead to the development of severe late-season drought in some years (Hanson *et al.*, 2003c) leading to reduced foliar assimilation, conductance (Wilson & Hanson, 2003) and stand-level water use (Wullschleger *et al.*, 2003b). Consistent with field observations on the TDE (Wilson & Hanson, 2003)

and more detailed laboratory characterizations of other species (Bota *et al.*, 2004) water deficits were assumed to have their primary effect through reductions in stomatal conductance. Reductions in assimilation were thus primarily associated with reductions in leaf internal [CO₂]. Altered Rubisco activity and RuBP content associated with changes in the parameter settings for V_{cmax} in the Farquhar model were assumed to develop only for severe drought conditions (e.g. plant water potential less than -1.5 MPa). This assumption would need to be reassessed for other species and ecosystems.

Chronic precipitation increases did not result in significant or sustained changes in leaf, stem, or soil respiration (Edwards & Hanson, 2003; Hanson *et al.*, 2003b; Wilson & Hanson, 2003), and thus no changes were modeled with respect to the precipitation scenario.

Contrary to strong physiological responses to late-season drought, the TDE study demonstrated a general insensitivity of tree growth responses to chronic 33% increases or 33% decreases in throughfall inputs from 1993 to 2000. The insensitivity is the result of a disconnect between the occurrence of growth in the early summer and soil water deficits late in the growing season (Hanson *et al.*, 2001, 2003e). Seedling and sapling mortality was, however, shown to decrease for increasing precipitation scenarios (Hanson *et al.*, 2001, 2003e). Nevertheless, the overall impact of increased seedling/sapling survival on standing biomass was small and adjustments to the live respiration biomass were not included in the current simulations for precipitation change (i.e. no biomass change in Table 3).

Long-term changes in element cycling have been hypothesized to result from chronic acid leaching of the Walker Branch forest (Johnson & Todd, 1990; Johnson *et al.*, 2000) and such changes might be exacerbated by a 20% increase in winter precipitation. Measured changes in soil solution chemistry on the TDE site from 1993 to 2000 (Johnson *et al.*, 2002, 2003) demonstrated significant changes in leachable elements, but the impact of those chronic treatments has yet to be translated to significant changes in growth or canopy function. Although a scenario of altered nutrient cycling in the year 2100 model scenarios has not been included, the impact of potential changes in element cycles on the results is developed further in the discussion.

Elevated O₃. While some crop and tree species are known to be highly sensitive to O₃ exposure (Davidson & Barnes, 1998; Isebrands *et al.*, 2001; Karnosky, 2003; Morgan *et al.*, 2003), the majority of the tree species found on Walker Branch Watershed do not show significant growth responses to incremental increases

in O₃ exposure (Chappelka & Samuelson, 1998). Reductions in foliar assimilation and conductance are, nonetheless, commonly observed as a function of cumulative O₃ exposures (Kolb & Matyssek, 2001; Samuelson & Kelly, 2001). For this paper, the foliar responses of northern red oak to internal O₃ uptake observed by Hanson *et al.* (1994) were used to drive reductions in foliar assimilation and conductance response. No effect of O₃ on leaf or other organ respiration was simulated (Wullschlegel *et al.*, 1996). Indirect responses of O₃ on canopy transpiration resulted from modeled reductions in assimilation and stomatal conductance.

Samuelson *et al.* (1996) found no change in lower or midcanopy stem growth or leaf production after 3 years of exposure of large northern red oak trees to twice current O₃ exposures (a higher O₃ exposure than the +20 ppb O₃ scenario considered here). In the same study, Kelting *et al.* (1995) found a 33% reduction in mature tree fine-root production and a 42% reduction in turnover. However, because our simulated year 2100 O₃ scenario is lower than the twice-current-concentration exposures used by Kelting *et al.* (1995), and because Topa *et al.* (2004) have concluded that O₃ does not have a direct effect on carbon transport processes, the simulations assume no effect of O₃ on belowground production and root turnover (Table 3). This paper only assumes insignificant O₃-induced growth effects for the upland-oak forest and the specific scenarios discussed here. Simulations for other species might appropriately assume significant growth reductions in response to O₃ exposures for alternate scenarios and growth conditions.

Combined effects. Growth responses for the combined effects of CO₂ and temperature treatments have been observed in some experimental studies as described above, but insufficient data are available to provide unambiguous assessments of multiple treatment effects in long-term simulations. Norby & Luo (2004) reported limited statistical interactions (i.e. nonadditive effects) between [CO₂] and temperature for a 4-year experiment with *A. saccharum* and *A. rubrum*. To facilitate the modeling of multifactor responses in this paper, fractional growth response to individual factors were multiplied together to yield a response for the combined scenarios of future environmental change. For example, for the future scenario including [CO₂] of +385 ppm and temperature of +4 °C, observed wood growth increases under elevated CO₂ (+13%) were multiplied by decreases at elevated temperatures (−17%) to yield a combined result of −6% (i.e. $1.13 \times 0.83 = 0.94$). Individual and combined responses to CO₂ and O₃ treatments reported by Isebrands *et al.* (2001) also support this approach.

Modeling single-variable and integrated responses

The relative importance of future changes in atmospheric CO₂, O₃, temperature, precipitation, and their combined effect on key ecosystem carbon and water cycling processes were evaluated with a stand-level model appropriate for hourly, daily and annual integration of carbon and water cycle fluxes of the Walker Branch watershed (INTRASTAND; Hanson *et al.*, 2004). The model was used to run single-factor simulations for each environmental variable and multi-factor runs representing current conditions and the 2100 climate scenarios from Table 1 including:

1. Elevated CO₂: + 385 ppm,
2. temperature increases: + 4 °C,
3. increased winter precipitation: + 20% from November to March,
4. increased O₃: + 20 ppb, and
5. the combined response to all four changes.

Carbon cycle model predictions discussed in this paper include net ecosystem exchange of carbon for daily or annual time steps (NEE_d or NEE_a), and some of the components of NEE including: gross primary production (GPP), canopy leaf respiration (R_{leaf}), and soil respiration (R_{soil}). Water cycle outputs to be discussed include transpiration (T) and soil drainage.

Outputs from INTRASTAND, along with relevant assumptions from Tables 2 and 3 and the climate scenarios outlined above, were also used to execute multiyear simulations using the individual-based model of forest succession LINKAGES (Pastor & Post, 1988). This model incorporates ecosystem functions of soil-water balance, litter return and decomposition along with nitrogen dynamics, and the effect of these factors on tree establishment and growth. Because stand dynamics are so strongly coupled with the forest water, carbon, and nitrogen cycles, LINKAGES is well suited for the study of long-term forest responses to environmental change, where feedbacks because of plant competition and constraints imposed by interactions between the C and N cycles may be important in determining the productivity and species composition of future forests.

INTRASTAND

INTRASTAND is an hourly time step model designed for use in the interpolation of measured physiological data over time for the calculation of daily and intra-annual forest stand carbon and water budgets. The model structure contains three canopy foliage layers, branch and bole stem components, four soil layers, and stem capacitance. By design, the structural detail is

limited so as not to exceed the availability of measured input data. Carbon uptake is based on the coupled Farquhar/Ball-Berry photosynthetic and stomatal conductance model as described by Harley *et al.* (1992) and parameterized according to data in Harley & Baldocchi (1995) and Wilson *et al.* (2001). The model used in this paper includes an improved $V_{\text{cmax}}/J_{\text{max}}$ relationship (Leuning, 1997) and adjusted temperature coefficients as recommended by Bernacchi *et al.* (2001, 2003). A modified version of the water budget model PROSPER (Huff *et al.*, 1977) is used with the inclusion of a stem capacitance. Stem respiration is modeled based on Edwards & Hanson (1996), and a model of forest floor CO₂ efflux follows Hanson *et al.* (1993, 2003b).

The canopy is divided into three layers of equal LAI, and diffuse and direct light penetration is calculated as suggested by Norman (1982). The modeled canopy net foliar assimilation rates were calibrated to yield maximum assimilation in early June following full leaf expansion in accordance with reported values for the upland-oak forest on Walker Branch watershed (Verma *et al.*, 1986; Harley & Baldocchi, 1995; Baldocchi & Vogel, 1996; Baldocchi, 1997). Isoprene emission was also estimated for this stand (a small component of carbon flux) based on the observations and models of Harley *et al.* (1997). Respiratory costs of growing plant structures were calculated by a modified Penning de Vries approach as outlined by Amthor (1996). The model is coded using 'Stella' modeling software (ISEE systems Inc., Lebanon, NH, USA). Published results for the water budget and carbon flux components can be found in Edwards & Hanson (1996), Hanson *et al.* (1998, 2001, 2003a,b, 2004), and Johnson *et al.* (2002). A hypersensitive response to drought stress noted for INTRASTAND in Hanson *et al.* (2004) was corrected for the simulations in this paper.

Climate variables used for these studies were measured as a part of the Walker Branch TDE (Hanson *et al.*, 2003c) from 1993 to 2003 including: canopy air temperature and relative humidity, soil temperature, incident photosynthetically active radiation, above-canopy wind speed, and rainfall. Mean annual [CO₂] data were observed to follow the northern hemisphere averages reported in the Carbon Dioxide Information Analysis Center's (CDIAC) TRENDS archive (<http://cdiac.esd.ornl.gov/trends/trends.htm>). Intra-annual and diurnal patterns of [CO₂] were not ignored. A 4-year record of measured [CO₂] was averaged to yield seasonal and diel patterns of [CO₂]. The mean hourly pattern of annual [CO₂] was converted to a multiplier ranging from 0.85 to 1.25 for application to the mean annual [CO₂] data from CDIAC. Hourly [O₃] specific to the local region from 1993 to 2003 were obtained from the Environmental Protection Agency's Aerometric

Information Retrieval System for the Freels Bend location near Oak Ridge, Tennessee (<http://www.epa.gov/ttnairs1/index.html>).

The INTRASTAND model was developed for application to intra-annual carbon and water budgeting (Hanson *et al.*, 2004) but has been used here over a multiyear period assuming that plant biomass and carbon pools approximate current or future steady-state conditions. Growth of stems, roots, and leaves, the timing of leaf out and leaf senescence, and required physiological variables for the current condition are inputs from direct measurements on the study site for the period from 1993 to 2003. Simulated changes in the amount of growth of stems and roots (Table 3) are assumed to follow the observed seasonal phenology for current conditions on Walker Branch watershed (Hanson *et al.*, 2003d; Joslin & Wolfe, 2003). The amount of leaf growth is distributed under the observed current growth phenology or an expanded phenology when temperature increases are simulated to produce an elongation of the growing season.

Assimilates in excess of growth and respiration demands accumulate in a total nonstructural carbohydrate (TNC) pool representing the combined soluble sugar and starch reserves of the live plant biomass. The modeled TNC pool capacity is not tied to a specific organ type or volume, and there is no intra- or interannual feedback on growth rates or physiological processes from the TNC pool. While a limit on TNC storage based on available plant volume would be a logical addition to the INTRASTAND model for the simulation of physiological feedbacks, it has not been included for lack of direct experimental evidence. A benefit of this approach is that the model simulations are not confounded with the experimental observations (Tables 2 and 3) that we are trying to evaluate.

LINKAGES v2.2

LINKAGES v2.2 (Wullschleger *et al.*, 2003a; Hanson *et al.*, 2004) is derived from LINKAGES (Pastor & Post, 1985, 1988) to study the effects of climatic change on long-term forest dynamics. Unlike the original version of the model, which simulated soil and plant-based components of the water cycle on a monthly time-step, soil and plant water relations in LINKAGES v2.2 are modeled daily assuming a single big-leaf canopy and a multilayered soil. Soil evaporation and canopy transpiration are treated separately (Shuttleworth & Wallace, 1985; Federer, 1995). The decomposition and nitrogen dynamics are similar to those in the FORTNITE model (Aber & Melillo, 1982). LINKAGES simulates a range of plant and ecosystem dynamics by considering interactions between physiological

processes and individual tree growth, demographic processes and tree-population dynamics, microbial processes and nitrogen availability, and the roles played by climate and soils as they combine to influence site water balance (Shugart *et al.*, 1992).

A maximum stomatal conductance is specified for the stand and transpiration is modeled based on the response of stomatal conductance to radiation, temperature, vapor pressure deficit, and extractable soil water. Interception losses are determined from leaf area and stem area index. The bucket model of soil water extraction in LINKAGES, which was predicted on the basis of a single soil layer, was replaced with an approach that used multiple soil layers and a scheme that extracted water for transpiration from each soil layer as modified by the relative distribution of roots within the soil profile (Wullschleger *et al.*, 2003a). Fractional drought days are calculated according to the time of year that soil water deficits occurred. In addition, rather than allow seedlings, saplings, and mature trees to have equal access to all soil layers, and thus to all extractable soil water, roots were restricted to specific soil layers based on whether plants were designated seedlings, saplings, or mature trees. Seedlings occupied the soil layers from 0 to 50 cm, saplings occupied soil layers from 0 to 70 cm soil layers, and mature trees occupied the entire soil profile. The number of drought days for each size class was estimated separately and, as a result, the model mimicked the differential susceptibility of seedlings, saplings, and mature trees to drought. Other modifications included replacing the parabolic dependency of diameter growth on growing degree days in LINKAGES with an asymptotic function. Such a change mimicked the lower portion of the temperature-response function, but did not impose a growth reduction at higher temperatures (Talkkari *et al.*, 1999; Bugmann & Solomon, 2000). Furthermore, canopy leaf area development was made a function of air temperature, allowing for year-to-year variation in stand phenology.

An environmental data set was compiled from 28 years (1973 to 2000) of weather data collected on or near Walker Branch watershed. Hourly data were available for radiation, air temperature, precipitation, relative humidity, and wind speed. Daily averages were derived from these data. Long-term simulations (i.e. 200 years) were accomplished by running the model using repeated cycles of the 28-year climate data set. Simulations were run from bare ground for 100 years, at which time climate change scenarios were imposed. Increases in air temperature (+4°C) and winter precipitation (+20%) were changed in a linear fashion over a second 100-year period. The CO₂ concentrations

were increased gradually starting in 2000 to attain 760 ppm by 2100. Direct effects of elevated CO₂ on the growth of individual trees in LINKAGES v2.2 were simulated by altering diameter increment (i.e. variable DINC) each year so as to achieve a +17% difference in stand-level NPP (wood only) for the 760 ppm [CO₂] at the end of the simulation. Canopy conductance was incrementally reduced during each year of the simulation in order to match a 12% reduction in canopy conductance because of elevated CO₂ as predicted by the physiology-based model INTRASTAND. Total stand biomass and species composition are reported for the average of 200 model plot simulations.

Results

Simple environmental simulations

The mean annual pattern of cumulative NEE and *T* for current conditions (1993–2003) and for the single-environmental factor changes proposed for 2100 are plotted in Fig. 1 along with a prediction of the combined simple response. NEE_a values show carbon loss until leaf emergence around day 115 followed by carbon gain throughout the growing season until the return to carbon loss following complete leaf senescence (~ day 330 in Fig. 1a). Transpiration was initiated around day 115 followed by consistent increases until canopy senescence (Fig. 1b).

Current conditions from 1993 to 2003 yielded a mean annual cumulative NEE_a value of $266 \pm 23 \text{ g C m}^{-2} \text{ yr}^{-1}$ where the standard error term represents interannual variation in weather. The elevated CO₂ and temperature scenarios produced nearly opposite effects with respect to NEE_a at current conditions. The elevated CO₂ scenario resulted in a 191% increase in carbon accumulation ($774 \pm 29 \text{ g C m}^{-2} \text{ yr}^{-1}$), expressed in the model as a high (and probably unreasonable) accumulation of the nonstructural carbohydrate pool (data not shown). The temperature scenario led to a 206% decrease in NEE_a ($-283 \pm 29 \text{ g C m}^{-2} \text{ yr}^{-1}$). The scenario of increased winter precipitation had no effect on NEE_a, but increased O₃ yielded a 35% loss of carbon gain with respect to the current conditions ($174 \pm 21 \text{ g C m}^{-2} \text{ yr}^{-1}$). When modeled simultaneously, the combined impact of all four treatments produced a 29% reduction in NEE_a ($188 \pm 31 \text{ g C m}^{-2} \text{ yr}^{-1}$).

Current conditions yielded a mean annual cumulative *T*_a of $441 \pm 7 \text{ mm yr}^{-1}$ where the standard error term represents interannual variations in weather for the 1993 to 2003 time sequence. The elevated CO₂ and temperature scenarios produced nearly opposite effects with respect to *T*_a at current conditions. The elevated CO₂ scenario resulted in a 20% decrease in water use

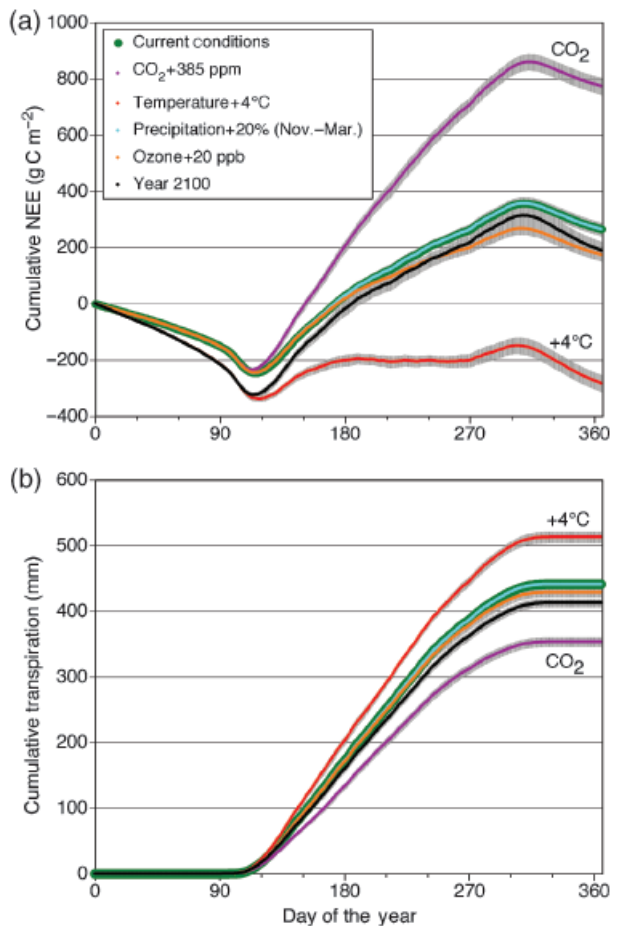


Fig. 1 Mean (\pm SE) of the cumulative annual net ecosystem exchange of carbon (top graph) and transpiration (bottom graph) from 1993 to 2003 based on current physiological characteristics, biomass distribution, and litter/soil carbon pools. Simulations are provided for the current conditions (1993–2003) and for year 2100 climate scenarios as described in Table 1.

($353 \pm 7 \text{ mm yr}^{-1}$) similar to observed FACE data, and the temperature scenario a 16% increase ($513 \pm 8 \text{ mm yr}^{-1}$). Consistent with the results for NEE_a, the scenario of increased winter precipitation had no effect on water use. Increased O₃ yielded a modest 3% reduction in water use ($429 \pm 6 \text{ mm yr}^{-1}$) with respect to current conditions. When modeled simultaneously, the simple combination of all four treatments produced a 6% reduction in *T*_a ($413 \pm 6 \text{ mm yr}^{-1}$).

Model simulations including physiological and biomass adjustments

Figures 2–4 show the interannual range of annual carbon and water cycle components in box-and-whisker plots for all of the simple single-factor and

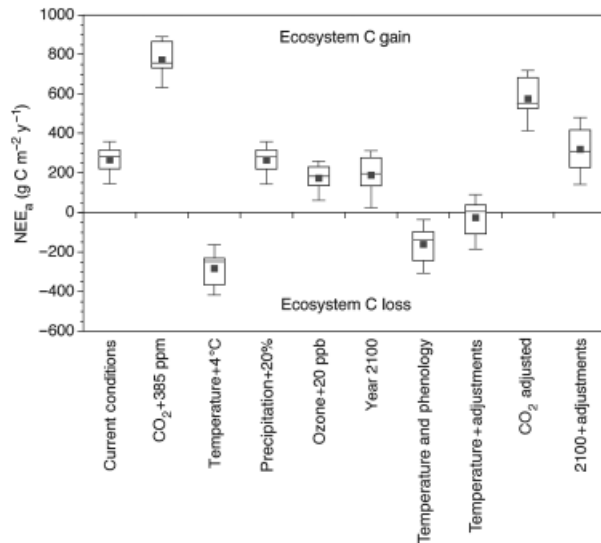


Fig. 2 Mean (solid square), median (middle line), 50% range (box) and maximum range (whiskers) of annual net ecosystem exchange (NEE_a) demonstrating the interannual variation in NEE from 1993 to 2003 for a variety of environmental scenarios. Scenarios include current conditions, single environmental change scenarios for CO_2 (+ 385 ppm), temperature (+ 4 °C), precipitation (+ 20% November–March), tropospheric ozone (+ 20 ppb O_3), a combination of all single factor changes (Year 2100), a scenario of increased temperature change with growing season elongation (Temp. + Phenology), scenarios of temperature and CO_2 increases for 2100 that include adjustments (Tables 2 and 3) for experimentally observed changes in physiological characteristics and biomass distribution (Temp. or CO_2 + Adjustments), and finally the combined influence of the 2100 environmental change plus vegetation adjustments (2100 + adjustments).

combined-factor model runs described above, together with additional runs showing (1) the impact of temperature-induced elongation of the growing season, (2) temperature treatments including physiological and biomass adjustments, (3) CO_2 treatments with physiological and biomass adjustments, and (4) the fully combined model simulations for year 2100.

Carbon cycle. When growing season elongation was added to the simulations as a response to the 4 °C temperature scenario, NEE_a increased by $122 \text{ g C m}^{-2} \text{ yr}^{-1}$ from -283 to $-161 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Fig. 2). Further increases of $135 \text{ g C m}^{-2} \text{ yr}^{-1}$ were obtained when adjustments were applied to leaf respiration and production rates yielding an NEE_a of $-26 \pm 32 \text{ g C m}^{-2} \text{ yr}^{-1}$. Therefore, experimentally observed adjustments to organ physiology and production (Tables 2 and 3) limited the negative impact of a 4 °C temperature increase from -206% of current to only -110% . Similarly, the inclusion of experimentally observed adjustments in CO_2 simulations (e.g. altered LMA and leaf N) also reduced the

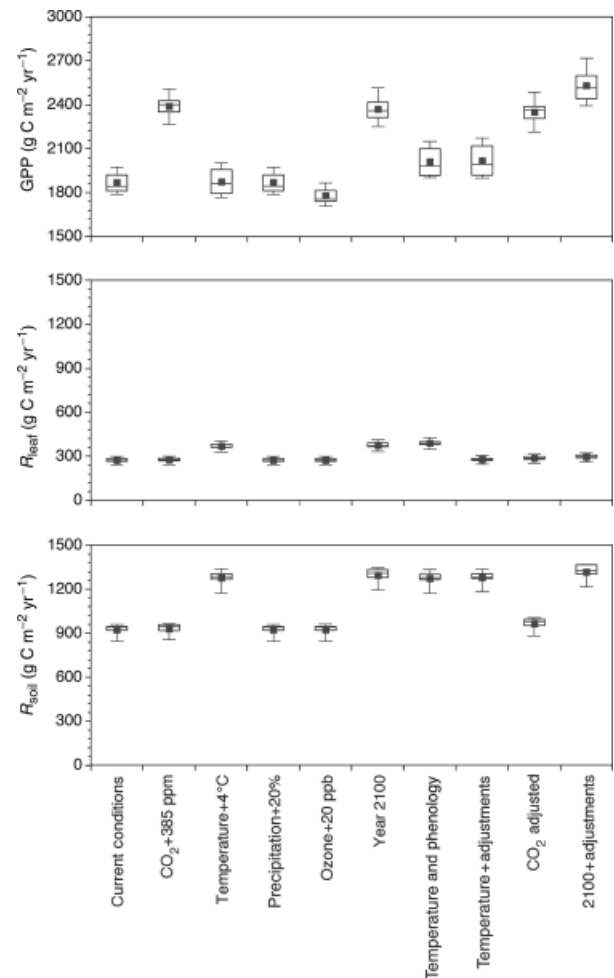


Fig. 3 Mean (solid square), median (middle line), 50% range (box) and maximum range (whiskers) for gross primary production (GPP; upper), leaf respiration (R_{leaf} ; middle) and soil respiration (R_{soil} ; lower) showing their respective interannual variation from 1993 to 2003 for a variety of environmental scenarios. Scenarios are as described in the caption for Fig. 2.

strong positive effect of elevated CO_2 by $198 \text{ g C m}^{-2} \text{ yr}^{-1}$ to yield an adjusted mean NEE_a value of $576 \pm 34 \text{ g C m}^{-2} \text{ yr}^{-1}$ (117% over current conditions). The combined influence of all four environmental scenarios plus their ecosystem adjustments produced a mean annual NEE_a of $319 \pm 38 \text{ g C m}^{-2} \text{ yr}^{-1}$, a net 20% increase over current conditions. Physiological acclimation and biomass adjustments associated with long-term CO_2 and temperature treatments were of opposite direction and similar magnitude, leading to offsetting changes in the combined response.

Figure 3 shows the relative importance of each environmental driver and their various combinations to components of NEE_a for current conditions. GPP (top panel) responded most strongly to increasing atmospheric CO_2 , was reduced slightly by exposure to

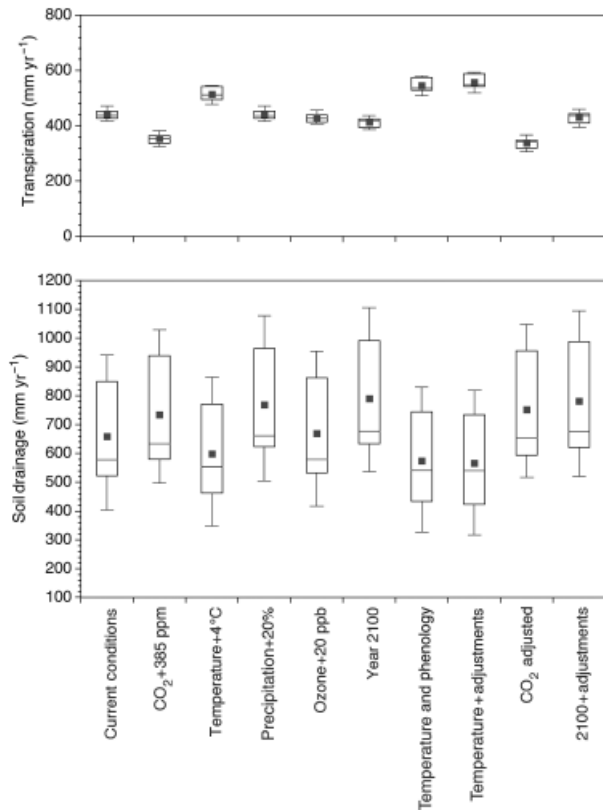


Fig. 4 Mean (solid square), median (middle line), 50% range (box) and maximum range (whiskers) for transpiration (upper graph) and soil drainage (lower graph) showing their respective interannual variation from 1993 to 2003 for a variety of environmental scenarios. Scenarios are as described in the caption for Fig. 2.

increased O₃, showed increases from growing season elongation, and was highest for the year 2100 scenario including all adjustments (+35% over current conditions). Simple temperature increases led to a 36% increase in R_{leaf} (Fig. 3, middle panel) with a slight additional increase from the longer growing season (i.e. +38%), but such changes were negated by long-term acclimation of leaf physiology for the year 2100 scenario. R_{soil} was increased by warming temperatures (+39%), but a greater increase was associated with the adjusted year 2100 scenario (+47%), presumably from the combined influence of warming and experimentally dictated adjustments to fine root turnover.

Water cycle. When growing season elongation was simulated in response to a warming of 4°C, T_a was slightly increased from 513 to 545 mm yr⁻¹ (Fig. 4, upper panel). Long-term experimental adjustments to physiology, biomass pools, and growth rates produced small changes in the CO₂ effect, reducing T_a by 16 mm yr⁻¹ for a combined effect of -24%. The

combined influence of all four environmental scenarios plus their ecosystem adjustments produced a mean annual T_a of 430 mm yr⁻¹ representing only a 2% reduction in T_a from current conditions. The positive increases in T_a driven by increased vapor pressure deficits from warming appear to be offset by stomatal-closure-induced reductions in canopy conductance driven by elevated CO₂. Increased November to March precipitation is predicted to have little impact on T_a , but it does result in a 17% increase in leachate drainage from the soil profile (Fig. 4, lower panel). Drainage is further increased by 2% because of transpiration reductions associated with the elevated CO₂ scenario.

Annual sums of the daily soil water potential in MPa days for the rooted soil profile has been shown to be a good index of soil water deficits for comparisons across years and termed the water stress integral (WSI; Myers, 1988; Hanson *et al.*, 2003c). Figure 5 shows calculated WSI for current conditions and all combinations of single factor and combined environmental drivers. Elevated CO₂ and warming reduce and exacerbate the WSI, respectively, but the combined influence of future environmental conditions and ecosystem adjustments shows an overall reduction in WSI indicating fewer and less extreme droughts.

Analysis of daily predictions

Intra-annual patterns of NEE_d (Fig. 6) and T_d (Fig. 7) for current conditions, and key treatments with and with-

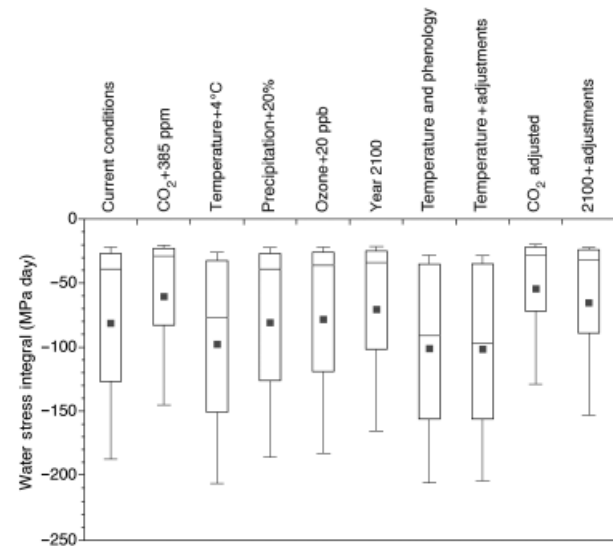


Fig. 5 Mean (solid square), median (middle line), 50% range (box) and maximum range (whiskers) for the water stress integral showing its respective interannual variation from 1993 to 2003 for a variety of environmental scenarios. Scenarios are as described in the caption for Fig. 2.

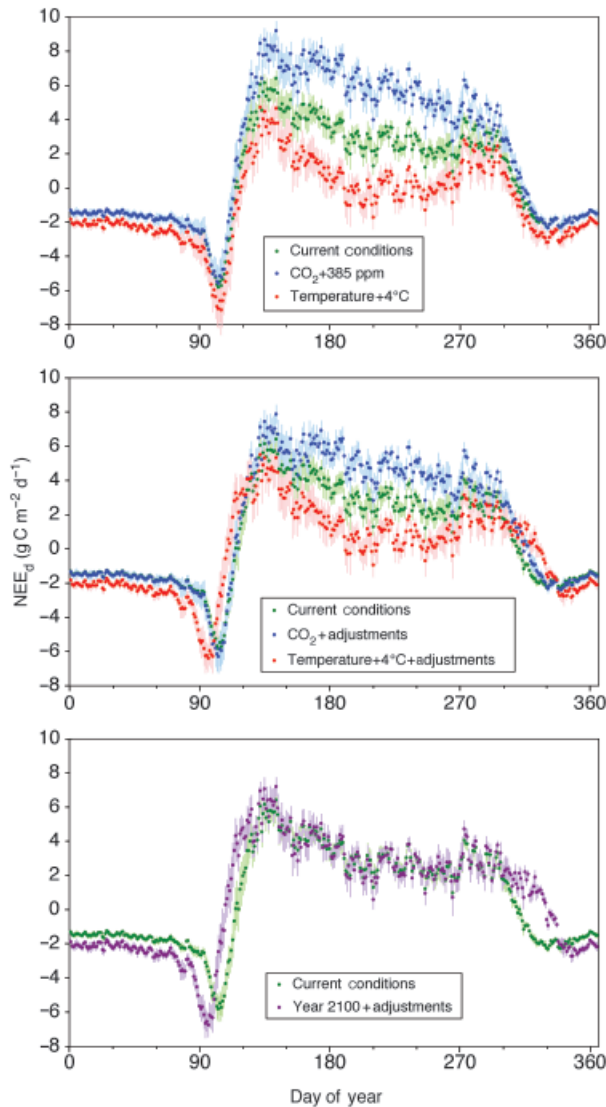


Fig. 6 Mean (\pm SE) of daily net ecosystem exchange of carbon (NEE_d) contrasting current conditions with simple environmental changes (upper graph; +385 ppm CO_2 or +4 °C), environmental changes plus experimentally observed plant adjustments (middle graph; CO_2 or Temp. + Adjustments), and the year 2100 climate plus adjustments (lower graph; Year 2100 + Adjustments).

out adjustments demonstrate further the dramatic potential for changes in temperature and [CO_2] to impact ecosystem functions (Figs 6 and 7, upper panels). However, with long-term organ acclimation and adjustments to biomass pools and growth rates the influence is diminished (Figs 6 and 7, middle panels). The net simulated effect of all treatments and their adjustments on NEE_d and T_d for 2100 shows incremental changes in daily rates that occur throughout the annual cycle, but the most dramatic influence on daily

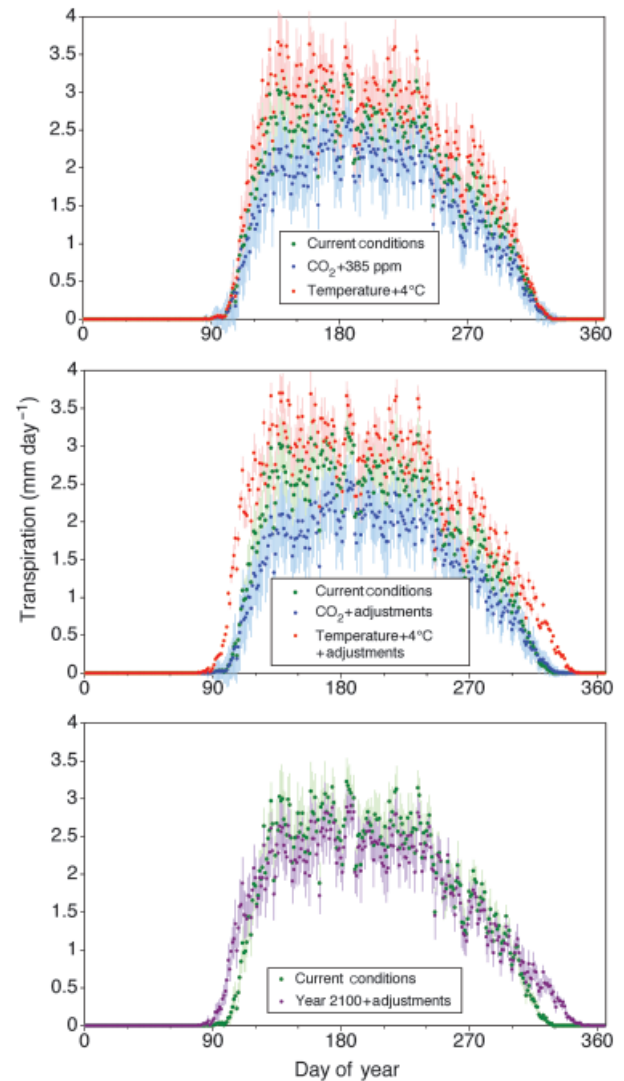


Fig. 7 Mean (\pm SE) of daily transpiration contrasting current conditions with simple environmental changes (upper graph; +385 ppm CO_2 or +4 °C), environmental changes plus experimentally observed plant adjustments (middle graph; CO_2 or Temp. + Adjustments), and the year 2100 climate plus adjustments (lower graph; Year 2100 + Adjustments).

rates of NEE_d or T_d are driven by the temperature-induced elongation of the growing season and increasing dormant-season respiration (Figs 6 and 7, lower panels).

Long-term simulations 2003–2100

Multifactor simulations with LINKAGES v2.2 indicated that a combination of CO_2 , temperature, and precipitation would result in a stand biomass of 329 $Mg\ ha^{-1}$ in 2100 compared with 296 $Mg\ ha^{-1}$ under current climate conditions (Fig. 8, upper panel). This increase (i.e. 11%)

was due primarily to the positive effects of elevated $[\text{CO}_2]$ simulated in the model as an increase in annual stem increment. Growing degree days and leaf area duration increased in response to a $+4^\circ\text{C}$ increase in temperature, but their impact contributed only slightly to observed changes in stand biomass. Evapotranspiration (ET) increased with growing season length and rising temperature (707 vs. 790 mm yr^{-1}), but those effects were dampened by CO_2 -induced reductions in canopy conductance (data not shown). Drought days did not accumulate to any appreciable extent in response to warming temperatures. Increased ET was balanced by additional inputs from increased wintertime precipitation, such that soil water drainage, which averaged 670 mm yr^{-1} , was similar for current and future climates. Therefore, leaching of soil nitrogen was not a major concern. Interannual variation in soil nitrogen availability ranged from 77 to $97\text{ kg ha}^{-1}\text{ yr}^{-1}$ over the final 100 years of the simulation (Fig. 8, lower panel), but there were few differences between current and future climate scenarios. Despite modest increases in stand biomass because of CO_2 , temperature and

precipitation, species composition did not change in response to altered climate; *L. tulipifera*, *Q. alba*, *Q. prinus*, and *A. rubrum* accounted for the majority (i.e. $>65\%$) of standing live biomass in simulations of both current and future climates.

Discussion

Relative importance of single environmental variables

As parameterized in this study, INTRASTAND simulated the relative importance of the four environmental drivers to NEE_a in the absence of long-term adjustments as $[\text{CO}_2] = \text{temperature} > [\text{O}_3] > \text{precipitation}$ change. The importance ranking for NEE_a does not hold for all component ecosystem processes. While $[\text{CO}_2]$ is the dominant driver for GPP, temperature is the key environmental driver controlling plant respiration. The increasing $[\text{CO}_2]$ and temperature scenarios have nearly opposite effects on T_a , and winter precipitation is the primary variable responsible for changing patterns of soil drainage.

The dramatic modeled effect of single-factor $[\text{CO}_2]$ increases on NEE were expressed in the INTRASTAND model as an increasing pool of TNCs. While inter- and intra-annual variability in such a pool is known (Körner, 2003; Tschaplinski & Hanson, 2003), sustained accumulation over multiple years is not a reasonable response. Tschaplinski & Hanson (2003) showed maximum dormant-season TNC accumulation in branches and boles of 27.3% and 15.5%, respectively. This level of storage would correspond to a maximum dormant-season TNC pool for branches, boles, and coarse roots of approximately $700\text{ g TNC-C m}^{-2}$ ground area for the Walker Branch upland-oak forest. Additional TNC storage would also be likely within the fine root biomass pool (Tschaplinski & Blake, 1995). Unpublished results from the ORNL Sweetgum FACE project (T. Tschaplinski, personal communication) showed transient increases in dormant-season, organ-specific TNC maxima, but those levels were not sustained. Therefore, no change in organ-specific storage capacity with exposure to elevated $[\text{CO}_2]$ is likely, but CO_2 -induced increases in wood volume with its associated incremental increase in sapwood would support additional TNC storage space. Storage space for TNC is, however, not included in the INTRASTAND simulation. Although annual TNC storage can be substantial, it cannot increase indefinitely even with increased stem and root volume. Interannual model simulations need to allow appropriate feedbacks between GPP, TNC storage, respiration, and other C losses to avoid unacceptably large accumulations.

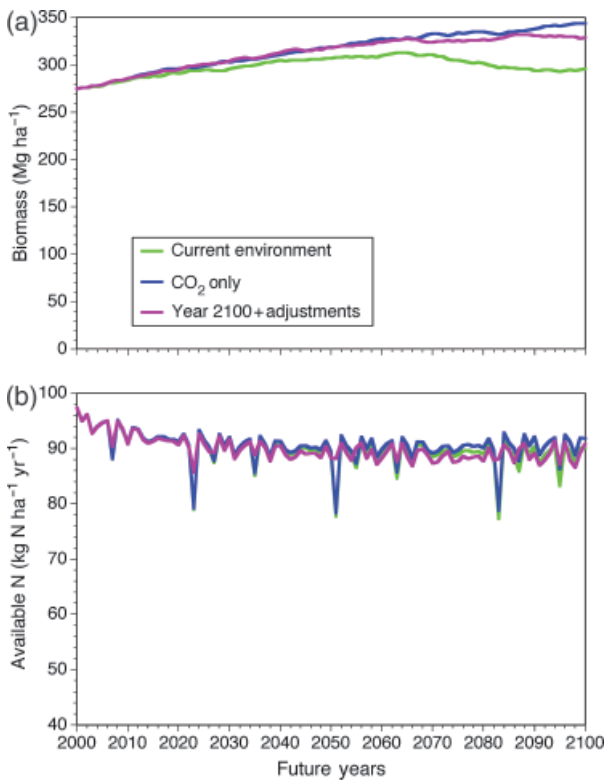


Fig. 8 Predicted standing biomass (upper panel) and annual nitrogen availability for Walker Branch soils (lower panel) for current conditions modeled through 2100 (current environment), an elevated CO_2 simulation (CO_2 only), and for the year 2100 climate scenarios with vegetation adjustments (Year 2100 + Adjustments).

The increasing $[O_3]$ scenario was translated by the model as a cumulative reduction in GPP capacity with small associated changes in stomatal conductance. For the model runs, the 5% O_3 -induced reduction of GPP ($90 \text{ g C m}^{-2} \text{ yr}^{-1}$) was translated nearly directly to a $92 \text{ g C m}^{-2} \text{ yr}^{-1}$ annual change in NEE_a , corresponding to a 35% reduction with respect to the current-condition simulation (Figs 2 and 3). When the O_3 effect is combined with the $[CO_2]$ scenario, the O_3 -induced reductions are limited to 2–3% of GPP (calculations not shown). This attenuation of the O_3 response is consistent with experimental observations on a number of hardwood species (Broadmeadow *et al.*, 1999; Karnosky *et al.*, 2003; Rebbeck *et al.*, 2004).

In addition to the direct effect of warming on physiological processes, temperature increases were defined to have an independent effect on growing season duration. By itself, growing season elongation was predicted to enhance GPP by $121 \text{ g C m}^{-2} \text{ yr}^{-1}$, but, when additional leaf respiration was accounted for, the increase in NEE_a was only $32 \text{ g C m}^{-2} \text{ yr}^{-1}$. Growing season elongation also increased T_a by $27 \text{ mm H}_2\text{O yr}^{-1}$ (Figs 2–4). The predicted levels of change associated with growing season elongation are relatively small fractions of observed GPP and NPP, consistent with the weak correlation between modeled NEE_a and growing season duration found by White & Nemani (2003). The magnitude of the changes in NEE_a driven by growing season elongation are also consistent with observed changes in NEE_a from long-term eddy covariance observations at Harvard Forest (Goulden *et al.*, 1996; Barford *et al.*, 2001) and a mixed forest in Belgium (Carrara *et al.*, 2003).

The relative rankings among environmental variables are, of course, dependent on the scenarios established in Table 1. Alternative choices for levels of change would result in different levels of limitations (e.g. greater warming or altered timing of precipitation events). For example, the current scenarios only simulated precipitation additions to winter events observed from 1993 to 2003. If new precipitation events had been simulated during the depth of drought periods in 1993, 1995, 1998, and 2002, the relative importance of precipitation increases on GPP would have been greater. That is, elimination of strong soil moisture deficits would have allowed for greater GPP.

Multifactor responses

The complete year 2100 analysis, including physiological and growth rate adjustments, produced increases in NEE_a (20%), GPP (35%), and soil water drainage (19%), but decreases in leaf respiration (–3%) and transpiration (–3%). Ollinger *et al.* (2002) simulated changes in

forest systems driven by $[CO_2]$, $[O_3]$, nitrogen deposition, and their combination between 1700 and 2000, and they predicted a reduced overall response for the combined treatments analogous to the observations reported here. Similarly, the global scale simulations of Cramer *et al.* (2001) showed reduced NEE predictions when the influence of increasing $[CO_2]$, temperature and precipitation were combined. However, Cramer and others' predictions for 2100 vs. 2000 showed an approximate 100% increase in net ecosystem production (NEP) that is much larger than our final projected increase in NEE_a of only 20%. The inclusion of experimentally observed adjustments to plant functions and plant growth rates was key to the NEE_a predictions for Walker Branch, and these adjustments are likely to be just as important for ecosystem forecasting at the global scale.

Decadal responses

As discussed previously, INTRASTAND was developed as a computational tool to simulate stand carbon and water cycles at intra-annual time scales. Feedbacks that do occur within the model are driven largely by fast dynamics in photosynthesis, autotrophic and heterotrophic respiration, leaf area development, and stand biometry. INTRASTAND does not represent potential feedbacks because of nitrogen limitations or [TNC]. In contrast, LINKAGES v2.2 simulates the growth of individual trees, albeit with less physiological mechanism than INTRASTAND, but explicitly considers how NPP, stand biomass, and species composition are impacted by interactions between carbon and nitrogen cycles over decades to centuries. Simulations with LINKAGES v2.2, both in this and previous studies (Bugmann *et al.*, 2001; Wullschleger *et al.*, 2003a), adequately predicted biomass, stem density, age-class distribution, and species composition for 50–100-year-old stands growing under current climatic conditions on the Walker Branch watershed. As used in this study, LINKAGES v2.2 also appeared to yield reasonable estimates for stand biomass and species composition given future climate conditions. Elevated $[CO_2]$ alone contributed to a 16% increase in stand biomass (i.e. 344 Mg ha^{-1}) compared with current climate conditions, whereas standing biomass was reduced to 329 Mg ha^{-1} in combination with temperature and winter-time precipitation. Not surprisingly, the effects of elevated $[CO_2]$, represented here as an increase in annual stem increment, dominated the multifactor simulations with LINKAGES v2.2. Interactions between CO_2 and temperature were limited and, while the results of the current simulation appear reasonable, additional studies are needed in order to

more thoroughly evaluate the utility of this class of models to represent multifactor interactions. Loehle & LeBlanc (1996) highlight several limitations of gap models in this regard and argue that changes must be made in the representation of various processes in these models in order to achieve greater confidence in model predictions. Steps are being taken to include physiological mechanism in gap models and to ensure that (where appropriate) monthly and annual representations of important processes are replaced by hourly and daily time steps (Smith *et al.*, 2001; Wullschleger *et al.*, 2003a). Such efforts will facilitate the direct incorporation of data obtained in field studies and hopefully expand the utility of this class of models in climatic change research.

Nutrient limitations

Large CO₂-induced increases in carbon uptake by vegetation predicted by some global model outputs (e.g. Cramer *et al.*, 2001) and the simplistic single-factor CO₂ scenario of this paper can be criticized for not accounting for limitations imposed by nutrient availability (Hungate *et al.*, 2003; Beedlow *et al.*, 2004; Luo *et al.*, 2004). In this paper, the INTRASTAND simulations do not include feedbacks associated with nutrient supply and a key question is: Can the predicted NEE or NPP responses for year 2100 be supported by available nutrients?

For the current environment and composition of the upland-oak forest on Walker Branch watershed, mean annual NPP is observed to be $729 \pm 69 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Hanson *et al.*, 2003a). The annual N requirement for this level of NPP ranges from 95 to $120 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (Johnson & Henderson, 1989; Johnson & Todd, 1990). In 1983, when the stand was 20 years younger, Johnson & Henderson (1989) estimated that the annual N requirement to support NPP ranged from 93 to $103 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ from a combination of mineralization ($62\text{--}67 \text{ kg N ha}^{-1} \text{ yr}^{-1}$), atmospheric deposition ($13 \text{ kg N ha}^{-1} \text{ yr}^{-1}$), and retranslocation from vegetation storage pools ($26\text{--}39 \text{ kg N ha}^{-1} \text{ yr}^{-1}$). Because leaf and fine root components of NPP cycle rapidly in contrast to wood, long-term C accumulation in wood is limited by the availability of nutrient elements. In the case of N, the logical source for Walker Branch is atmospheric deposition.

Current data for atmospheric deposition of N to Walker Branch watershed are available from published articles and online archives. The National Atmospheric Deposition Program shows a long-term (1980–2003) mean wet deposition value of $4.9 \pm 0.2 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (NADP, 2004). Dry deposition values of $\sim 1.9 \pm 0.1 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ are also available for two eastern

Tennessee sites in the Clean Air Status and Trends Network (CASTNet, 2004). Direct annual foliar uptake of NO₂ has also been estimated to be $2.8 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (Hanson *et al.*, 1992). The combined total N deposition for current conditions is thus approximately $10 \text{ kg N ha}^{-1} \text{ yr}^{-1}$. This level of N deposition for sapwood containing between 0.002 and 0.005 g N g^{-1} dry wood could support annual wood C production of $200\text{--}235 \text{ g C m}^{-2} \text{ yr}^{-1}$, consistent with the observed range from 1993 to 2003 of $166\text{--}255 \text{ g C m}^{-2} \text{ yr}^{-1}$.

For the year 2100 scenario, annual wood production is expected to increase 17%, leading to a long-term increase in live-wood biomass C. Future increased nitrogen deposition associated with increased winter precipitation, and increased dry N deposition from increased oxidant activity of the atmosphere might be expected to yield N deposition rates of $\sim 15 \text{ kg N ha}^{-1} \text{ yr}^{-1}$. That level of N deposition would support future wood C production of $300\text{--}352 \text{ g C m}^{-2} \text{ yr}^{-1}$ and accommodate the simulated increases associated with the 2100 scenario discussed here (i.e. $319 \text{ g C m}^{-2} \text{ yr}^{-1}$). Temperature-induced increases in litter turnover are expected to enhance N mineralization rates and sustain N supplies for leaf production and fine root turnover. Johnson *et al.* (2004) reported that nutrient limitations associated with elevated CO₂ exposures for the sweetgum FACE study would not be large, and that the ultimate limitations would be driven by the combination of N demand, deposition and mineralization. It is important to point out that the soils of the upland-oak forests on Walker Branch have lower N pools than the sweetgum FACE study site. Nevertheless, the LINKAGES simulations showed sustained N availability driven by temperature-induced mineralization of N stocks (Fig. 8, lower panel).

Can other elements be assumed to be nonlimiting? The simple answer is no. Complete budget analyses must be accomplished in conjunction with ongoing experiments to identify the level of flexibility present for a given ecosystem. In addition to N, phosphorous has recently been reemphasized as another key element that can commonly limit the responsiveness of vegetation in established ecosystems (Wardle *et al.*, 2004), and base cation supplies were previously suggested as a potentially limiting factor associated with long-term exposure to acidic precipitation (Johnson & Todd, 1990).

From the multiyear manipulated increases in precipitation on the TDE study (+33%), Johnson *et al.* (2002) concluded that enhanced precipitation would cause long-term depletion of soil base cations. Using the Nutrient Cycling model (NuCM), Johnson *et al.* (2000) had already predicted this possibility, but cautioned that their simulations did not adequately

capture the interactive effects that vegetation might play in future nutrient cycles. To ensure that model simulations do not continue to predict unreasonable responses in the presence of logical element-cycle limitations, existing plant-based carbon and water cycling models must be improved to include integrated biogeochemical cycles for the major elements limiting plant growth. In a recent example of such integration, Aber *et al.* (2002) demonstrated the importance of combining the effects of environmental drivers with predictions of element cycling processes to adequately capture current patterns of nitrogen loss from forested watersheds.

Gradual vs. abrupt CO₂ changes

Forest responses to a gradually increasing atmospheric [CO₂] may differ from the responses to an abrupt change in [CO₂] as occurred in the FACE experiment and is represented in the INTRASTAND model. Klironomos *et al.* (2005) demonstrated that an abrupt increase in [CO₂] caused an immediate change in the structure and function of the mycorrhizal community that altered belowground plant production, whereas similar changes did not occur if the [CO₂] concentration was increased gradually. Luo & Reynolds, (1999) simulated how the fluxes of C between pools with different turnover rates could be different in response to a sudden influx of C compared with gradual changes. Luo *et al.* (2004) also presented the related hypothesis of progressive N limitation, whereby initial increases in plant growth reduces N availability to create a negative feedback limiting further growth increases. INTRASTAND is not sensitive to any of these mechanisms because, as an intra-annual model, information is not passed from 1 year to the next, and it does not operate at a level of detail to incorporate complicated interactions such as the effect of mycorrhizal function on plant C allocation. Because of this limitation, it is possible that superimposed experimental input data from abrupt changes in [CO₂] associated with FACE studies would exaggerate the effects of a gradually rising [CO₂] on forest NPP. However, the FACE data used in this exercise excluded first-year responses where artifacts of the abrupt increase would be most likely to express themselves. Over 7 years there has been no evidence of a negative feedback related to N limitation in the sweetgum FACE study (Norby *et al.*, 2004; Norby & Luo, 2004).

Conclusion

Although it is impossible to be certain of the magnitude of future environmental changes or the resulting

response of ecosystem processes, it is clear that ecosystem responses will involve complex interactions among variables driving positive or negative changes in ecosystem functions. This paper has shown that reasonable scenarios of environmental change for a typical upland-oak forest of the eastern United States can produce very different responses (negative vs. positive carbon gain) depending on the inclusion of critical information from long-term experimental manipulations. Such a conclusion was made possible because results from appropriate long-term studies were available. This conclusion underscores the need to consider similar analyses for understudied but valuable ecosystems to enable accurate forecasts of ecosystem response to climatic change variables. Plans for long-term manipulative research should take advantage of the current and future analyses conducted using alternative and perhaps more sophisticated ecosystem models. The combined results from various efforts will be needed for planning the efficient use of available scientific resources, and to suggest necessary directions for model improvement and experimentation.

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