# Importance of carbon-nitrogen interactions and ozone on ecosystem hydrology during the 21st century

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Received 20 July 2008; revised 3 November 2008; accepted 19 December 2008; published 18 March 2009.

[1] There is evidence that increasing $CO_2$ concentrations have reduced evapotranspiration and increased runoff through reductions in stomatal conductance during the twentieth century. While this process will continue to counteract increased evapotranspiration associated with future warming, it is highly dependent upon concurrent changes in photosynthesis, especially due to $CO_2$ fertilization, nitrogen limitation, and ozone exposure. A new version of the Terrestrial Ecosystem Model (TEM-Hydro) was developed to examine the effects of carbon and nitrogen on the water cycle. We used two climate models (NCAR CCSM3 and DOE PCM) and two emissions scenarios (SRES B1 and A2) to examine the effects of climate, elevated $CO_2$, nitrogen limitation, and ozone exposure on the hydrological cycle in the eastern United States. While the direction of future runoff changes is largely dependent upon predicted precipitation changes, the effects of elevated $CO_2$ on ecosystem function (stomatal closure and $CO_2$ fertilization) increase runoff by 3–7%, as compared to the effects of climate alone. Consideration of nitrogen limitation and ozone damage on photosynthesis increases runoff by a further 6–11%. Failure to consider the effects of the interactions among nitrogen, ozone, and elevated $CO_2$ may lead to significant regional underestimates of future runoff.

**Citation:** Felzer, B. S., T. W. Cronin, J. M. Melillo, D. W. Kicklighter, and C. A. Schlosser (2009), Importance of carbon-nitrogen interactions and ozone on ecosystem hydrology during the 21st century, *J. Geophys. Res.*, *114*, G01020, doi:10.1029/2008JG000826.

## 1. Introduction

[2] Climate warming during the last several decades has likely led to increased frequency of heavy precipitation events [*Groisman et al.*, 2004] as well as severe droughts [*Dai et al.*, 2004]. Most future scenarios show that these trends are likely to continue and intensify in the future [*Intergovernmental Panel on Climate Change* (*IPCC*), 2007]. However, the changing hydrological cycle is not only a function of climate; vegetation plays a key part of the story over land. A recent study [*Gedney et al.*, 2006] has shown that while precipitation over land decreased in the latter half of the twentieth century, runoff actually increased and attributed the increase to the effect of higher atmospheric $CO_2$ levels on stomatal conductance. Other studies [*Betts et al.*, 2007; *Cramer et al.*, 2001; *Ollinger et al.*, 2007] have predicted this effect to continue into the future, and that even higher atmospheric $CO_2$ levels will lead to more runoff (or less of a reduction in runoff) due to reduced stomatal conductance. The effect of plants on regulating future hydrology is important [*Hornbeck et al.*, 1993; *Jones and Post*, 2004] and needs to be considered in light of multiple stresses on ecosystems, including changing concentrations of soil nutrients and atmospheric pollutants.

[3] Elevated $CO_2$ can affect runoff in two different ways (Figure 1). On the one hand, plants respond to higher atmospheric $CO_2$ by reducing their stomatal conductance, thereby reducing transpiration and increasing runoff (the direct effect). On the other hand, higher atmospheric $CO_2$ levels also lead to increased photosynthetic rates, thereby increasing stomatal conductance [*Ball et al.*, 1987] (the $CO_2$ fertilization effect). This increase in photosynthesis may also lead to greater Leaf Area Index (LAI), which would increase canopy conductance. Both *Gedney et al.* [2006] and *Betts et al.* [2007] show that, in model-based investigations, the effect of elevated $CO_2$ on stomatal conductance is dominated by the direct effect. Also, because $CO_2$ fertilization is expected to result in less than a doubling of photosynthetic rates with doubled atmospheric $CO_2$ levels, we would expect the direct effect to predominate over the $CO_2$ fertilization effect [*Medlyn et al.*, 2001].

[4] Ultimately, the ability of plants to respond to elevated $CO_2$ may be governed as much by factors such as nutrient limitation or air pollution, as by intrinsic kinetics of photosynthesis reactions. In nitrogen-limited conditions, $CO_2$ fertilization is minimal. While most boreal and temperate forests are nitrogen-limited to some extent [*Melillo and Gosz*, 1983; *Vitousek and Howarth*, 1991], anthropogenic additions of $NO_y$ to the atmosphere have alleviated nitrogen

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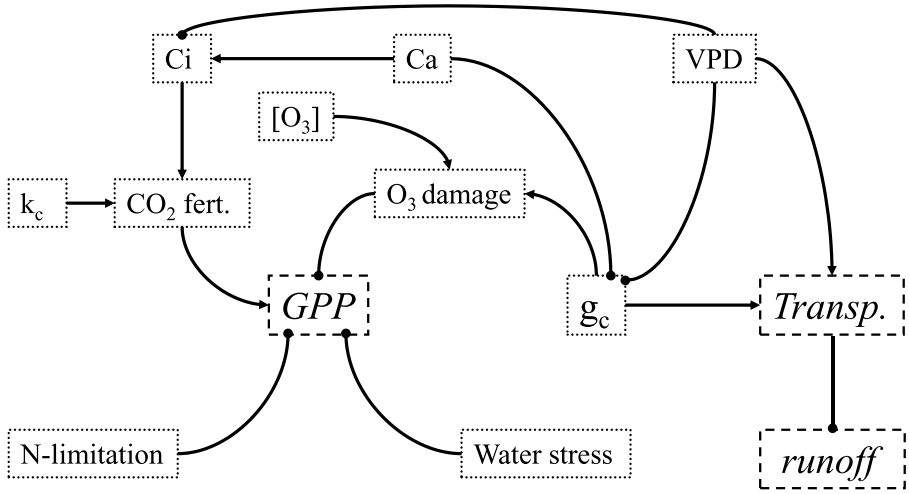


**Figure 1.** Carbon-nitrogen-water coupling in TEM-Hydro. Arrows indicate positive couplings, and circles represent negative couplings. Ci, interal $CO_2$; Ca, atmospheric $CO_2$; kc, half saturation constant for $CO_2$ fertilization; GPP, gross primary productivity; gc, canopy conductance; VPD, vapor pressure deficit.

limitation in many European and other temperate forests [*Magnani et al.*, 2007]. Pollutants like ozone may negate any positive benefits of $CO_2$ fertilization through direct cellular damage of photosynthetic machinery [e.g., *Felzer et al.*, 2004; *Karnosky et al.*, 2003]. The negative effects of nitrogen limitation and ozone on photosynthesis need to be weighed against the benefits of increased $CO_2$ fertilization in order to determine the net effects on photosynthesis and stomatal conductance (Figure 1).

[5] A more complete picture of connections among carbon, nitrogen, ozone, and water (Figure 1) is rather complex, and recent studies of the effects of elevated $CO_2$ on water cycling have generally not included interactions of elevated $CO_2$ with nitrogen limitation or ozone damage. In this study, we develop a biogeochemical model and perform sensitivity analyses using two different climate models and two emissions scenarios, to ascertain how climate, elevated $CO_2$, nitrogen limitation, and ozone combine to influence future hydrology in the eastern United States. We find that the effects of nitrogen limitation and increased ozone concentrations on future runoff are at least as large as the net effects of elevated $CO_2$ alone. To realistically model future runoff and surface hydrology therefore necessitates including not just plant carbon cycling, but also carbon-nitrogen interactions and considerations of ozone.

## 2. Methods

### 2.1. Model Description

[6] The biogeochemical model we developed (TEM-Hydro) is based on the Terrestrial Ecosystem Model (TEM) [*Felzer et al.*, 2004; *Raich et al.*, 1991; *Tian et al.*, 2003], modified to enable us to explore more thoroughly the linkages between the water, carbon, and nitrogen cycles (Figure 2). To capture the role of stomatal conductance in transpiration, $CO_2$ and ozone uptake, we explicitly model specific components of vegetation, rather than a single aggregated pool for all vegetation carbon. We have thus developed a multiple pool model for vegetation carbon and nitrogen, consisting of leaves, active and inactive stem tissues (e.g., sapwood and heartwood), fine roots, and a labile pool for storage. A summary of this model follows, but a complete description can be found in Text S1 (available as auxiliary material).[1]

[7] Each of the vegetation pools serves a specific function. Leaves are the photosynthetic organs, active stem tissue provides hydraulic transport and resource storage, inactive stem tissue is solely structural, fine roots mediate nutrient and water uptake, and the labile pool embodies the resource reserve used for growing new structural tissue or maintaining existing tissue. The full set of coupled differential equations is given in Text S1, section 1. Fluxes into and out of the pools include photosynthesis, nitrogen uptake, respiration, litterfall, and allocation. Each compartment, with the exception of the labile pool, has a plant functional type (PFT) dependent C:N ratio.

[8] Photosynthesis depends upon several environmental variables (Text S1, section 2), which scale the maximum rate of carbon assimilation (*Cmax*). Because we now model leaf area index (LAI) explicitly, calculated from leaf carbon with a PFT-dependent specific leaf area (SLA), *Cmax* now represents a leaf-level, rather than canopy-level, rate. The environmental factors that affect photosynthesis, as represented by gross primary productivity (GPP) are solar radiation, air temperature, soil moisture, $CO_2$, ozone damage, and nitrogen uptake. A complete description is given in Text S1, section 2, but here we describe those elements that rely upon the new model structure. The dependence of leaf GPP on photosynthetically active radiation (PAR) is hyperbolic, and the canopy expression is an integral over LAI that uses Beer's law. The dependence of GPP on internal carbon dioxide concentration is also hyperbolic; internal $[CO_2]$ depends upon atmospheric $[CO_2]$, vapor pressure deficit (VPD), and a stomatal slope parameter (described below).

[1]Auxiliary materials are available in the HTML. doi:10.1029/2008JG000826.

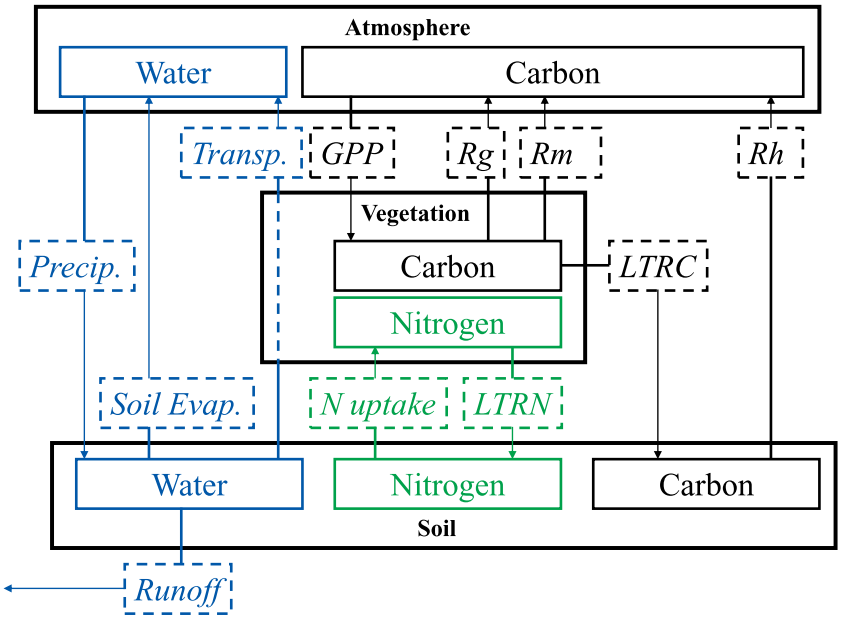


**Figure 2.** TEM-Hydro overview. TEM-Hydro considers interactions between the atmosphere, vegetation, and soil. Carbon fluxes between the atmosphere and vegetation include GPP (gross primary productivity) and growth and maintenance respiration (Rg, Rm). LRTC and LTRN are the carbon and nitrogen litterfall rates, respectively, from vegetation to soil. Heterotrophic respiration (Rh) represents microbial soil decomposition, and Nuptake represents the uptake of inorganic nitrogen from the soil. Soil evaporation and plant transpiration are considered separately. The carbon and nitrogen in vegetation is further divided between four structural pools (fine roots, leaves, sapwood, and heartwood), and a labile pool for storage (see text).

The effect of ozone on GPP is largely cumulative, so at each time step, the change in total ozone damage is calculated, as the difference between healing and new damage. Healing occurs both with new growth, and the addition of new leaves. New damage is based on the *Reich* [1987] and *Ollinger et al.* [1997] formulation used by *Felzer et al.* [2004, 2005]. Now, however, the stomatal conductance that determines new ozone damage is integrated into the model structure rather than being determined by an empirical formula. Nitrogen uptake is now dependent on fine root biomass, in addition to soil moisture, respiration rates, and ozone (Text S1, section 3). Nitrogen limitation causes downregulation of GPP (Text S1, section 4).

[9] Respiration consists of both maintenance and growth respiration (Text S1, section 5). Maintenance respiration is a function of temperature and tissue nitrogen, and is calculated for the labile pool, leaves, active stems, and fine roots. Growth respiration is 25% of the total carbon allocated to new tissue at the time of allocation. Litterfall rates are based on residence times for each pool (Text S1, section 6).

[10] Allocation from the labile pool to the structural pools is based on a cost:benefit analysis of adding new tissue (Text S1, section 7). An investment in new leaves is made if the marginal benefit of more leaf area outweighs the marginal cost of adding new leaves, with carbon as the currency. More leaves increase GPP, allowing for greater carbon gain; the marginal benefit of added leaf area is calculated by differentiating GPP with respect to LAI. The marginal cost is the sum of direct maintenance costs to support new leaves and direct construction costs resulting from lost carbon used to create new leaf tissue. There are also indirect costs from other plant tissue required to support the new leaves; these indirect costs also break down into maintenance and construction. The direct maintenance costs are calculated by differentiating the leaf maintenance respiration with respect to LAI, while the direct construction costs depend on the carbon content of additional leaves, and the expected leaf lifetime. The indirect costs are based on a PFT-dependent leaf allocation fraction and the ratio of stem to root allocation (see Text S1, section 7, for details). Rules are developed based upon evergreen, cold-deciduous (temperature-limited), and stress-deciduous (both temperature and moisture-limited) PFTs to determine the timing of allocation and litterfall.

[11] The hydrology is a modified version of the original Water Balance Model (WBM) developed by *Vorosmarty et al.* [1989], which has a simple 1-pool (bucket) model of soil moisture. We have modified the calculation of evapotranspiration, and now employ the *Shuttleworth and Wallace* [1985] formulation, which is similar to the Penman-Monteith approach, except that it explicitly considers both soil evaporation and plant transpiration [*Federer et al.*, 1996]. The method is a flow-resistance model that determines water vapor fluxes from the canopy and soil based on meteorological conditions and aerodynamic resistances, including the canopy stomatal resistance ($r_c = 1/g_c$, where $g_c$ is the canopy conductance), the soil surface resistance [*Choudhury and Monteith*, 1988], and three other aerodynamic resistances between the soil, canopy, canopy airspace, and atmosphere. To determine $g_c$, we employ the approach of *Ball et al.* [1987] and *Leuning* [1995] in which canopy stomatal conductance is a linear function of GPP.

The slope of the linear function is the product of a PFT-dependent stomatal parameter (used in the determination of internal $CO_2$) and a hyperbolic function of VPD (so that drier conditions lead to lower stomatal conductance), divided by atmospheric $CO_2$ concentration (so that increasing $CO_2$ leads to lower stomatal conductance at a given GPP). The intercept of the linear function is equal to the product of LAI and a parameter relating to minimum stomatal conductance. This construction is consistent with the hypothesis that plants maintain a relatively stable ratio of internal to atmospheric $CO_2$, which governs both the direct effect of $CO_2$ and the indirect effect of $CO_2$ fertilization on transpiration.

### 2.2. Experimental Design

[12] We test different hypotheses about the interactions of $CO_2$, nitrogen availability, and ozone on the water cycle in the context of changing climate using a historical climate data set and four future climate scenarios. The historical climate is based on the $0.5° \times 0.5°$ data set of temperature, precipitation, and cloudiness from the Climatic Research Unit [*Mitchell et al.*, 2003] from 1901 to 2000. Future climate scenarios (2001–2099) are based on the National Center for Atmospheric Research (NCAR) CCSM3 model and the Department of Energy (DOE) Parallel Climate Model (PCM), using the SRES A2 and B1 emissions scenarios. We use data from the World Climate Research Programme's (WCRP's) Coupled Model Intercomparison Project phase 3 (CMIP3) multimodel data set. The A2 scenario is a "warm" scenario representing a heterogeneous world with increasing population and regional economic growth; greenhouse gas emissions have still not peaked by the end of the 21st century. The B1 scenario is a relatively "green" scenario, representing a convergent world with declining population toward the end of the century, development of a service and information economy, and technological advances in use of energy resources [*IPCC*, 2007]. This scenario is consistent with the target of stabilizing $CO_2$ at 550 ppmv. The ozone data is based on the AOT40 index, which is the accumulated hourly ozone over 40 ppb. We use the modeled historical ozone data set developed by *Felzer et al.* [2005]. For the future, we keep ozone levels constant at late twentieth century levels in the B1 scenario and allow them to increase according to the POL case of *Felzer et al.* [2005], which is broadly consistent with assumptions in the A2 scenario.

[13] General Circulation Model (GCM) data needs to be bias-corrected before they are used in climate impact studies. In addition, the coarse resolution of these global models (gridded equivalents $1.4° \times 1.4°$ for CCSM3 and $2.8° \times 2.8°$ for PCM) requires spatial downscaling to the $0.5° \times 0.5°$ grid. We use a simple delta/ratio approach, where we first linearly interpolate the model output to the half degree grid, and then add the monthly anomalies from the model baseline (1970–1999) for temperature or multiply the monthly ratios for precipitation and cloudiness to the observed baseline monthly mean [*Kittel et al.*, 1995]. The result of this downscaling (Table 1) is that the temperature difference from the end of the 21st century (2070–2099) to the end of the twentieth century (1970–1999), averaged over temperate forests in the conterminous United States, is 1.9°C for the CCSM3 and 1.5°C for the PCM B1 scenarios, 4.3°C for the CCSM3 A2 scenario, and 2.5°C for the PCM A2 scenarios. The B1 scenario has the same climate sensitivity for both models, whereas the climate sensitivity to the A2 emissions is much greater in the CCSM3 model.

**Table 1.** Model Sensitivities for U.S. Temperate Forests[a]

| Scenario | ΔTemperature (°C) | ΔPrecipitation (%) |
|---|---|---|
| CCSM3-B1 | 1.9 | 9.0 |
| PCM-B1 | 1.5 | 3.5 |
| CCSM3-A2 | 4.3 | 9.2 |
| PCM-A2 | 2.5 | 3.4 |

[a]Change in temperature (°C) and change in precipitation (%) between future (2070–2099 mean) and present baseline (1970–1999 mean). Data from PCMDI, NCAR, and DOE. Spatial downscaling using historical CRU data.

**Table 2.** Experimental Design[a]

| | $CO_2$ Fertilization | Ozone Damage | Nitrogen Limitation |
|---|---|---|---|
| Climate | no | no | no |
| Elevated $CO_2$ | yes | no | no |
| N-lim. + Ozone | yes | yes | yes |

[a]No $CO_2$ fertilization means that $CO_2$ levels are held constant at 2001 values (369.5 ppm) for the 21st century. Photosynthesis either responds to ozone (yes) or does not (no). Future ozone is held at current values for the B1 scenario and increased for the A2 scenario (see text). The rows are the experiments, and the columns are the stressors.

[14] We perform a series of three sensitivity experiments (Table 2). The first experiment explores the effects of climate alone (via the precipitation and temperature anomalies), holding $CO_2$ concentrations constant over the 21st century, and assuming no nitrogen limitation or ozone damage effects on photosynthesis. The next experiment incorporates elevated $CO_2$ according to the emissions scenario used, and uses a low $CO_2$ fertilization half saturation constant of 200. The half saturation constant is based on the assumption of a hyperbolic relationship between atmospheric $CO_2$ and GPP (GPP reaches half of its maximum at a concentration equal to the half-saturation constant), and is determined from experimental increases in photosynthesis or biomass with elevated $CO_2$ [*Sokolov et al.*, 2008]. The value we have chosen for the $CO_2$ fertilization half saturation constant represents the lower end of the uncertainty range from the literature [*Kimball*, 1983; *Norby et al.*, 1999], and has been shown to mimic the $CO_2$ fertilization response of other carbon-only ecosystems models [*Sokolov et al.*, 2008]. The final experiment adds in the effects of nitrogen limitation and ozone damage, both of which decrease photosynthesis. Most northern forests are nitrogen limited, though anthropogenic nitrogen deposition has reduced nitrogen limitation in certain industrial regions, like the eastern United States [*Melillo and Steudler*, 1989; *Magnani et al.*, 2007]. Chemical reactions of these nitrogen compounds in the atmosphere are also responsible for the production of ozone, which has a damaging effect on photosynthesis. All experiments are run for grid cells originally covered by temperate deciduous and coniferous forests in the conterminous United States.

## 3. Results

[15] We first check the model against historical evapotranspiration (ET) and runoff in 12 river basins (Figure 3). Observed ET is determined by subtracting USGS river

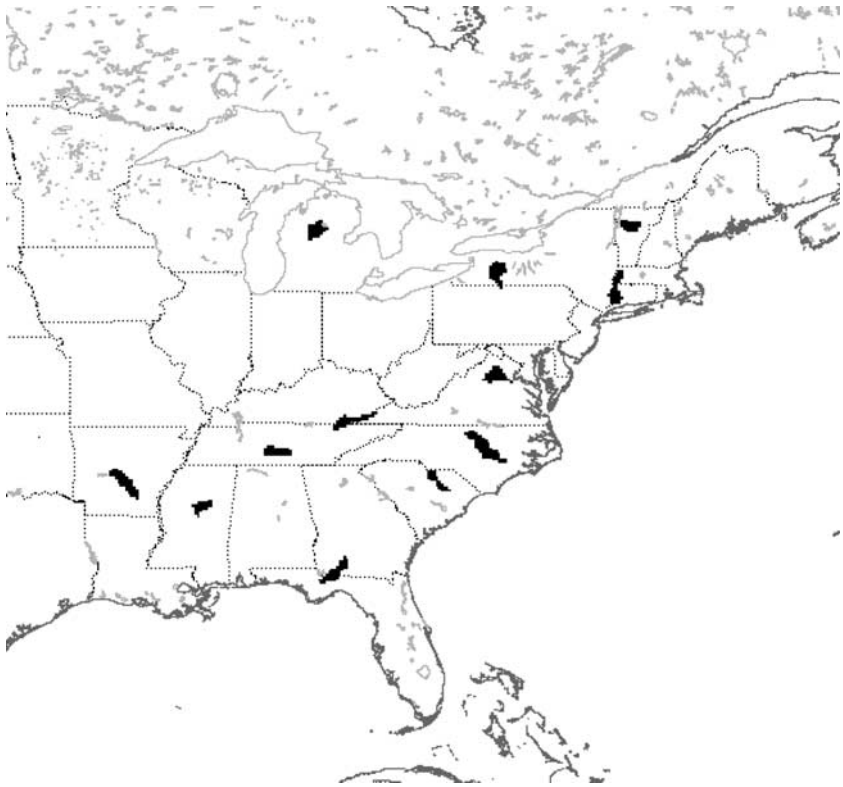

**Figure 3.** Location of twelve river basins used in this study (B. Fekete, personal communication, 2006).

gauge runoff from CRU precipitation for each basin (and assuming negligible trends in storage) during the baseline period of 1970–1999 (Figure 4). This observed measure of average annual basin ET shows a strong correlation with modeled values, having an $r^2$ of 0.93 along the 1–1 line. To determine how well the model captures both seasonal and interannual variabilities in runoff, we use the Nash-Sutcliffe coefficient of efficiency (NS) to evaluate the similarity between observed and modeled runoff (Table 3). The NS coefficient is a common measure of error used in hydrology [*Gordon et al.*, 2004] and is represented as the ratio of the mean square error to the variance in the measured data subtracted from unity. The NS coefficient ranges from $-\infty$ (poor model) to 1 (perfect model). Values greater than zero indicate that the mean square error is less than the variance of the observed data. For the monthly estimates, all river basins but two (Muskegon and Gennessee) have positive values, while the strongest fits are for the Big Black, Cumberland and Duck River basins. The interannual NS coefficients (Table 3) also show only two basins with negative values (Muskegon and Lynches), and that the error in annual runoff is less than half the interannual variability at five of the twelve basins (NS > 0.5).

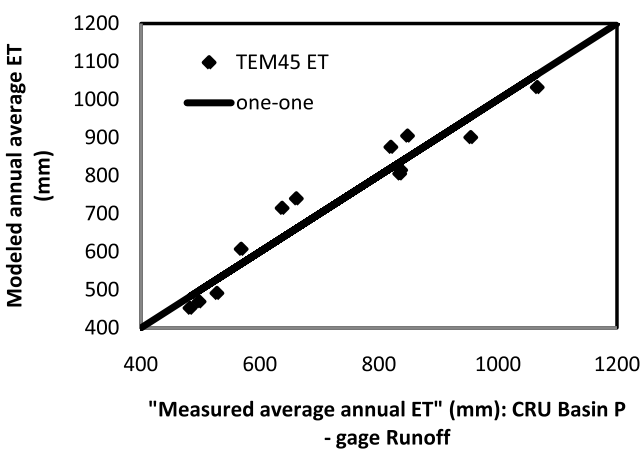


**Figure 4.** Scatterplot of modeled evapotranspiration (ET) versus observed ET calculated as the difference between precipitation (from the Climatic Research Unit [*Mitchell et al.*, 2003]) and runoff (from the USGS river gauge data) in mm $a^{-1}$ for the period 1970–1999 for the 12 watersheds used in this study.

[16] A comparison of ET for the different sensitivity experiments over the temperate forests of the United States

**Table 3.** River Basin Statistics, Including Area and Nash-Sutcliffe Coefficients for Monthly and Annual Runoff Values

| River Basin | Area ($km^2$) | NS (Monthly) | NS (Interannual) |
|---|---|---|---|
| Saline R., AR (Rye) | 5309 | 0.64 | 0.66 |
| Housatonic R, CT (Stevenson) | 4051 | 0.37 | 0.63 |
| Ochlockonee R., FL (Bloxham) | 4988 | 0.40 | 0.48 |
| Cumberland R., KY (Williamsberg) | 4259 | 0.70 | 0.29 |
| Muskegon R., MI (Evart) | 3546 | −0.87 | −0.10 |
| Big Black R., MS (West) | 2787 | 0.75 | 0.78 |
| Neuse R., NC (Kinston) | 7329 | 0.50 | 0.38 |
| Genessee R., NY (Mt. Morris) | 4010 | −0.13 | 0.39 |
| Lynches R., SC (Effingham) | 2653 | 0.40 | −0.01 |
| Duck R., TN (Columbia) | 3521 | 0.70 | 0.60 |
| Rappahannok R., VA (Fredericksburg) | 4161 | 0.48 | 0.07 |
| Winouski R., VT (Essex Jct.) | 2741 | 0.03 | 0.61 |
| Average | 4113 | 0.33 | 0.40 |

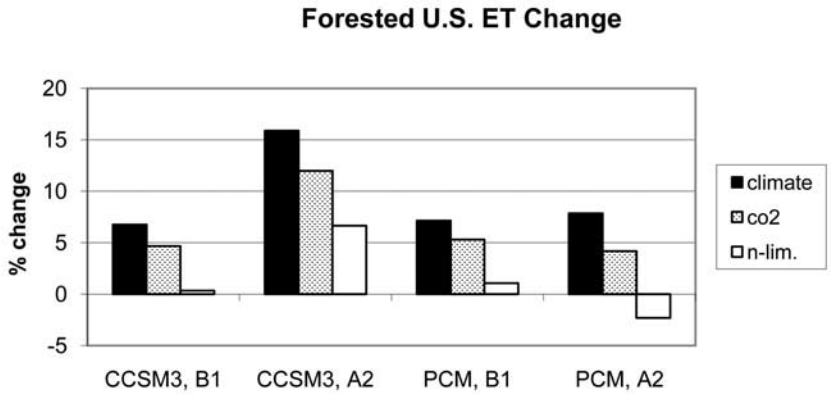


**Figure 5.** Percent change in evapotranspiration between future (2070–2099 mean) and baseline (1970–1999 mean) for U.S. temperate forests. Experiment descriptors are defined in Table 2.

(Figure 5) shows the range of changes in ET due to climate, elevated $CO_2$, nitrogen limitation, and ozone. Evapotranspiration values increase in the future in all cases except the N-limited case for the PCM A2 scenario. In each scenario, ET is greatest for climate alone, decreases when the net effects of elevated $CO_2$ are considered, and decreases further when nitrogen limitation and ozone are allowed to restrict photosynthesis. There are clear offsetting influences between the effects of higher temperatures and higher $CO_2$ levels on ET, with higher temperatures leading to increased ET and higher $CO_2$ levels leading to damped ET increases through reductions in stomatal conductance. Differences in runoff within a scenario are directly related to ET; the larger the increase in ET, the smaller the increase in runoff (Figure 6). Differences in runoff between scenarios are also driven by differences in precipitation. The PCM scenarios have smaller increases, or decreases, in runoff compared to CCSM3 because of the smaller increase in precipitation in the PCM (Table 1).

[17] The effect of elevated $CO_2$ (i.e., difference between the elevated $CO_2$ simulation results and the climate-only simulation results) on runoff by the end of the 21st century for the two models averages to a 3.3% increase over present for the B1 scenarios and a 6.2% increase for the A2 scenarios (Table 4). When nitrogen limitation and ozone are included, the increase over the elevated $CO_2$ experiment is 6.8% for the B1 scenarios and 9.6% for the A2 scenarios. Therefore the effects of N limitation and ozone on runoff are larger than the effect of elevated $CO_2$. The differences between the models, which are one measure of climate uncertainty, are larger than both of these for the B1 scenario (about 15.5% for both elevated $CO_2$ and N limitation/ozone experiments) and less for the A2 scenario (1.5–3.4%). So, in some cases, the biases from not considering the effects of nitrogen limitation and ozone damage to photosynthesis are larger than the uncertainties in climate.

[18] The amount of future increase in ET is directly dependent on the role of increasing gross primary productivity (GPP) on stomatal conductance. Changing climate alone results in modest increases in GPP (Figure 7), by increasing metabolic rates and by lengthening the growing season throughout much of the simulated region. The largest enhancement of GPP is due to elevated $CO_2$ and governed by atmospheric $CO_2$ concentrations, which are higher in the A2 than B1 scenarios. Nitrogen availability and ozone damage significantly limit $CO_2$ fertilization, but the degree of limitation is less in the warmest scenario (CCSM3, A2), due to the increased mineralization of soil nitrogen at higher temperatures [*Sokolov et al.*, 2008].

[19] Since our new modeling framework enables us to distinguish between canopy transpiration and soil evaporation, we can determine how the two covary. For the present-

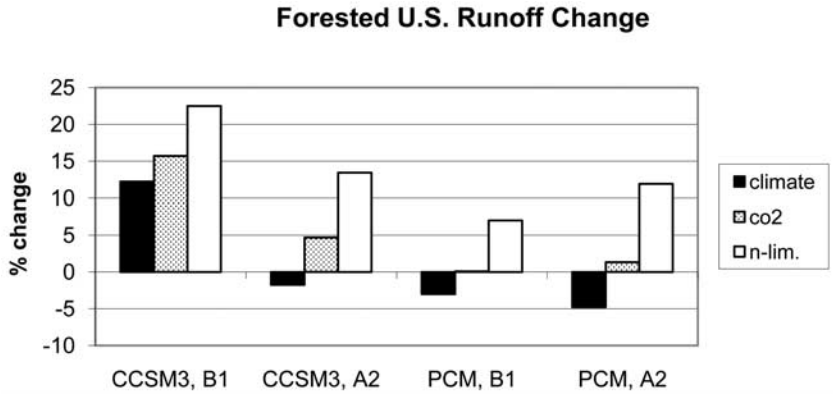


**Figure 6.** Percent change in runoff between future (2070–2099 mean) and baseline (1970–1999 mean) for U.S. temperate forests. Experiment descriptors are defined in Table 2.

**Table 4.** Percent Differences Between Future (2070–2099 Mean) and Baseline (1970–1999 Mean) for Evapotranspiration, Gross Primary Productivity, and Runoff[a]

| Percent ET Difference | CCSM3, B1 | PCM, B1 | CCSM3, A2 | PCM, A2 |
|---|---|---|---|---|
| Climate | 6.8 | 7.1 | 15.9 | 7.9 |
| $CO_2$ | 4.7 | 5.3 | 12.0 | 4.2 |
| N-lim. | 0.3 | 1.1 | 6.7 | −2.3 |
| Percent GPP difference | | | | |
| Climate | 11.4 | 9.2 | 11.8 | 7.7 |
| $CO_2$ | 36.1 | 34.0 | 55.1 | 50.2 |
| N-lim. | 19.4 | 17.5 | 26.8 | 17.9 |
| Percent runoff difference | | | | |
| Climate | 12.2 | −3.0 | −1.7 | −4.8 |
| $CO_2$ | 15.7 | 0.1 | 4.7 | 1.3 |
| N-lim. | 22.5 | 7.0 | 13.4 | 11.9 |

[a]For scenarios where only climate changes (climate), climate + elevated $CO_2$ ($CO_2$), climate + elevated $CO_2$ + N limitation + ozone (N-lim.). Evapotranspiration, ET; gross primary productivity, GPP.

day, the model results indicate that transpiration is 61% of the total evapotranspiration. Warming alone increases transpiration by 13–25% and soil evaporation by 2–10% in our model experiments. The effect of elevated $CO_2$ is to damp increases in transpiration because of lowered stomatal conductance. If this were the only effect of elevated $CO_2$ on ecosystems, we would expect this damping of transpiration to be accompanied by a slight rise in soil evaporation to balance the energy budget. However, in our model elevated $CO_2$ has the effect of decreasing soil evaporation, due to greater LAI, and thus less solar radiation at the soil surface, in response to the enhanced GPP. Including ozone damage and nitrogen limitation reduces transpiration, with concomitant increases in soil evaporation because of both energy balance and shadiness considerations.

[20] Water use efficiency (WUE), defined as GPP/transpiration, is expected to increase in the future as plants respond to elevated $CO_2$ levels through reduced stomatal conductance. For a given emissions scenario and climate model, the increase in WUE is always largest when considering elevated $CO_2$ but not nitrogen limitation and ozone. The smallest WUE increases occur with the climate-only runs. Averaging over each set of four runs (CCSM3 and PCM models, B1 and A2 scenarios) with elevated $CO_2$ and N limitation with ozone, the increase in WUE is 28% and 18%, respectively. This result is due to the reduced photosynthesis in the runs with N limitation and ozone, and the nonlinear dependence of transpiration on stomatal conductance. The increases in WUE in the PCM simulations are larger than the CCSM3 simulations for the A2 scenarios but smaller for the B1 scenarios.

## 4. Discussion

[21] Stomatal response to elevated $CO_2$ is affected by a complex set of plant physiological responses to concurrent changes in climate, N deposition, and ozone. Other studies of the effects of plant physiology on runoff have focused on the role of elevated $CO_2$ on stomatal conductance and not on the effects of reduced photosynthesis caused by nitrogen limitation and ozone damage. *Gedney et al.* [2006] indicate that increased runoff over land since 1960 is best explained as a result of elevated $CO_2$ reducing stomatal conductance rather than changes in land use, climate, or aerosol concentration. *Betts et al.* [2007] show a 6% increase in global runoff when considering the effects of a doubling of atmospheric $CO_2$ on plant physiology with the HadSM3 model, and also look at structural changes due to increasing LAI, which they show do not compensate for the reduced stomatal conductance. *Leipprand and Gerten* [2006] conclude that structural changes in vegetation can compensate for functional changes resulting from increasing vegetation cover in barren or partly barren areas, which would not apply to the eastern United States. *Cramer et al.* [2001] use an older version of the Hadley model to force several DGVMs and also conclude that terrestrial ecosystems increase runoff because of reduced transpiration due to higher $CO_2$ concentrations, which is similar to our results. However, our study suggests that other aspects of changing atmospheric chemistry may also be influencing stomatal conductance and runoff in addition to $CO_2$ concentrations.

[22] In a previous study, *Ollinger et al.* [2007] used the PnET-CN model, which includes nitrogen and ozone effects on photosynthesis, to simulate carbon and water dynamics at five sites in the northeastern United States forced by the HadCM3 and PCM models for the SRES A1fi and B1 scenarios. They ran experiments with and without the effect of $CO_2$ on both GPP and stomatal conductance and found higher runoff in an elevated $CO_2$ environment with these

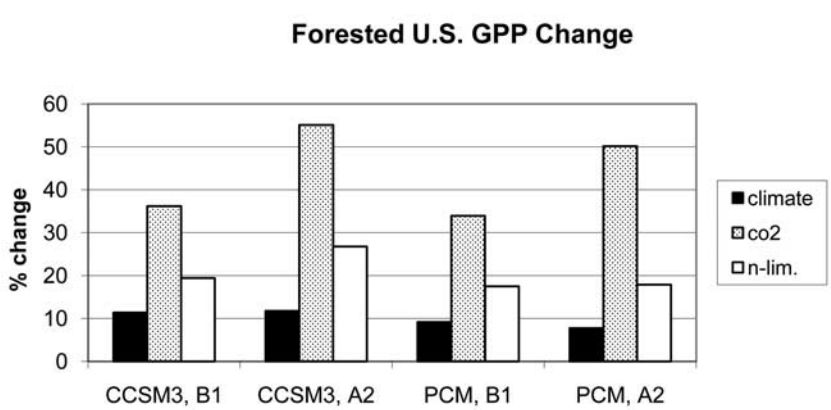


**Figure 7.** Percent change in gross primary productivity between future (2070–2099 mean) and baseline (1970–1999 mean) for U.S. temperate forests. Experiment descriptors are defined in Table 2.

plant physiological effects included. However, they did not separately examine the potential effects of nitrogen limitation and ozone damage on runoff in their study. With nitrogen limitation and ozone damage, our results show more of an increase in runoff due to dramatically lower photosynthetic rates in the future. For the A2 scenario, increasing ozone suppresses future photosynthesis in our study. For both scenarios, nitrogen limitation suppresses future $CO_2$ fertilization. We show that the effects of nitrogen limitation and ozone on runoff are potentially larger than the effects of elevated $CO_2$. Without these plant physiological effects, climate change itself often leads to reduced runoff, but the effects of plants on the hydrological cycle leads to increasing runoff.

[23] The effect of elevated $CO_2$ is to increase $CO_2$ fertilization and reduce stomatal conductance, which, as already noted, has compensating effects on evapotranspiration and the resulting runoff. In our model, nitrogen limitation reduces the magnitude of $CO_2$ fertilization, and the half-saturation constant kc becomes relatively unimportant for determining future GPP. In the carbon-only simulations, $CO_2$ fertilization becomes more important and sensitive to the choice of kc [*Sokolov et al.*, 2008]. Experimental evidence for larger $CO_2$ fertilization effects [*Curtis and Wang*, 1998; *Gunderson and Wullschleger*, 1994; *Kimball*, 1983; *Norby et al.*, 1999, 2005] and hence larger kc values, would result in more evapotranspiration and less runoff.

[24] Most temperate and boreal ecosystems are nitrogen limited, as evidenced by high C:N ratios and studies showing that nitrogen fertilization increases productivity [*Melillo and Gosz*, 1983; *Vitousek and Howarth*, 1991]. Nitrogen limitation may be alleviated in these systems by the presence of nitrogen fixers or atmospheric nitrogen deposition. Because nitrogen deposition results from fossil fuel combustion ($NO_x$) and agriculture (NHx), it has significantly decreased the degree of nitrogen limitation in temperate and boreal forests [*Magnani et al.*, 2007; *Melillo and Steudler*, 1989] and can be expected to do so even more in the future. Most studies have shown that nitrogen deposition increases carbon sequestration, but the magnitude of the effect has been the source of much debate. *Magnani et al.* [2007] have shown a large effect on carbon sequestration in European forests, on the order of 175–225 gC $gN^{-1}$ [*Magnani et al.*, 2008], while *Nadelhoffer et al.* [1999] have postulated a much smaller effect (50 gC $gN^{-1}$), assuming that less nitrogen remains in the live biomass and more in the litter and soils, which have a lower C:N. While we have not explicitly modeled nitrogen deposition in this study, we have observed in our simulations that enhanced nitrogen availability associated with increased net nitrogen mineralization increases GPP [*Sokolov et al.*, 2008], effectively increasing stomatal conductance and thereby reducing runoff. This result is consistent with field experiments which have found that under warmer conditions, increased nitrogen mineralization rates make more inorganic nitrogen available and increase NPP [*Melillo et al.*, 2002].

[25] Ozone damage to photosynthesis will offset some of the gains resulting from $CO_2$ fertilization [*Karnosky et al.*, 2003] and nitrogen deposition [*Felzer et al.*, 2007; *Ollinger et al.*, 2002]. A wide variety of studies have documented decreased growth due to ozone in eastern U.S. forests [e.g., *Chappelka and Samuelson*, 1998; *Heck and Furiness*, 2001; *Teskey*, 1996], though there are significant differences among species [*Pye*, 1988]. In the Aspen Free Air $CO_2$ Enrichment Experiment (FACE) at Rhinelander, WI, for example, *Karnosky et al.* [2005] found 29–40% reductions in GPP for aspen, whereas birch was largely affected only under elevated $CO_2$ conditions, and maple was not responsive at all. There is considerable uncertainty as to how ozone affects stomatal conductance. Since ozone uptake occurs through the stomata, many studies have shown reduced ozone damage under drought conditions [*Runeckles and Chevone*, 1992; *Showman*, 1991; *Smith et al.*, 2003]. Other studies, however, have shown greater ozone damage under moisture-stress conditions [*Bartholomay et al.*, 1997; *McLaughlin and Downing*, 1995, 1996]. Recent studies by *McLaughlin et al.* [2007a, 2007b] at mixed forest sites in Tennessee, show that ozone increases water stress by increasing stomatal conductance and therefore reducing runoff, which counters many other studies based on seedlings in Open Top Chambers that show reduced stomatal conductance resulting from ozone [*Reich and Amundson*, 1985; *Reich*, 1987]. Increased stomatal conductance and additional water stress would lead to even more ozone damage to photosynthesis. In this study, we assume that the only effect of ozone on stomatal conductance is the indirect reduction of stomatal conductance due to reduced GPP. Therefore, in our model, moisture stress leads to reduced stomatal conductance, which limits ozone damage.

[26] In a recent meta-analytic review by *Wittig et al.* [2007], they determined that ozone increases during the twentieth century have reduced light-saturated photosynthesis by 11% and stomatal conductance by 13%. When comparing our experiments with and without ozone, we find a 4.3% decrease in GPP and a 1.6% decrease in stomatal conductance for nitrogen-limiting conditions, and a 5.5% decrease in GPP and a 2.2% decrease in stomatal conductance for non-nitrogen-limiting conditions. Our more conservative estimates may be due to the effects of stomatal conductance on ozone uptake, the limitations resulting from monthly estimates of ozone uptake instead of instantaneous fluxes, or smaller regional ozone concentrations than those used in the meta-analysis.

## 5. Conclusions and Implications

[27] Our modeling study agrees with other studies that conclude that stomatal response to elevated $CO_2$ will affect future runoff, leading to larger increases or smaller decreases in runoff. However, the importance of this plant physiological response for predicting future runoff may be significantly larger than indicated by previous studies due to the suppression of $CO_2$ fertilization by nitrogen limitation and ozone exposure. Smaller than expected increases in photosynthesis, whether due to nitrogen limitation, saturation of $CO_2$ fertilization, or higher tropospheric ozone concentrations, will result in larger than expected increases in runoff. The degree to which elevated $CO_2$ will affect runoff for a given amount of precipitation is a function of the influences of nitrogen availability and ozone on plant photosynthesis. In combination with elevated $CO_2$ concentrations, nitrogen limitation and ozone will also limit the

expected increase in evapotranspiration resulting from future global warming.

[28] Future $CO_2$ and ozone concentrations, and nitrogen deposition, will be determined largely by the collective actions of humankind. Furthermore, these variables are not independent: the same fossil fuels that are responsible for rising atmospheric $CO_2$ concentrations also release other pollutants to the atmosphere, which can contribute both to the formation of tropospheric ozone, and the deposition of nitrogen on ecosystems. Policies enacted to reduce the emission of greenhouse gases will have a synergistic benefit of also reducing precursors of ozone and nitrogen deposition. Similar to elevated $CO_2$, the effects of these stresses on ecosystems are offsetting to some degree: ozone serving to decrease plant productivity and increase runoff, and nitrogen deposition acting to increase plant productivity and decrease runoff. However, unlike $CO_2$, nitrogen deposition and ozone pollution are largely regional problems, because of the shorter residence times of ozone and reactive nitrogen compounds in the atmosphere. Also, the spatial distribution of these stresses, while linked, is not exactly coincident; because of photochemical processes, maximum ozone occurs to the south of maximum nitrogen deposition [*Felzer et al.*, 2007]. While cleaning up pollution may have an immediate effect in terms of increasing plant productivity by removing ozone damage, the footprint of nitrogen deposition will persist in the form of elevated ecosystem nitrogen stocks. Policies on the regional scale will thus be important in determining how ozone damage and nitrogen limitations evolve over time. For example, both surface ozone [*Lin et al.*, 2001] and nitrogen deposition [*CASTNET*, 2007] precursors in the eastern United States have decreased since the 1980s as a result of pollution policies. The effects of ozone and nitrogen deposition on plant productivity and runoff are a complex product of pollution policies, climate, atmospheric chemistry, and ecosystem inertia due to large reservoirs.

[29] While other studies have shown that $CO_2$ fertilization can have a significant effect on increasing runoff levels in the future, our study shows that the consideration of nitrogen limitation and ozone damage on photosynthesis may have an even larger effect than elevated $CO_2$. It is therefore necessary for future modeling studies to account for these terms in order to accurately determine the effects of a changing climate on the fate of terrestrial water cycling.

[30] **Acknowledgments.** This study was funded by the Interdisciplinary Science Program of the U.S. National Aeronautics and Space Administration (NNG04GJ80G, NNG04GM39G), the Dynamic Global Economic Modeling of Greenhouse Gas Emissions and Mitigation from Land-Use Activities of the U.S. Environmental Protection Agency (XA-83240101), and the Nonlinear Response to Global Change in Linked Aquatic and Terrestrial Ecosystems of the U.S. EPA (XA-83326101). Thanks to B. Fekete at University of New Hampshire for the river basin network and to the U.S. Geological Survey (USGS) for river discharge data. We acknowledge the modeling groups, the Program for Climate Model Diagnosis and Intercomparison (PCMDI) and the WCRP's Working Group on Coupled Modeling (WGCM) for their roles in making available the WCRP CMIP3 multimodel data set. Support of this data set is provided by the Office of Science, U.S. Department of Energy.

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