**Biogeosciences
Discussions**

Predicting photosynthesis and transpiration responses to ozone: decoupling modeled photosynthesis and stomatal conductance

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Abstract

Plants exchange carbon dioxide and water, two key greenhouse gases, with the atmosphere through the processes of photosynthesis and transpiration, making them essential in climate regulation. Carbon dioxide and water exchange are typically coupled through the control of stomatal conductance, and the parameterization in many models often predict conductance based on photosynthesis values. Some environmental conditions, like exposure to high ozone (O_3) concentrations, alter photosynthesis independent of stomatal conductance, so models cannot accurately predict both. The goals of this study were to test direct and indirect photosynthesis and stomatal conductance modifications based on O_3 damage in a coupled Farquhar/Ball-Berry model. The same modifications were then tested in the Community Land Model (CLM) to determine the impacts on gross primary productivity (GPP) and transpiration. Modifying the V_{cmax} parameter and directly modifying stomatal conductance best predicts photosynthesis and stomatal conductance responses to chronic O_3 over a range of environmental conditions. On a global scale, directly modifying conductance reduces the effect of O_3 on both transpiration and GPP compared to indirectly modifying conductance, particularly in the tropics. The results of this study suggest that independently modifying stomatal conductance can improve the ability of models to predict hydrologic cycling, and therefore improve future climate predictions.

1 Introduction

Surface vegetation has a strong, direct effect on climate through regulating both carbon and hydrologic cycles on regional and global scales (Bonan, 2008). Often, carbon and water exchange between plants and the atmosphere is closely coupled. On a leaf level, stomatal aperture controls the amount of carbon entering and water exiting the leaf, and responds to changes in many environmental parameters, such as light, temperature, and carbon dioxide concentrations (Jones, 1998; Schroeder et al., 2001).

Though regulation of stomatal conductance is the primary mechanism plants use to regulate water loss via transpiration, it is only one of the mechanisms controlling photosynthetic carbon gain; biochemical assimilation of carbon (carboxylation) also plays a large role (Cowan and Troughto, 1971; Jones, 1998; von Caemmerer and Farquhar, 1981). Under circumstances where carboxylation is damaged or not limited by stomatal conductance, photosynthesis and conductance can become decoupled. For example, many C_3 plants do not completely close stomatal guard cells at night, resulting in water loss during a time when carboxylation does not occur due to a lack of light (Caird et al., 2007). Also, when plants are exposed to high light levels or high ozone (O_3) concentrations, membranes and photosystems become oxidized, decreasing carboxylation rates often without decreasing stomatal conductance at the same rate or magnitude (Calatayud et al., 2007; Demmig-Adams and Adams, 2006; Francini et al., 2007; Maiermaercker and Koch, 1991; Matyssek et al., 1991; Paoletti, 2005; Pearson and Mansfield, 1993; Tjoelker et al., 1995). In all of these scenarios, photosynthesis and stomatal conductance can become decoupled, changing the relationship between carbon gain and water loss.

Models are a primary method of studying how vegetation interacts with climate on regional and global scales. Often, models scale leaf-level physiology to ecosystem and global levels by assuming that photosynthesis and transpiration are closely coupled and, in fact, calculate stomatal conductance based on photosynthetic values. For example, the physiological model of photosynthesis derived by Farquhar (Farquhar et al., 1980) and the Ball-Berry model of stomatal conductance (Ball, 1987) are commonly used together in regional and global models and accurately predict observed photosynthesis and stomatal conductance under many conditions (Collatz et al., 1991; Harley et al., 1992; Misson et al., 2004; von Caemmerer and Farquhar, 1981). In this formulation, the photosynthesis calculations are influenced by feedbacks from changes in stomatal conductance because conductance regulates internal carbon dioxide (CO_2) concentration (c_i), which drives the biochemical components of photosynthesis (see Eq. 1). In contrast, the Ball-Berry conductance equation is calculated directly from photosynthetic

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rates (see Eq. 2), in addition to other factors like ambient CO_2 concentration ($[CO_2]$), a relative humidity gradient, and atmospheric partial pressure.

Despite the accuracy of the Farquhar/Ball-Berry physiological model in many situations, conditions that increase or decrease carboxylation without subsequent changes in stomatal conductance cannot be accurately predicted due to the direct dependence of stomatal conductance calculations on the photosynthetic rate. For example, the relationship between photosynthesis and transpiration changes after chronic O_3 exposure due to damage to functional aspects of both carboxylation and stomatal conductance, causing larger decreases in photosynthesis than transpiration (Calatayud et al., 2007; Francini et al., 2007; Maiermaercker and Koch, 1991; Matyssek et al., 1991; Paoletti, 2005; Pearson and Mansfield, 1993; Tjoelker et al., 1995). Models using Farquhar/Ball-Berry equations to predict O_3 damage to photosynthesis with proportional responses in conductance (Felzer et al., 2004; Ollinger et al., 1997; Sitch et al., 2007), therefore predict overly large decreases in stomatal conductance (Lombardozzi et al., 2012), which, when scaled from leaf-level responses to regional and global responses through time result in large inaccuracies in predicted transpiration. Sitch et al. (2007) predicted that O_3 has a large, indirect impact on climate through suppressing photosynthesis, resulting in more CO_2 in the atmosphere. However, the method used assumes a proportional decrease in stomatal conductance. Considering differential responses of photosynthesis and stomatal conductance will allow transpiration to decrease less than predicted by such simulations, resulting in relative increases in atmospheric water vapor, an important greenhouse gas, in addition to increasing CO_2 concentrations, potentially exacerbating warming more than currently predicted.

Ozone damage to plants is a unique yet important scenario to incorporate into models because many regions already experience damaging concentrations (>40 ppb) that change the ability of plants to exchange carbon and water with the atmosphere (Wittig et al., 2007), an important ecosystem service in regulating climate (Bonan, 2008). Damage to photosynthesis, quantified in several meta-analyses and reviews (Feng et al., 2008; Morgan et al., 2003; Wittig et al., 2007), is caused by mechanisms that

include reductions in leaf chlorophyll content that impact electron transport (Heagle et al., 1996; Sharma, 2003), declines in carboxylation efficiency through reductions in the quantity and activity of the primary carboxylation enzyme Rubisco (Fiscus et al., 2005), and/or direct damage to stomatal cells (Hassan et al., 1994; Manes et al., 2001; Torsethaugen et al., 1999). Though stomatal cells can impose a diffusional limitation to photosynthesis, several studies suggest that carboxylation and mesophyllic limitations are more important than stomatal limitation in trees exposed to O_3 (Francini et al., 2007; Matyssek et al., 1991; Noormets et al., 2001; Reichenauer et al., 1997). Typically, stomata close in response to O_3 as an indirect response to increasing internal CO_2 concentration (c_i) that results from decreases in carbon fixation (Paoletti, 2005). However, the magnitude of stomatal decrease is seldom equal to the magnitude of total photosynthetic decrease under chronic O_3 exposure (Calatayud et al., 2007; Francini et al., 2007; Maiermaercker and Koch, 1991; Matyssek et al., 1991; Novak et al., 2005; Paoletti, 2005; Pearson and Mansfield, 1993; Tjoelker et al., 1995).

Acute instantaneous exposure at moderate or high concentrations of O_3 can cause instantaneous reductions in conductance similar in magnitude to photosynthesis (Farage et al., 1991). In contrast, chronic exposure often leads to sluggish stomatal responses to environmental stimuli due to loss of stomatal functioning and a decoupling of conductance from photosynthesis due to direct damage to biochemical carboxylation (Paoletti, 2005; Tjoelker et al., 1995). In fact, several studies demonstrate that sluggish stomatal cells can also result in increases in conductance and/or integrated diurnal transpiration (Hassan et al., 1994; McLaughlin et al., 2007). These observations suggest that models can better represent the influence of chronic O_3 through modifying parameters that estimate responses of carboxylation rather than total photosynthesis and directly modifying stomatal conductance because it often responds independent of photosynthesis.

To date, regional and global models that have incorporated O_3 damage to plants change only photosynthesis and assume a tight correlation between photosynthetic rate and stomatal conductance (Felzer et al., 2004, 2005; Ollinger et al., 1997, 2002;

Ren et al., 2011; Sitch et al., 2007), allowing photosynthesis to ultimately drive changes in transpiration. Since experimental data suggest O_3 damage to plants changes the relationship between photosynthesis and conductance, the standard Farquhar/Ball-Berry parameterization that couples these processes will not be capable of accurately predicting both processes. As a result, there are currently no accurate estimates of changes in some of the most important climate controls – transpiration, latent heat flux, hydrology and water cycling – due to O_3 damage to plants.

The objectives of this work were to: (1) determine the best photosynthesis and stomatal conductance parameterization to predict physiological responses to O_3 in a leaf-level Farquhar photosynthesis/Ball-Berry conductance model; and (2) to incorporate the most accurate O_3 parameterization into the Community Land Model version 4 (CLM4SP; described in Lawrence et al., 2011), the land component of the Community Earth System Model (CESM). To determine the best predictors of O_3 damage, we expanded upon work by Lombardozzi et al. (2012) to test an additional method of modifying photosynthesis and stomatal conductance in a Farquhar photosynthesis/Ball-Berry conductance model. Using CLM4SP, we then determined the differences in global gross primary productivity (GPP) and transpiration due to direct changes to photosynthesis and stomatal conductance compared to indirect changes that alter transpiration by modifying photosynthesis.

2 Methods

2.1 Farquhar photosynthesis/Ball-Berry conductance model description

The Farquhar/Ball-Berry model predicts leaf-level photosynthesis and stomatal conductance over a range of environmental conditions. The specific implementation used here is the model used by Lombardozzi et al. (2012) and is a variant of the Ball-Berry stomatal conductance model (Ball, 1987; Collatz et al., 1991), the Farquhar et al. (1980) C_3 photosynthesis model extended to include product-limited photosynthesis

(Harley and Sharkey, 1991; Harley et al., 1992) and C_4 photosynthesis (Collatz et al., 1992). In this parameterization, the model represents photosynthetic uptake of CO_2 as limited by: (i) Rubisco-limited photosynthesis, A_c, (ii) RuBP-limited photosynthesis, A_j, or (iii) product-limited photosynthesis, A_p (see Equations in Bonan et al., 2011). The net CO_2 assimilation rate, A_n, is:

$$A_n = \min(A_c, A_j, A_p,) - R_d \tag{1}$$

where R_d is dark respiration. The required internal leaf CO_2 concentration (c_i) is calculated from the diffusion equations:

$$A_n = (c_a - c_s)(g_b/1.4) = (c_s - c_i)(g_s/1.6) \tag{2}$$

where c_a is the ambient [CO_2], c_s is the [CO_2] at the leaf surface, g_b is the leaf boundary layer conductance, and g_s is the stomatal conductance. The photosynthesis model is coupled to the Ball-Berry stomatal conductance model (Ball, 1987; Collatz et al., 1991), in which stomatal conductance, g_s, is calculated based on the relationship:

$$g_s = b + m A_n h_s / c_s \tag{3}$$

where b is the minimum stomatal conductance when $A_n \leq 0$, m is the Ball-Berry slope of the conductance-photosynthesis relationship, and h_s is the fractional humidity at the leaf surface. Additional details are given in Bonan et al. (2011). The coupling of photosynthesis and stomatal conductance models results in a direct dependence of stomatal conductance on photosynthesis, while stomatal conductance plays a role in predicting photosynthesis by controlling c_i, which is obtained from the diffusion equation and therefore depends on g_s. The model is forced with specified environmental variables, with c_a ranging from 50–2000 μmol CO_2 mol^{-1} air, light ranging from 0–2000 μmol photons m^{-2} s^{-1}, temperature = 22 °C, h_s = 0.70, and g_b = 0.05 m s^{-1}.

2.1.1 Ozone response relationships

Photosynthesis. Two methods of simulating O_3-induced decreases in photosynthesis were compared. The first method of modifying photosynthesis expanded on work by

Lombardozzi et al. (2012) and is denoted here as the Psn modification. This modification mimicked observed decreases in photosynthesis using an O_3 factor developed by Lombardozzi et al. (2012), F_{AO3}, calculated from a linear regression of treatment to control response ratios against cumulative O_3 uptake (CUO):

$$F_{AO3} = 1.0421 - 0.2399 \times CUO \tag{4}$$

where F_{AO3} is the response ratio of treatment to control photosynthesis, 1.0421 and 0.2399 are empirically derived intercept and slope coefficients, respectively, and CUO is the cumulative O_3 uptake. The calculation for CUO assumes that the $[O_3]$ inside the leaf is zero and is calculated as:

$$CUO = \Sigma(k_{O3}/g_s)[O_3] \tag{5}$$

similar to Reich (1987), Nunn et al. (2006) and Wittig et al. (2007), where $k_{O3} = 1.67$ and is the ratio of leaf resistance to O_3 to leaf resistance to water, g_s is leaf-level stomatal resistance, and $[O_3]$ is the O_3 concentration. CUO is summed through time, with units of mmol m^{-2}. The Psn modification occurs post hoc in which net photosynthesis, after it is calculated using the leaf photosynthesis/stomatal conductance model, is multiplied by F_{AO3}. This method of modifying photosynthesis is similar to parameterizations in most other models that incorporate O_3 damage to physiology (e.g. Felzer et al., 2004, 2005; Ollinger et al., 1997, 2002; Ren et al., 2011; Sitch et al., 2007).

The second method of modifying photosynthesis, denoted here as Rub, impacts the biochemical aspects of photosynthesis directly through altering the V_{cmax} parameter in the Farquhar model. V_{cmax} integrates mesophyllic conductance with enzyme amount and activity and therefore estimates aspects of biochemical carbon fixation that are often damaged with O_3 exposure (Calatayud et al., 2010; Cardoso-Vilhena et al., 2004; Farage and Long, 1999; Feng et al., 2008; Fiscus et al., 2005; Noormets et al., 2001; Ojanpera et al., 1998; Pellegrini et al., 2010; Zheng et al., 2002). This modification mimicked observed decreases in V_{cmax} using an O_3 factor calculated from work by Lombardozzi et al. (2012), F_{RO3}:

$$F_{RO3} = 0.9888 - 0.1976 \times CUO \tag{6}$$

where F_{RO3} is the response ratio of treatment to control V_{cmax}. The Rub modification multiplies V_{cmax} by F_{RO3}, using the O_3-modified V_{cmax} in photosynthesis calculations. This method of modifying photosynthesis through changing V_{cmax} is similar to parameterizations used in Martin et al. (2000) to simulate photosynthetic responses to acute O_3 exposure and Constable and Taylor (1997) to simulate chronic exposure.

Stomatal Conductance. A new method of simulating O_3-induced decreases in stomatal conductance by altering the V_{cmax} parameter in photosynthesis calculations was compared to the Cnd modification developed by Lombardozzi et al. (2012). The Cnd modification altered stomatal conductance directly using an O_3-factor calculated by Lombardozzi et al. (2012), F_{GsO3}, calculated from a linear regression of treatment to control response ratios against cumulative O_3 uptake (CUO):

$$F_{GsO3} = 1.0884 - 0.1998 \times CUO \tag{7}$$

where F_{GsO3} is the response ratio of treatment to control stomatal conductance, and 1.0884 and 0.1998 are empirically derived intercept and slope coefficients, respectively. The Cnd modification multiplies stomatal conductance by F_{GsO3} after stomatal conductance is calculated and does not alter the photosynthesis calculations in the model.

The second method of altering stomatal conductance, denoted as Rub, modified conductance indirectly using the new modification to the photosynthesis model, which modified V_{cmax} by F_{RO3} (described above). This simulation relied on photosynthetic decreases to indirectly drive stomatal conductance decreases, similar to methods used by Martin et al. (2000) and Constable and Taylor (1997).

2.1.2 Simulations

Each photosynthesis (Psn, Rub) and stomatal conductance (Cnd, Rub) modification simulated light curves at three O_3 uptake levels (0, 2 and 4.2 mmol m^{-2}) by calculating photosynthesis and stomatal conductance over a range of light values from 0 through 2000 µmol m^{-2} s^{-1} with [CO_2] at 380 ppm and a temperature of 25 °C. Additionally, each

photosynthesis modification simulated A-c_i curves at all three O_3 uptake levels by calculating photosynthesis over a range of [CO_2] from 50 to 2000 ppm with light equal to 2000 µmol m^{-2} s^{-1} and a temperature of 25 °C. The simulated plants were individualized through changing dark respiration (R_d) rates and model parameters V_{cmax} and J_{max} were set to appropriate values based on measured rates for the experimental plants. The model was evaluated by comparing predictions of photosynthesis and stomatal conductance with plant responses measured in Lombardozzi et al. (2012).

2.1.3 Statistical analysis

Results of the simulations were analyzed to determine which modification allowed the model to best fit the data using R$^{©}$ version 2.11.1. Simulations were analyzed for root mean squared error (RMSE) to quantify the variance and mean bias (MB) to determine the magnitude and direction of the model bias. Linear mixed-effects models with plant as the random factor were fit to the experimental data using the nlme package in R (Pinheiro, 2011). The model with the highest likelihood was selected as the best model.

2.2 Testing the community land model

The CLM4SP represents biophysical land surface processes within the context of a global climate simulation model and is described in Lawrence et al. (2011). In this study, the model was run in offline mode forced with a historical atmospheric dataset that includes observed precipitation, temperature, downward solar radiation, surface windspeed, specific humidity, and air pressure from 1948 through 2004 (Qian et al., 2006). The CLM4SP uses coupled Farquhar photosynthesis and Ball-Berry stomatal conductance models (Bonan et al., 2011; Oleson, 2010) to simulate plant physiology.

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2.2.1 Ozone Effects

To incorporate the effects of O_3 on photosynthesis and stomatal conductance into the CLM4SP, we used the Rub photosynthesis modification and the Cnd stomatal conductance modification to the Farquhar/Ball-Berry model. The Rub modification had the highest likelihood of accurately predicting photosynthesis through modifying the V_{cmax} parameter in the model. Likewise, the Cnd modification had the highest likelihood of predicting stomatal conductance through directly modifying the conductance variable. Additionally, the Cnd modification allowed the most flexibility in simulating other situations where stomatal conductance responds independently of photosynthesis. For example, stomata sometimes respond sluggishly after chronic O_3 exposure (e.g. Paoletti, 2005), so the Cnd parameterization can be used to simulate O_3-induced changes in diurnal transpiration. Nighttime transpiration and damage from photo-oxidation can also be simulated using the Cnd modification.

Ozone effects on both photosynthesis and stomatal conductance were included in the CLM4SP based on the O_3 response factors calculated for the Farquhar/Ball-Berry model. Cumulative O_3 uptake (CUO) was calculated by the CLM4SP rather than being specified as in the leaf-level simulations. Therefore, four key differences existed in the calculations of CUO. First, CUO in the CLM was calculated using the sum of stomatal, boundary layer, and aerodynamical resistances. Second, a critical uptake threshold of $0.8 \, \text{nmol} \, O_3 \, \text{m}^{-2} \, \text{s}^{-1}$ was used as an instantaneous, flux-based threshold (similar to methods used in Sitch et al., 2007). Third, because O_3 damage is cumulative, we included a leaf-turnover O_3 decay rate so that accumulated O_3 damage did not accrue beyond the average leaf lifetime for evergreen plants. Last, CUO was only integrated over the time when leaf area index (LAI) was above a minimum value of 0.5. This threshold was chosen based on modeled LAI values because LAI values often asymptote in the model rather than reaching 0 (see Fig. 1), causing O_3 accumulation to be too high. For a deciduous tree species, the 0.5 LAI threshold did not significantly change accumulated O_3 damage.

2.2.2 Simulations

Since photosynthesis and stomatal conductance were inherently linked in the CLM due to the traditional Ball-Berry formulation, calculations for both variables were made three times during each simulation to allow for separation between optimal rates and O$_3$-influenced rates. The first calculations provided optimal levels of photosynthesis (Psn$_{opt}$) and stomatal conductance (g_{sopt}) and were calculated in the absence of O$_3$. The second set of calculations directly modified photosynthesis (Psn$_{O3}$) for O$_3$ and allowed stomatal conductance (g_{sfb}) to respond indirectly and through feedback loops. The third set of calculations modified stomatal conductance (g_{sO3}) for O$_3$ and allowed photosynthesis (Psn$_{fb}$) to respond via feedback loops. We used this parameterization to run four different experimental simulations (see Table 2) that determined the magnitude of direct and indirect responses in addition to feedback loops between photosynthesis and stomatal conductance. This verified that the indirect responses could be eliminated. Simulations were named with letters "p" when photosynthesis was modified and "g" when stomatal conductance was modified, with a capital letter (e.g. P and G) signifying that the modification was direct and a lower case letter (e.g. p and g) signifying that the modification was indirect. The objective of each simulation was to determine the optimal or O$_3$-influenced photosynthesis and stomatal conductance values to be used in the downstream calculations like GPP and transpiration. For example, to determine whether O$_3$-modified photosynthesis could be calculated without influencing transpiration, the model used modified photosynthesis, Psn$_{O3}$, and optimal conductance, g_{sopt}, for all downstream calculations.

To create a new modeling framework that would allow for decoupled behavior of photosynthesis and stomatal conductance, we took several steps to test the model behavior and make observed differences large. First, all simulations were run at a constant O$_3$ concentration of 100 ppb. This is an unrealistically high global concentration of O$_3$, but it helped to determine whether O$_3$ damage could be independently incorporated for photosynthesis and stomatal conductance and to identify hotspots where O$_3$

damage might have a large impact on GPP and transpiration. Second, for simplicity all O_3 modifications were based on data collected on tulip poplar seedling responses to O_3 (Lombardozzi et al., 2012). Plant species-specific responses representing multiple plant functional types should be used once these data become available. Each simulation was run for a total of 25 years, with the first 5 years being discarded in analyses to allow for stabilization of accumulated O_3 damage.

3   Results

3.1   Farquhar Photosynthesis/Ball-Berry conductance model

All stomatal conductance modifications to the Farquhar/Ball-Berry model decreased predicted conductance with increasing O_3 uptake, though the magnitudes varied (Fig. 2a–c; Table 1). When comparing the ability of each modification to predict the observed conductance light curves, the Cnd modification, which changed conductance directly, best predicted the observation (neg. log likelihood = 199.0) and was selected for use in CLM simulations. The Rub modification, which changed predicted conductance indirectly, did not perform as well as the Cnd modification (neg. log likelihood = 200.7) and had a higher mean bias (bias = 0.027) compared to the Cnd simulation (bias = 0.020). At low light levels, modifications predicted conductance values lower than observed conductance values. Root mean square error was the same for both simulations (Rub and Cnd RMSE = 0.051).

Both the Psn modification and the Rub modification decreased predicted net photosynthetic rates with increasing O_3 uptake, similar to observed net photosynthetic rates. Photosynthesis modifications predicted light curves more accurately than A-c_i curves at all O_3 uptake values (Fig. 2d–f and 2g–i), with mean biases for light curves close to 0 for both modifications (Psn = 0.07; Rub = −0.008) and RMSE approximately 1.2 μmol CO_2 m^{-2} s^{-1}. The Rub modification predicted observed responses to light better than the Psn modification (Fig. 2d–f; Rub neg. log likelihood = −158.6; Psn neg. log

likelihood $= -164.6$). When compared to observed A-c_i curves, the Rub modification outperformed the Psn modification at each O_3 uptake value (Fig. 2g–i; Rub neg. log likelihood $= -227.658$; Psn neg. log likelihood $= -312.390$). Both modifications were positively biased, though the RMSE of the Rub modification was $0.93\,\mu mol\,CO_2\,m^{-2}\,s^{-1}$ less than the Psn modification. Overall, the Rub modification predicts photosynthesis more accurately in both A-c_i and light curves than the Psn modification (Table 1; Fig. 2). Consequently, the Rub photosynthesis modification was selected for use in all CLM simulations.

3.2 CLM simulations

Analysis initially focused on a 5×5 grid centered on Ithaca, NY, where photosynthetic and stomatal modifications were developed. In the simulated region surrounding Ithaca, NY, transpiration and photosynthesis decreased in response to O_3 exposure. When O_3 directly altered conductance in the PG simulation, transpiration decreased ($r^2 = -0.90$; rate $= -8.68$) at a slower rate than photosynthesis ($r^2 = -0.89$; rate $= -10.44$) for the same O_3 uptake (Fig. 3a; $p = 0.192$). At an O_3 uptake of $4\,mmol\,m^{-2}$ in the PG simulation, photosynthesis decreased by 85 %, whereas transpiration only decreased by 76.5 %. Indirect changes in conductance in the Pg simulation resulted in more similar rates of change in photosynthesis ($r^2 = -0.92$; rate $= -9.12$) and transpiration ($r^2 = -0.91$; rate $= -9.23$; $p = 0.781$), where photosynthesis decreased by 85.8 % and transpiration decreased by 81 % at an O_3 uptake of $4\,mmol\,m^{-2}$ (Fig. 3b).

When simulations were analyzed globally, global transpiration decreased in all simulations when O_3 modifications caused decreases in stomatal conductance. The Pg simulation, which modified photosynthesis directly and conductance indirectly, caused substantially larger decreases in transpiration than the PG simulation, which changed photosynthesis and stomatal conductance directly. Compared to control simulations, transpiration rates decreased more than 50 % in many areas in the Pg simulation, with

the largest decreases in the tropics and other regions with high control transpiration rates (Fig. 4b). In contrast, the PG simulation produced smaller decreases in transpiration in tropical regions (Fig. 4c), typically less than 50 %, and similar decreases in mid- and high-latitudes (40–80 %). Relative differences between the Pg and PG simulations (Fig. 4d) show that the PG simulation, changing conductance directly, results in higher transpiration rates – greater than 25 % in most tropical regions – than predicted by the Pg simulation in almost all locations. In a few temperate locations, however, the PG simulation caused transpiration to decrease up to 10 % more than the Pg simulation.

Independently modifying photosynthesis and conductance in the CLM (the PG simulation) reduced the effect of O_3 on GPP in regions with high control photosynthetic rates compared to the Pg simulation. The Pg simulation decreased GPP in most locations, with decreases of more than 70 % in the tropics and high latitudes (Fig. 5b). The PG simulation also reduced GPP globally, though the decreases were less than 50 % in most tropical regions (Fig. 5c) and the largest decreases were in the high latitudes, which decrease GPP by 50 % or more from control simulations. Differences between the Pg and PG simulations (Fig. 5d) demonstrate that the PG simulation, through modifying conductance directly, results in GPP nearly 50 % higher in the tropics than predicted by the Pg simulation. Differences between the PG and Pg simulation are smaller (+/- 20 %) at mid- and high- latitudes, with the PG simulation resulting in both higher and lower GPP than the Pg simulation.

Directly modifying stomatal conductance in the CLM changed the rate of O_3 uptake in the PG simulation compared to the Pg simulation (Fig. 6). Average uptake rates in the Pg simulation ranged from 1–3 mmol m^{-2} in the mid- and high-latitudes and approached 5 mmol m^{-2} in the tropics (Fig. 6a). Average O_3 uptake rates in the PG simulation were similar to those in the Pg simulation at mid- and high-latitudes, though only reached 2.5–3 mmol m^{-2} in the tropics (Fig. 6b).

The Pg and the PG simulations caused small changes in relative humidity (RH) compared to control simulations (Fig. 7). Most changes in RH were similar in the PG and Pg simulations, though RH decreased slightly less in the tropics in the PG simulation,

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resulting in a relative increase in RH compared to the Pg simulation (Fig. 7d). Though RH did not change in all locations, it decreased 1–2 % on average in Pg and PG simulations compared to the control simulation (Fig. 7b and c). However, RH increased up to 1 % in Australia and in a few locations in Asia, Africa, and North America.

While changes to stomatal conductance were implemented differently in the Pg (indirect) and PG (direct) simulations, changes made to photosynthesis were the same with differences only expected due to different O_3 uptake rates. To ensure that GPP responds the same in both the Pg and PG simulations at the same O_3 uptake rate, the PG and Pg simulations were forced with a constant O_3 uptake rate of $3\,mmol\,O_3\,m^{-2}$ (Fig. 8). Both simulations had the same O_3 uptake rates (Fig. 8a) and similar GPP (Fig. 8b) in the single-year analysis. Transpiration, however, differed between the simulations with +/- 10 % differences between the PG and Pg simulations.

To determine whether the photosynthesis and conductance modifications were truly independent, each direct parameter change was run independently without any indirect changes to the other parameter (Fig. 9). Simulation P, where only photosynthesis modifications were implemented, had no effect on transpiration with 0% changes from control transpiration rates in all regions (Fig. 9b), though the effect on GPP was quite large, with decreases close to 100 % in most locations (Fig. 9a). Simulation G, where only stomatal conductance modifications were implemented, resulted in decreases in transpiration nearly identical to the PG case, with decreases up to approximately 50 % in the tropics (Fig. 9d). Simulation G also changed GPP in some locations, causing decreases from control GPP that were less than 15 % and increases in other locations up to 30 %, though there were almost no changes in GPP in tropical locales.

4 Discussion

Many land surface components of climate models, such as the CLM, use the coupled Farquhar/Ball-Berry model to predict photosynthesis and stomatal conductance, which are then scaled to tree, canopy, ecosystem or global areas. However, changing

photosynthesis in response to chronic O_3 exposure within the current Farquhar/Ball-Berry formulation does not accurately represent changes in stomatal conductance. Even small errors in stomatal conductance, when scaled to ecosystem or global areas, can propagate large errors in transpiration that then impact climate. Despite this fact,

5 most studies modeling regional and global responses to O_3 (e.g. Felzer et al., 2004, 2005; Ollinger et al., 1997, 2002; Ren et al., 2011; Sitch et al., 2007) focus primarily on changes in carbon and do not verify the accuracy of stomatal conductance predictions.

Implementing stomatal conductance responses to O_3 independently of photosynthetic responses, the Cnd modification, improved the ability of the coupled

10 Farquhar/Ball-Berry model to predict observed conductance values (Table 1; Fig. 2). This is different than the results of Martin et al. (2000), which found that altering V_{cmax} accurately predicted conductance. However, the simulations in Martin et al. (2000) were based on responses of wheat to acute, rather than chronic, O_3 exposure where conductance and photosynthesis decreased at similar rates in response to high $[O_3]$

15 over a short period of time. Since chronic O_3 exposure often causes conductance and photosynthesis to decrease at different rates (Calatayud et al., 2007; Francini et al., 2007; Matyssek et al., 1991; Maurer et al., 1997; Mikkelsen, 1995; Novak et al., 2005b; Paoletti and Grulke, 2005; Soldatini et al., 1998; Tjoelker et al., 1995), as it did in the plants used to parameterize these simulations, the ability of the Cnd modi-

20 fication to improve the model was expected. The parameters in this modification can be adjusted to capture different responses based on the type of plant being simulated, including plants that increase stomatal conductance and transpiration in response to O_3 exposure (Freersmith and Dobson, 1989; Maiermaercker and Koch, 1991; Manes et al., 2001, 1998; McLaughlin et al., 2007; Mills et al., 2009).

25 The Rub modification to the coupled Ball-Berry/Farquhar model, which modifies the V_{cmax} parameter within the photosynthesis equation, improved the ability of the model to predict photosynthetic responses to internal CO_2 (A-c_i) and light curves compared to the Psn modification (Table 1, Fig. 2). Applying a post hoc decrease to the photosynthesis value, such as in the Psn model, is the method used in most models that

incorporate the effects of O_3 on photosynthesis (Felzer et al., 2004; Ollinger et al., 1997; Sitch et al., 2007). While this method did predict decreases in photosynthesis, the Rub modification is more representative of physiological responses to O_3 because it alters the biochemical aspects of photosynthesis directly, and therefore more accu-
5 rately predicted photosynthesis over a range of environmental conditions.

Accounting for direct, independent O_3 damage to photosynthesis and stomatal conductance improves the accuracy of stomatal conductance predictions in the Farquhar photosynthesis/Ball-Berry stomatal conductance model, so we wanted to test this method in the CLM. The objective of the CLM simulations was to determine the magni-
10 tude of change in GPP and transpiration between direct modifications to stomatal conductance and indirect modifications driven by photosynthesis. The simulations were run at $[O_3]$ of 100 ppb and parameterized on a single plant functional type. These simulations are not detailed depictions of global responses to O_3 because they do not include responses from a full array of plant functional type or continuous atmospheric
15 $[O_3]$. However, they do demonstrate the differences in GPP and transpiration that may occur based on the parameterization used to estimate stomatal conductance.

Allowing conductance to change independently of photosynthesis in the CLM (the PG simulation) caused transpiration to decrease at a slower rate than photosynthesis for the same O_3 uptake. This trend was most clear when focused on the 5 × 5 grid
20 centered on Ithaca, NY, where the photosynthetic and stomatal modifications were developed. In this region, transpiration decreased less than photosynthesis in the PG simulation where conductance was directly modified (Fig. 3), similar to experimental observations that demonstrate larger decreases in photosynthesis than conductance in deciduous trees exposed to chronic O_3 (Calatayud et al., 2007; Francini et al., 2007;
25 Maurer et al., 1997; Mikkelsen, 1995; Novak et al., 2005b; Paoletti and Grulke, 2005; Soldatini et al., 1998; Tjoelker et al., 1995).

When changes in conductance were directly driven by photosynthetic changes in the Pg simulation, similar to most other model parameterizations, photosynthesis and transpiration had similar rates of decrease. These results are similar to those generated by

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simulations of ponderosa pine using the TREGRO model (Constable and Taylor, 1997), the only simulation to our knowledge that reports changes in transpiration caused by O_3. The similar rates of decrease in photosynthesis and transpiration in these simulations, however, do not represent changes measured in many O_3-exposure experiments. Maiermaercker (1997) and McLaughlin et al. (2007), for example, found that transpiration increased in trees exposed to elevated O_3, opposite of typical photosynthetic responses. Several studies similarly determined that photosynthesis decreases more than stomatal conductance, the primary plant control over transpiration, in response to O_3, uncoupling stomatal conductance from photosynthesis (Calatayud et al., 2007; Francini et al., 2007; Novak et al., 2005). The similar rates of decrease in photosynthesis and transpiration in the Pg simulation do not match these experimental results, suggesting that changing only photosynthesis likely over-predicts decreases in transpiration and is therefore not accurately capturing changes in atmospheric water vapor, a key greenhouse gas.

On regional and global scales, O_3 can have large impacts on hydrology and atmospheric water vapor by changing transpiration rates. In one of the few studies examining how hydrology responds to chronic O_3, Felzer et al. (2009) found that O_3, when coupled with nitrogen limitation, had a larger effect on runoff than did elevated CO_2, highlighting the importance of O_3 in the hydrologic cycle. The parameterization of TEM-Hydro used by Felzer et al. (2009) was similar to the Pg simulation in the CLM, where O_3 caused decreases in conductance indirectly through reduced photosynthesis. The accuracy of predicted hydrology can be improved by directly modifying stomatal conductance.

Independently incorporating O_3-induced decreases in photosynthesis and stomatal conductance (PG simulation) into the CLM yielded higher transpiration compared to simulations where photosynthesis indirectly changed stomatal conductance (Pg simulation; Fig. 4). Higher transpiration rates in the PG simulation were expected because stomatal conductance decreased at a slower rate than photosynthesis, which drove stomatal decreases in the Pg simulation. Unsurprisingly, the differences driven by

changing conductance directly compared to indirectly were particularly evident in regions with high photosynthetic rates, such as tropical latitudes where the Pg simulation drove decreases in transpiration that were 30 % larger than in the PG simulation. Estimates of atmospheric water vapor, an important greenhouse gas, are therefore largely
5   underestimated in these regions. The largest transpiration decreases in the PG simulation occurred in the mid-to high latitudes of the northern hemisphere and were similar in magnitude in the Pg simulation.

Though photosynthesis modifications were identical in the PG and Pg simulations, GPP was typically higher in the PG simulation (Fig. 5) suggesting that differences in
10   conductance changed the rate of O_3 uptake or altered the rate of carbon acquisition through changing c_i. Ollinger et al. (1997), using PnET to determine the impacts of O_3 on NPP in the northeastern United States, ran a sensitivity analysis in which O_3 caused conductance to increase, rather than decrease. In this sensitivity analysis, increasing conductance resulted in higher O_3 uptake, doubling the decrease in NPP. Similarly, we
15   expected that the slower decrease in conductance in the PG simulation compared to the Pg simulation would result in higher O_3 uptake rates, causing GPP to decrease more in the PG simulation. However, O_3 uptake was higher in the Pg simulation compared to the PG simulation (Fig. 6) and caused larger decreases in GPP, opposite of expected results. Though the differences were most striking in tropical latitudes, small
20   increases and decreases (+/- $10\,g\,C\,m^{-2}\,yr^{-1}$) in GPP were also observed in mid- and high-latitudes in the PG compared to the Pg simulation.

We conducted a sensitivity analysis to determine whether O_3 uptake was driving the differences in GPP. When the Pg and PG simulations were forced at a constant O_3 uptake, one-year averages demonstrated no differences in O_3 uptake, and almost
25   no differences in GPP (Fig. 8a–b), though transpiration did change due to different methods of modifying stomatal conductance (Fig. 8c). The similarity of GPP in both simulations at the same O_3 uptake suggest that the difference in O_3 uptake, which was higher in the Pg simulation, was the primary factor driving larger decreases in GPP in the Pg simulation. Higher O_3 uptake was expected in the PG simulation and it is

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not clear why O_3 uptake was lower in this simulation. Perhaps regions with initially high conductance rates in the PG simulation, such as tropical latitudes, allowed for high initial O_3 uptake rates. These initially high rates of O_3 uptake might act to reduce conductance quickly at the start of the simulation, resulting in lower conductance rates later in the simulation. Because conductance limits O_3 uptake, the lower conductance rates later in the simulation result in lower O_3 uptake. Ultimately, the differences in conductance caused changes in O_3 uptake, resulting in the differences in GPP between the PG and Pg simulations.

Relative humidity (RH) is a factor that could be strongly related to O_3 uptake in the simulations because both factors directly or indirectly influence leaf conductance and therefore potentially influence each other. For example, differences in stomatal conductance and transpiration caused by O_3 uptake could potentially force changes in RH, initiating a positive feedback cycle among stomatal conductance, transpiration and RH that could lead to divergence in O_3 uptake between the PG and Pg simulations. In both simulations, relative humidity changed in a range of locations, but those changes were small, within 2% of RH in control simulations (Fig. 7). Further, there were only small differences between the two simulations in a few tropical locales, with RH increasing in the PG simulation compared to the Pg simulation by only 1%. Given the small differences between the two simulations, changes in RH were likely not driving the larger differences in O_3 uptake observed in the tropics.

Photosynthesis and stomatal conductance modifications were run singly to determine the magnitude of feedbacks each modification caused. For example, stomatal conductance determines c_i, which is used in photosynthesis calculations. We therefore expected that changing only stomatal conductance (G simulation) would decrease photosynthesis due to feedbacks caused by a decrease in c_i values when conductance decreased. The G and the PG simulation decreased transpiration the same amount because the stomatal conductance modifications were identical. However, the G simulation caused GPP to increase relative to control simulations by 20% in many locations, though remained unchanged in the tropics and decreased in parts of North America,

Africa, and Asia (Fig. 9c–d). It appears that reductions in conductance stimulate photosynthesis compared to control simulations in several locations, though it is not clear why given the expected decrease c_i. The stimulation of photosynthesis in the G simulation helps explain why GPP increases in the PG simulation, where conductance is directly changed, compared to the Pg simulation. When only photosynthesis was modified (P simulation), stomata did not close in response to increasing O_3, resulting in extremely large O_3 uptake and corresponding decreases in photosynthesis (Fig. 9a). Transpiration did not change from control simulations (Fig. 9b) in the P simulation, suggesting that this method of modifying photosynthesis did not create any feedbacks that altered conductance.

A key finding in these simulations was that declines in GPP and transpiration were highest in tropical latitudes, similar to the findings in Sitch et al. (2007). Additionally, different methods of incorporating reductions in stomatal conductance in the Pg and PG simulations resulted in the largest differences in the tropics. Despite these large predicted changes in the tropics, very little experimental data documenting the physiological responses of tropical plants to chronic O_3 exposure exists, making it difficult to determine the accuracy of responses. Since simulations predict this region to be largely impacted by chronic O_3, gas exchange data for tropical plants is a critical research need.

The ability of transpiration to respond differently than photosynthesis in the PG simulation demonstrates that global models can allow for independent responses in photosynthesis and conductance. While this work focuses on O_3 oxidation damage, allowing photosynthesis and conductance to respond independently is critical for any situation that causes decoupling in these two parameters, such as oxidative damage caused by excessive light or nighttime transpiration. Though the parameterization of the CLM in these simulations is based on a single species at a single O_3 concentration, responses of multiple types of plants to realistic atmospheric O_3 can be incorporated into future simulations now that there is an established framework for varying photosynthesis and conductance separately. Ultimately, improving the ability of models to

predict conductance allows for more accurate predictions of the water cycle, including atmospheric water vapor, a key gas in regulating climate.

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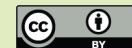Abstract | Introduction

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Table 1. Statistical results calculated for the Psn, Rub, and Cnd simulations in the Farquhar/Ball-Berry model. Intercept, slope, negative log likelihood, root mean square error (RMSE), and mean bias were calculated for both conductance and photosynthetic responses to varying levels of light (light curve) and photosynthetic responses to varying levels of CO_2 (A-c_i curve) at O_3 uptake values of 0, 2, and 4.2 mmol m^{-2}. Bolded values are the modifications within the response variable selected for use in the CLM simulations and are based on lowest negative log likelihood values.

Variable of Interest	Modification Name	Intercept	Slope	Negative Log Likelihood	RMSE	Mean Bias
			$A - c_i$ Curve			
Photosynthesis	Psn	2.21	1.07	−312.390	4.34	2.46
	Rub	**−0.04**	**1.32**	**−227.658**	**3.41**	**1.60**
			Light Curve			
Photosynthesis	Psn	0.54	0.84	−164.606	1.23	0.07
	Rub	**0.34**	**0.89**	**−158.600**	**1.22**	**−0.008**
Conductance	Psn	0.068	0.39	201.473	0.045	0.030
	Rub	0.065	0.41	200.668	0.051	0.027
	Cnd	**0.067**	**0.34**	**198.985**	**0.051**	**0.020**

Table 2. Description of the names, variables and simulations in the CLM.

	Variables	
Name	Variable	Description
G	g_{sO3}	O_3 affects conductance directly
g	g_{sfb}	O_3 indirectly affects conductance due to changes in photosynthesis
P	psn_{O3}	O_3 affects photosynthesis directly
p	psn_{fb}	O_3 indirectly affects photosynthesis due to changes in conductance

	Experimental Modifications	
Name	Variable	Description
Pg	psn_{O3} g_{sfb}	O_3 affects photosynthesis directly while indirectly changing conductance. Standard parameterization used currently in models.
P	psn_{O3} g_{sopt}	O_3 affects photosynthesis but does not change conductance because the links between photosynthesis and conductance have been cut.
G	psn_{opt} g_{sO3}	O_3 affects conductance but does not change photosynthesis because the links between conductance and photosynthesis have been cut.
PG	psn_{O3} g_{sO3}	O_3 affects conductance without indirect changes to photosynthesis and O_3 affects photosynthesis without indirect changes to conductance.

Predicting photosynthesis and transpiration responses to ozone

D. Lombardozzi et al.
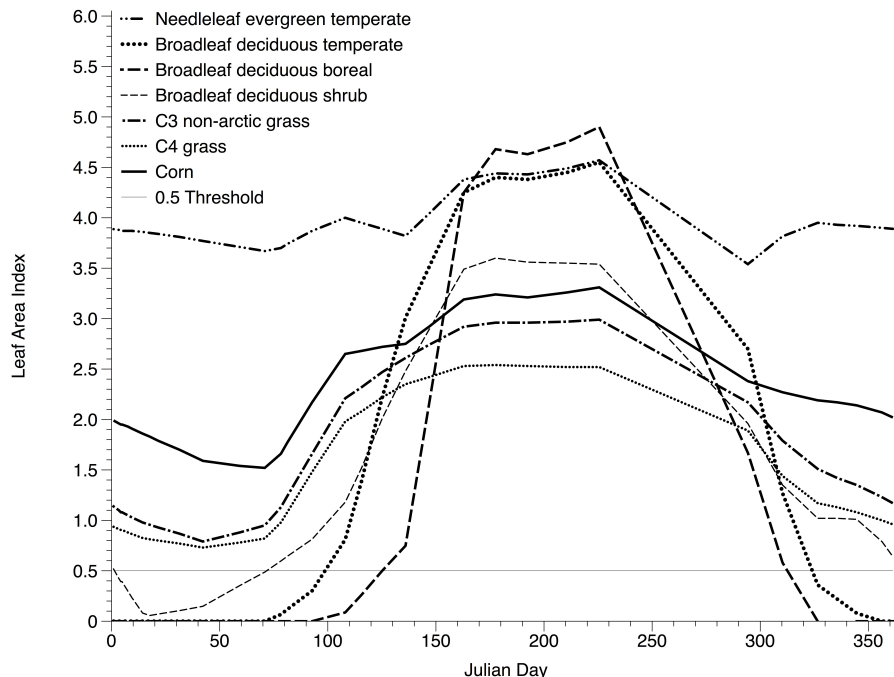
Fig. 1. Annual leaf area index (LAI) cycle for several plant functional types (PFTs) that are simulated in the CLM. The 0.5-LAI threshold (grey horizontal line), above which O$_3$ accumulates, demonstrates that O$_3$ accumulates at most times when LAI is positive, but minimizes uptake when LAI does not mathematically reach 0 when it should equal 0, particularly relevant in the broadleaf deciduous temperate and boreal trees.
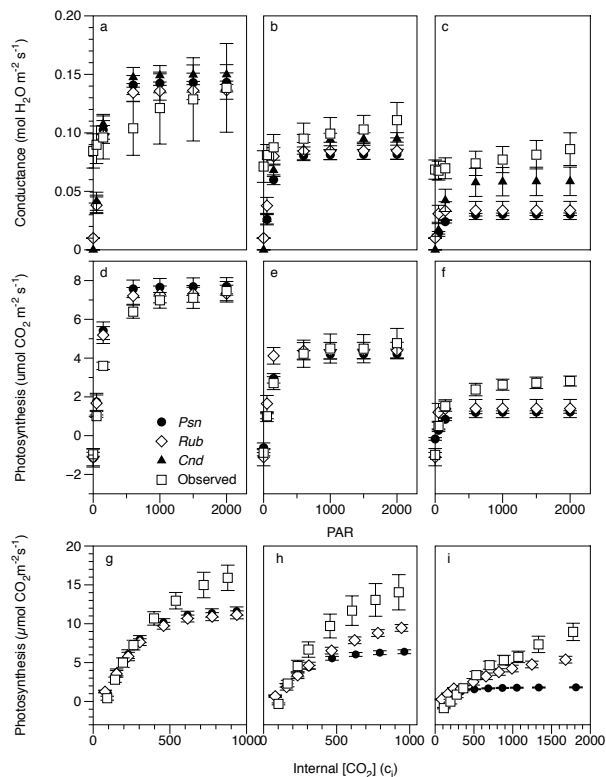
Fig. 2. Mean light and A-c_i curves predicted by different Farquhar/Ball-Berry model parameterizations compared with observed plant responses at various cumulative O_3 uptake (CUO) values. Simulations were run before the effects of O_3 (CUO = 0; **a**, **d**, and **g**); at CUO of $2 \, \text{mmol} \, \text{m}^{-2}$ (**b**, **e**, and **h**); and at a CUO of 4.2 (**c**, **f**, and **i**). The Cnd model predicts observed stomatal conductance responses to different light values **(a–c)** more accurately than the Psn or Rub models. The Rub model predicts observed photosynthetic responses to light **(d–f)** more accurately than the Psn model. Neither model predicts observed photosynthetic responses to A-c_i **(g–i)** as accurately as light, though the Rub model predicts A-c_i curves more accurately than the Psn model. Error bars represent mean standard error. See Table 1 for a description of the simulations.
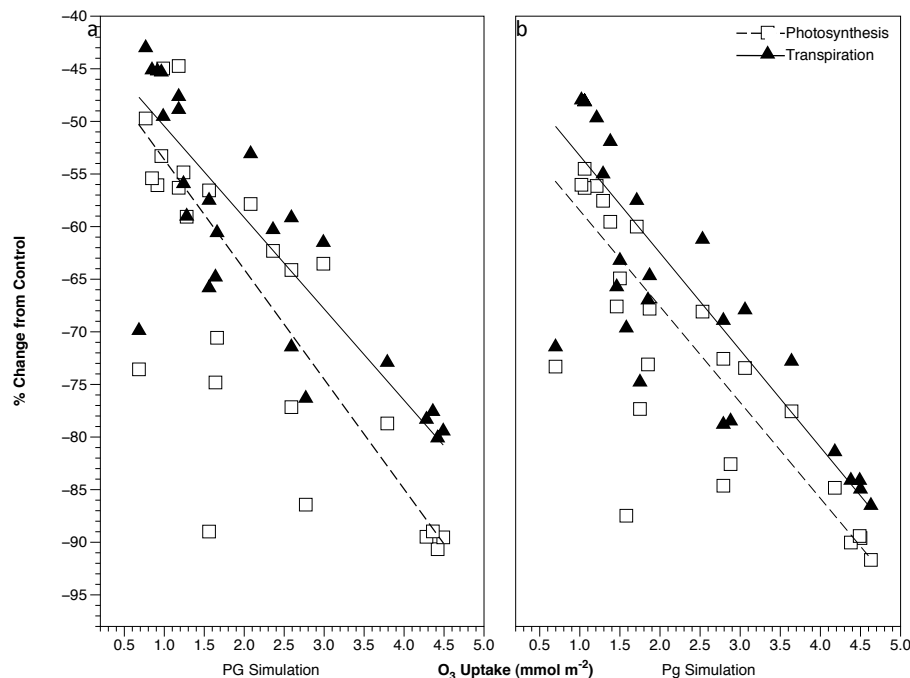
Fig. 3. Percent change from control CLM simulations in photosynthesis and transpiration over a range of O_3 uptake in the PG (direct change to conductance) **(a)**; and Pg (indirect change to conductance) **(b)** simulations. Results are from a 5 × 5 gridded region centered on Ithaca, NY (latitudes between 270–280 degrees; longitudes between 38–46 degrees) as modeled by the CLM. Points are gridcell averages from August of the 10th simulated year.
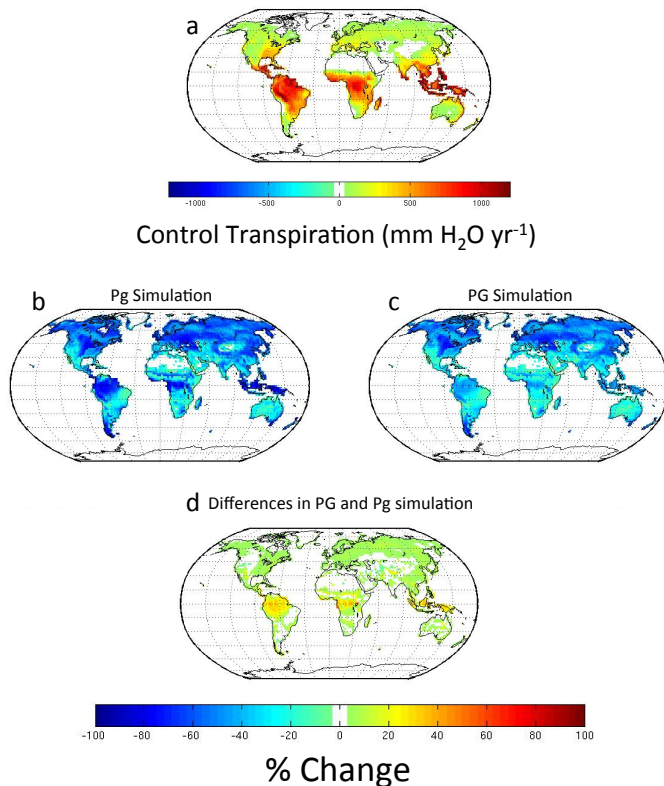
Fig. 4. Mean annual transpiration predicted in 20-year CLM simulations run at 100 ppb O_3. The control simulation **(a)** shows the average amount of water lost via transpiration annually in the absence of O_3. The percent changes from control were mapped for the **(b)** Pg simulation, where a direct change in photosynthesis causes indirect changes in conductance and for the **(c)** PG simulation, where direct changes to photosynthesis and conductance occur independently. Panel **(d)** illustrates the differences in transpiration between the PG simulation compared to the Pg simulation, also mapped as a percent change from control.

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Interactive Discussion

Control GPP (g C m^{-2} yr^{-1})

Pg Simulation

PG Simulation

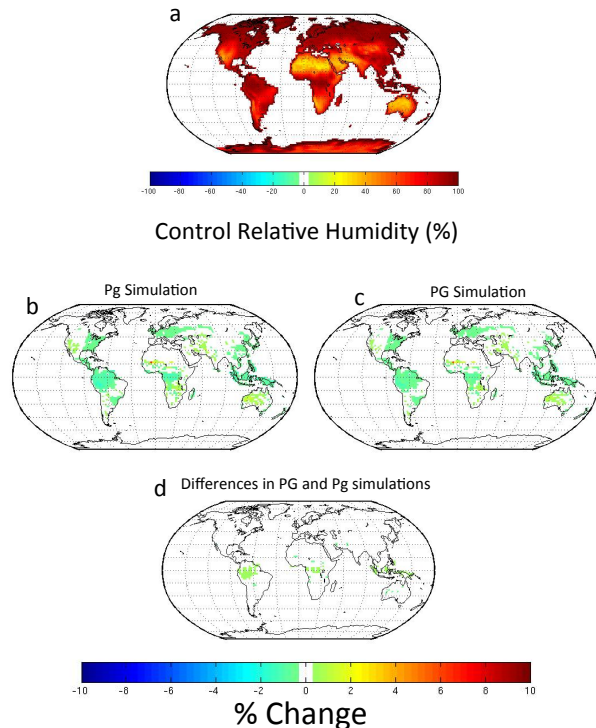Differences in PG and Pg simulations
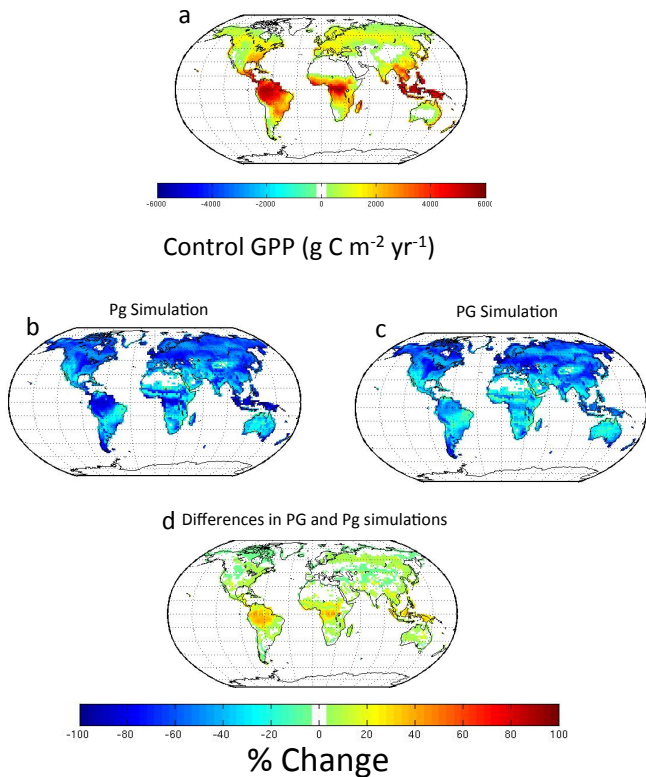
% Change

Fig. 5. Mean annual gross primary productivity (GPP) predicted in 20-year CLM simulations run at 100 ppb O$_3$. The control simulation **(a)** shows the average amount of carbon gained via photosynthesis annually in the absence of O$_3$. The percent changes from control were mapped for the **(b)** Pg simulation, where a direct change in photosynthesis causes changes in conductance and for the **(c)** PG simulation, where direct changes to photosynthesis and conductance occur independently. Panel **d** illustrates the differences in GPP between the PG compared to the Pg simulation, also mapped as a percent change from control.

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Fig. 6. Mean annual O_3 uptake predicted in 20-year CLM simulations run at 100 ppb O_3 in the **(a)** Pg simulation, where a direct change in photosynthesis causes changes in conductance and for the **(b)** PG simulation, where direct changes to photosynthesis and conductance occur independently. Ozone uptake is calculated as a function of O_3 concentration and stomatal conductance integrated over time.

Fig. 7. Mean annual relative humidity (RH) predicted in 20-year CLM simulations run at 100 ppb O₃. The control simulation **(a)** shows the average RH annually in the absence of O₃. The percent changes from control were mapped for the **(b)** Pg simulation, where a direct change in photosynthesis causes changes in conductance and for the **(c)** PG simulation, where direct changes to photosynthesis and conductance occur independently. Panel **d** illustrates the differences in RH between the PG compared to the Pg simulation, also mapped as a percent change from control. Note the difference in the scale of panels **b–d** compared to previous figures.
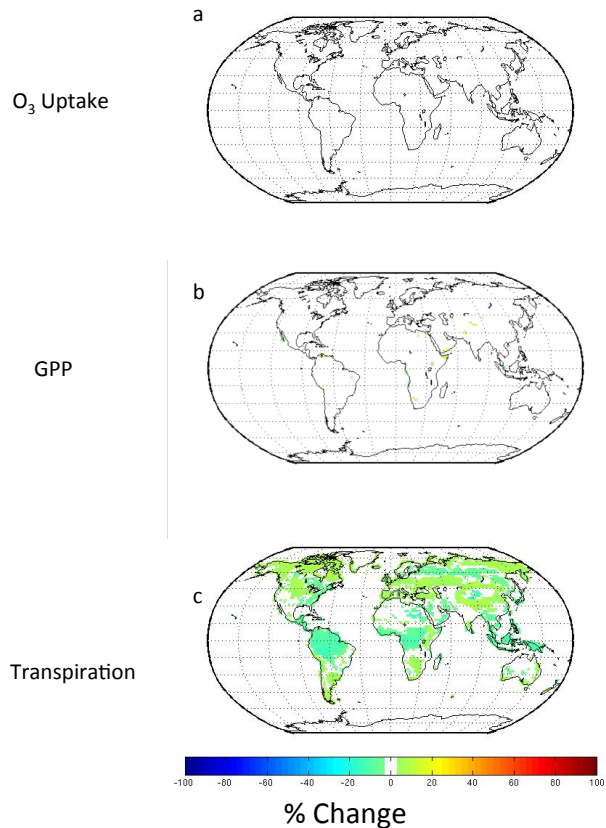
Fig. 8. A sensitivity analysis comparing the PG and Pg simulations at the same O_3 uptake rate. The differences in O_3 uptake **(a)**, GPP **(b)**, and transpiration **(c)** between the PG compared to the Pg simulation, mapped as a percent change from control in panels **(b)** and **(c)**. Annual means were calculated from a single-year CLM simulation where O_3 uptake was set at a constant rate of $3 \, \mathrm{mmol \, m^{-2}}$.
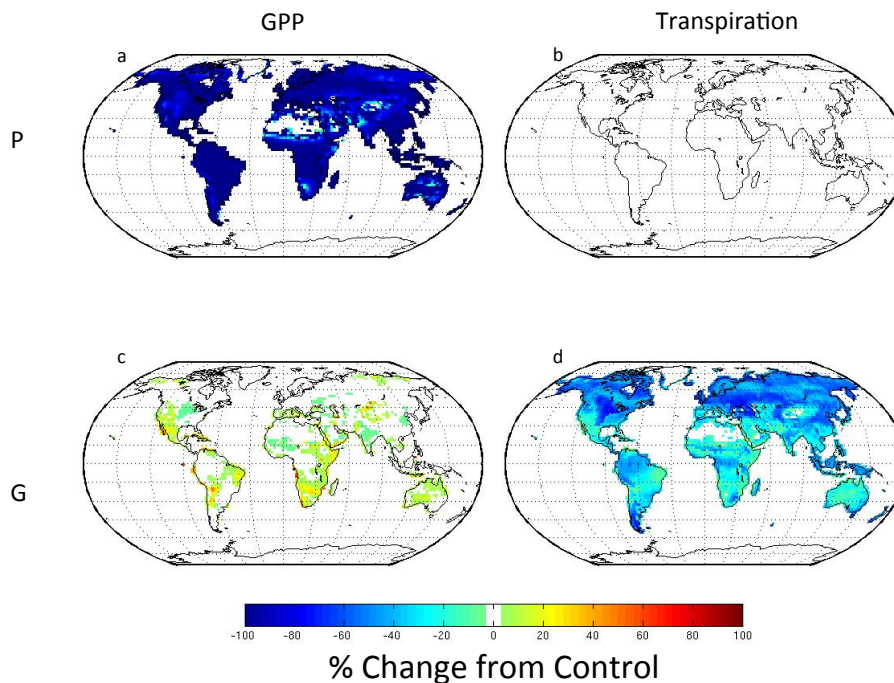
Fig. 9. Mean annual GPP and transpiration predicted in 20-year CLM simulations run at 100 ppb O_3. Percent differences from control were mapped for the P simulation **(a–b)**, where a direct change in photosynthesis caused decreases in GPP but did not cause indirect changes in conductance, and for the G simulation **(c–d)**, where a direct change in conductance caused decreases in transpiration and only affects photosynthesis through feedback loops.

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