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Key Points:

- Neglecting photosynthetic acclimation can impose model errors
- Errors at the leaf scale are similar or greater at the canopy scale
- Errors from neglecting acclimation cause productivity overestimation

Supporting Information:

- Readme
- Figure S1

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The influence of photosynthetic acclimation to rising CO₂ and warmer temperatures on leaf and canopy photosynthesis models

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Abstract There is an increasing necessity to understand how climate change factors, particularly increasing atmospheric concentrations of CO₂ ([CO₂]) and rising temperature, will influence photosynthetic carbon assimilation (*A*). Based on theory, an increased [CO₂] concomitant with a rise in temperature will increase *A* in C3 plants beyond that of an increase in [CO₂] alone. However, uncertainty surrounding the acclimation response of key photosynthetic parameters to these changes can influence this response. In this work, the acclimation responses of C3 photosynthesis for soybean measured at the SoyFACE Temperature by Free-Air CO₂ Enrichment experiment are incorporated in a leaf biochemical and canopy photosynthesis model. The two key parameters used as model inputs, the maximum velocity for carboxylation (*V_{c,max}*) and maximum rate of electron transport (*J_{max}*), were measured in a full factorial [CO₂] by temperature experiment over two growing seasons and applied in leaf- and canopy-scale models to (1) reassess the theory of combined increases in [CO₂] and temperature on *A*, (2) determine the role of photosynthetic acclimation to increased growth [CO₂] and/or temperature in leaf and canopy predictions of *A* for these treatments, and (3) assess the diurnal and seasonal differences in leaf- and canopy-scale *A* associated with the imposed treatments. The results demonstrate that the theory behind combined increases in [CO₂] and temperature is sound; however, incorporating more recent parameterizations into the photosynthesis model predicts greater increases in *A* when [CO₂] and temperature are increased together. Photosynthetic acclimation is shown to decrease leaf-level *A* for all treatments; however, in elevated [CO₂] the impact of acclimation does not result in any appreciable loss in photosynthetic potential at the canopy scale. In this analysis, neglecting photosynthetic acclimation in heated treatments, with or without concomitant rise in [CO₂], leads to modeled overestimates of carbon gain for soybean under future predicted conditions.

1. Introduction

Future agricultural production will encounter multifaceted challenges from global climate change. Atmospheric concentrations of carbon dioxide ([CO₂]) and several other radiatively active gases are increasing, and Earth system models predict further global warming above the temperature increases already observed [Collins *et al.*, 2013]. Mean land surface temperatures have already increased by over 1°C over the last century [Hartmann *et al.*, 2013] and are expected to increase further [Collins *et al.*, 2013]. Temperatures over the terrestrial areas of the planet are expected to increase faster than the global mean with specific regions experiencing increases of between 3 and 4°C by midcentury [Collins *et al.*, 2013]. Since 2000, the accumulation of greenhouse gases has accelerated to unprecedented rates, exceeding the most aggressive emission scenario [Peters *et al.*, 2013] and potentially leading to warming at or above the highest end of the predicted range.

The role of C3 crops in global food production is considerable, accounting for approximately 80% of human daily caloric intake derived directly from plants [Lobell and Gourdji, 2012]. Assessing the impact of future climate change on crop yields and net ecosystem production requires accurate assessments of climate change impacts on photosynthesis. As the entry point for carbon assimilation, the impact of global changes on C3 photosynthesis is a major determinant of overall crop productivity. The generally beneficial impact of rising [CO₂] on C3 plants has been well documented over many years through a combination of chamber and

open-air experiments. While environmental and growth conditions can cause variable plant responses, the overall effect of rising $[\text{CO}_2]$ generally results in higher rates of C3 photosynthesis [Lawlor and Mitchell, 1991; Curtis and Wang, 1998; Ainsworth *et al.*, 2002; Karnosky *et al.*, 2003; Long *et al.*, 2004; Nowak *et al.*, 2004; Ainsworth and Long, 2005; Bernacchi *et al.*, 2006; Ainsworth and Rogers, 2007; Leakey *et al.*, 2009]. Photosynthetic rates increase despite acclimation responses that drive down the expression and activity of key photosynthetic enzymes [e.g., Sage, 1994; Bernacchi *et al.*, 2005; Leakey *et al.*, 2009; Ge *et al.*, 2012]. Two biochemical processes that limit photosynthesis, the maximum rate of in vivo Rubisco carboxylation capacity of RuBP ($V_{c,\text{max}}$) and the rate of regeneration of RuBP associated with the maximum potential linear electron flux through photosystem II (J_{max}), have been shown to acclimate to long-term growth at elevated $[\text{CO}_2]$ [Wong, 1979; Sage *et al.*, 1989; Tissue *et al.*, 1993; Woodrow, 1994; Ghannoum *et al.*, 1997; Vu *et al.*, 1997; Sims *et al.*, 1998], although the down regulation of $V_{c,\text{max}}$ may have negligible impact on leaf photosynthesis for some plants grown in elevated $[\text{CO}_2]$ [Bernacchi *et al.*, 2005]. Elevated $[\text{CO}_2]$, however, is shown to have a much more variable impact on J_{max} ; while early studies show a range of responses based on species [e.g., Sage, 1994], J_{max} of herbaceous crops, such as soybean, shows little responses to elevated $[\text{CO}_2]$ [e.g., Bernacchi *et al.*, 2005].

As temperatures rise, the kinetics for the main carboxylating enzyme, Rubisco, increasingly favors oxygenation relative to carboxylation of RuBP [Jordan and Ogren, 1984; Long, 1991]. In C3 crops this results in increased photorespiration, an energetically wasteful process in which already fixed carbon is released as CO_2 [Ogren, 1984]. Increases in temperature have also been shown to reduce the amount of CO_2 that diffuses into the leaf due to decreased stomatal conductance (g_s), although this is likely a direct consequence of an increase in vapor pressure deficit that usually occurs as temperature rises [Farquhar and Sharkey, 1982]. While rising $[\text{CO}_2]$ almost universally increases rates of C3 photosynthesis, higher temperatures have been reported to result in an increase, decrease, or no change in photosynthesis depending on whether photosynthesis is operating below, at, or above the thermal optimum [Bernacchi *et al.*, 2001, 2003; Cen and Sage, 2005; Sage and Kubien, 2007]. Diurnal variation in temperature (e.g., hourly and daily) will lead to conditions where photosynthesis operates from below to above the thermal optimum. Longer-term changes in temperature (weekly, monthly, and seasonally) are anticipated to cause the temperature optimum of photosynthesis to approach the temperature to which the leaf is acclimated [Sage *et al.*, 1995; Sage and Kubien, 2007].

Increases in $[\text{CO}_2]$ and temperature were first hypothesized to increase C3 photosynthesis in a coupled manner over 20 years ago using in vitro-derived temperature functions [Long, 1991]. The combined effects of these variables on plants have been studied in various types of laboratory chambers and greenhouses [e.g., Ainsworth *et al.*, 2002], but similar experiments using open-air field-based experiments have been lacking. Photosynthetic measurements made on soybean over a wide range of meteorological conditions across growing seasons at the Soybean Free-Air CO_2 Enrichment (SoyFACE) research facility demonstrate that a positive correlation exists between temperature and photosynthesis [Bernacchi *et al.*, 2006] such that higher temperatures drive higher $[\text{CO}_2]$ -induced increases in photosynthesis. That analysis, however, was extracted from diurnal measurements of photosynthesis collected over three growing seasons and relied on natural climatic variability which is unavoidably confounded by variables other than just temperature. More recently with the advancement of in-field heating techniques [Kimball, 2005; Kimball *et al.*, 2008], experiments have been established to assess the responses of various ecosystems to combined increases in temperature and $[\text{CO}_2]$ [e.g., Ruiz-Vera *et al.*, 2013; Rosenthal *et al.*, 2014]. These experiments, in which full factorial treatments of $[\text{CO}_2]$ and temperature are applied under open-air growth conditions, provide a unique opportunity to assess whether physiological adjustments to growth in elevated $[\text{CO}_2]$ and temperature result in photosynthesis rates that conform to the theory-based expectations in Long [1991].

A major goal of in-field experimentation is to provide mechanistic understanding of plant physiological responses to changing environments that can better equip ecosystem-scale models with refined crop predictions [Twine *et al.*, 2013]. The biochemical and biophysical models of leaf photosynthesis [Farquhar *et al.*, 1980] are used extensively in leaf- to ecosystem-scale models and rely on input parameters of $V_{c,\text{max}}$ and J_{max} derived from in-field measurements while assuming standardized temperature responses of each model component. This study addresses the influence of growth in elevated $[\text{CO}_2]$ and/or higher temperature on acclimation of $V_{c,\text{max}}$ and J_{max} for one of the most widely grown food crops, soybean. The first objective is to reassess the theoretical impact of rising $[\text{CO}_2]$ and temperature on modeled leaf photosynthesis, accounting for physiological adjustments of $V_{c,\text{max}}$ and J_{max} to growth conditions. The second objective predicts how the

leaf-scale photosynthetic responses of soybean will manifest carbon uptake at the canopy scale. This objective builds upon recent measurements of photosynthetic physiology of soybean from a $[\text{CO}_2]$ by temperature factorial experiment at the Soybean Temperature by Free-Air CO_2 Enrichment (T-FACE) experiment [Ruiz-Vera *et al.*, 2013; Rosenthal *et al.*, 2014] and advances in canopy-scale photosynthesis modeling [Drewry *et al.*, 2010a]. The second objective uses a highly mechanistic multilayer canopy photosynthesis model, MLCan [Drewry *et al.*, 2010a], coupled with a parameterization of the leaf photosynthesis model [Farquhar *et al.*, 1980] over a wide range of temperatures [Bernacchi *et al.*, 2001, 2003]. This coupled measurement-modeling approach will use physiological and meteorological data from two growing seasons representing relatively typical conditions (2009) and much warmer and drier conditions (2011).

2. Methods

2.1. Modeling Leaf Photosynthesis

The response of A to the intercellular $[\text{CO}_2]$ (C_i) was modeled using the leaf biochemical photosynthesis model [Farquhar *et al.*, 1980; von Caemmerer, 2000], which assumes A to be limited by the slower of two processes, Rubisco (W_c) and maximum rate of RuBP regeneration (W_j).

$$A = W_c = (1 - \Gamma^*/C_i) \left\{ \frac{V_{c,\max} \cdot C_i}{C_i + K_c \cdot \left(1 + \frac{O}{K_o}\right)} \right\} - R_d \quad (1)$$

$$A = W_j = (1 - \Gamma^*/C_i) \left\{ \frac{J \cdot C_i}{4.5C_i + 10.5\Gamma^*} \right\} - R_d \quad (2)$$

In these two equations, $(1 - \Gamma^*/C_i)$ accounts for the proportion of CO_2 assimilated that is lost through photorespiration where Γ^* is the photosynthetic CO_2 compensation point in the absence of mitochondrial respiration (R_d). The terms K_c and K_o represent the Michaelis-Menten constants for CO_2 and O_2 , respectively, O is the chloroplastic oxygen concentration, and R_d is mitochondrial respiration in the light. In equation (2), the constants 4.5 and 10.5 reflect the electron transport requirements for the production of ATP from ADP and NADPH from NADP^+ to meet the demands for RuBP regeneration [von Caemmerer, 2000]. The values for Γ^* , K_c , and K_o are generally considered to be conserved among C3 plants for modeling purposes, although recent work suggests that variations may be important [von Caemmerer, 2013; Galmés *et al.*, 2014]. Thus, the values and temperature responses integrated into the MLCan model were based on those published previously for tobacco [Bernacchi *et al.*, 2001, 2003] unless otherwise noted.

The term J is defined as the linear electron flux through photosystem II:

$$J = \frac{Q_2 + J_{\max} - \sqrt{(Q_2 + J_{\max})^2 - 4 \cdot \Phi_{\text{PSII}} \cdot J_{\max}}}{2 \cdot \Phi_{\text{PSII}}} \quad (3)$$

$$Q_2 = Q \cdot \alpha \cdot \Phi_{\text{PSII}} \cdot \beta \quad (4)$$

where J_{\max} is the maximum potential electron flux through photosystem II, Q is photosynthetically active radiation, α is the leaf absorptance, Φ_{PSII} is the quantum yield of photosystem II, and β is the ratio of photosystem II to photosystem I. The temperature response for the functions specific to Rubisco-limited photosynthesis parameters is that reported by Bernacchi *et al.* [2001], and the temperature response for the parameters unique to the RuBP-limited photosynthesis model was used from Bernacchi *et al.* [2003] for tobacco plants grown at 25°C.

The parameters that are known to be highly variable among leaves, $V_{c,\max}$ and J_{\max} , were determined from A versus C_i response curves measured at 25°C (for detailed description see section 2.2 of Rosenthal *et al.* [2014]). The method of calculating $V_{c,\max}$, J_{\max} , and R_d from the A versus C_i responses curves was based on linearization of the two limiting processes (Rubisco and RuBP regeneration) from the leaf photosynthesis model [Farquhar *et al.*, 1980] following the method described previously [Long and Bernacchi, 2003]. The parameters $V_{c,\max}$ and J_{\max} were measured over two growing seasons (2009 and 2011) on regular intervals at 25°C as part of the SoyFACE T-FACE experiment, and each varied throughout the growing season [Rosenthal *et al.*, 2014].

Application of the leaf photosynthesis model generally assumes that the parameters, other than $V_{c,\max}$ and J_{\max} , are conserved for all higher C_3 species [Farquhar *et al.*, 1980; Harley and Tenhunen, 1991; von Caemmerer, 2000;

Bernacchi *et al.*, 2001; Long and Bernacchi, 2003]. Because of this, models are parameterized with $V_{c,max}$ and J_{max} measured at a standard temperature, generally 25°C, and the temperature functions associated with the model account for deviations at higher and lower temperatures. It is also assumed that growth conditions do not influence the temperature response of the parameters. Variation, however, does exist both between species [e.g., Galmés *et al.*, 2005] and, at least for J_{max} , within a species based on growth environment [Bernacchi *et al.*, 2003]. It is possible that growth conditions could influence the temperature responses of Γ^* , K_c , and K_o through different expression of genes coding for the Rubisco small subunit; however, at present this is highly speculative [Carmo-Silva *et al.*, 2014]. Thus, any means to account for these changes in models are nonexistent. While the influence of growth conditions on temperature functions for J_{max} are potentially relevant for modeling growth at different temperatures, only slight difference in the instantaneous temperature response of J_{max} has been observed for large changes in growth temperature [e.g., Bernacchi *et al.*, 2003]; thus, a “standard” temperature function based on growth at 25°C was incorporated in the modeling in this study.

The canopy modeling analysis presented here linearly interpolated measurements of $V_{c,max}$ and J_{max} to daily values over the two growing seasons (2009 and 2011). While R_d is known to vary as a result of leaf growth environment, values estimated from photosynthetic measurements are prone to significant variation resulting in no discernible differences among treatments. Thus, acclimation responses of R_d were not included in this analysis. The parameterization of the model is based on *in vivo* measurements of enzyme kinetics that are based on CO₂ concentrations in the intercellular airspaces (C_i) and not in the chloroplast. As a result, the instantaneous influence of temperature on mesophyll conductance (g_m) is built into the models. As g_m for soybean is not shown to change based on growth [CO₂] [Bernacchi *et al.*, 2005], its influence on model predictions for the elevated CO₂ scenarios are expected to be negligible. Soybeans were grown in a fully replicated ($n = 4$) complete block factorial experiment over two growing seasons under control (385 $\mu\text{mol mol}^{-1}$ [CO₂] and background canopy temperatures; 385-CON), elevated temperature (385 $\mu\text{mol mol}^{-1}$ [CO₂] and canopy temperatures warmed by 3.5°C; 385-HOT), elevated [CO₂] (585 $\mu\text{mol mol}^{-1}$ [CO₂] and background canopy temperatures; 585-CON), and elevated [CO₂] and temperature (585 $\mu\text{mol mol}^{-1}$ [CO₂] and canopy temperatures warmed by 3.5°C; 585-HOT). Photosynthetic CO₂ response curves were measured at 2 week intervals using the method described previously [Bernacchi *et al.*, 2005]. A complete description of the Soybean T-FACE experiment, measurements collected, and climatic conditions have been provided previously [Ruiz-Vera *et al.*, 2013; Rosenthal *et al.*, 2014].

2.2. Modeling Canopy Photosynthesis

Canopy photosynthesis was modeled using the MLCan model [Drewry *et al.*, 2010a] that divides the canopy into 15 horizontal layers, each composed of sunlit and shaded portions. The canopy model uses the leaf photosynthesis model [Farquhar *et al.*, 1980] as the basis for net carbon uptake and resolves radiation, air temperature, wind speed, [CO₂], water vapor, precipitation, and dew formation throughout the vertical canopy profile. Additionally, the model couples energy balance with physiological functioning at each canopy layer and has been evaluated using both canopy-scale flux data [Drewry *et al.*, 2010a] and physiological measurements [Drewry *et al.*, 2010b].

The canopy photosynthesis model was parameterized using the sunlit-shaded scaling approach [Norman, 1982; De Pury and Farquhar, 1997; Dai *et al.*, 2004] to scale leaf photosynthetic rates to the canopy. This scaling approach has been shown to properly account for the largest differentiator of intracanopy photosynthesis, radiative flux, and to be accurate at the diurnal and subdiurnal timescales used here [Medlyn *et al.*, 2003]. To accommodate this scaling approach, MLCan divides the incoming shortwave radiation into photosynthetically active (PAR) and near-infrared (NIR) radiation bands to allow for increased leaf absorptivity to PAR. These shortwave bands are further resolved into direct and diffuse radiation components, which are attenuated through the canopy layers according to Beer-Lambert law [Goudriaan, 1977]. Separating the shortwave bands into direct and diffuse components allows for the division of sunlit and shaded leaves, where sunlit portions of the canopy receive both direct and diffuse radiation and shaded portions receive only diffuse radiation. The fraction of leaves that is shaded and sunlit varies throughout the canopy and depends on the relative position of the Sun, canopy density, leaf orientation, and total radiative flux.

At each canopy layer photosynthesis is simulated using the leaf biochemical model described in the previous section. It is applied separately for shaded and sunlit leaves and is dependent on canopy structure in several ways. First, canopy structure modulates the microenvironment and radiative fluxes experienced

Table 1. Seasonal Mean (\pm SE) Values for the Maximum Velocity of Carboxylation ($V_{c,max}$; $\mu\text{mol m}^{-2} \text{s}^{-1}$) and Maximum Rate of Photosynthetic Electron Transport (J_{max} ; $\text{mmol m}^{-2} \text{s}^{-1}$) Used in the Photosynthesis Modeling^a

Treatment	$V_{c,max}$	J_{max}
2009		
385-CON	131.8 ± 3.0	214.6 ± 5.2
385-HOT	135.5 ± 3.0	198.8 ± 5.2
585-CON	115.7 ± 3.1	208.3 ± 5.3
585-HOT	118.0 ± 3.1	195.5 ± 5.3
2011		
385-CON	133.4 ± 3.2	192.7 ± 5.5
385-HOT	133.4 ± 3.2	176.8 ± 5.5
585-CON	113.3 ± 3.2	183.6 ± 5.5
585-HOT	115.9 ± 3.2	168.6 ± 5.5

^aThese values are derived from A versus C_i response curves measured at 25°C [Rosenthal *et al.*, 2014] in soybean leaves and exposed to control CO_2 and temperature (385-CON), control CO_2 and a temperature increase of 3.5°C (385-HOT), [CO_2] increased by 200 $\mu\text{mol mol}^{-1}$ above background and control temperature (585-CON), and both elevated temperature and [CO_2] (585-HOT) at the Soybean Free-Air CO_2 Enrichment (SoyFACE) Temperature by Free-Air CO_2 Enrichment (T-FACE) experiment. SE values were calculated using mixed model analysis of variance on measurements taken across 6 days in 2009 and 5 days in 2011 using a fully factorial design with four plots for each treatment.

by a leaf at a given canopy layer. Also, leaf photosynthetic capacity for sunlit and shaded portions of the canopy is assumed to decline from the top to bottom of the canopy as

$$V_{c,max}(L_{cum}) = V_{c,max}(0) \cdot \exp[-k_n \cdot L_{cum}] \quad (5)$$

where L_{cum} is the cumulative leaf area index (LAI) from the top of the canopy, $V_{c,max}(0)$ is $V_{c,max}$ at the top of the canopy, and k_n is an assumed exponential decay factor of canopy nitrogen equal to 0.5 [Drewry *et al.*, 2010a; Leuning *et al.*, 1995]. Analogous expressions for R_d and J_{max} are used to account for their related reductions throughout the canopy. Similarly, fluxes of energy and water are modeled separately for the shaded and sunlit portions of a canopy layer. This generally results in differing values of leaf state variables including g_s , leaf temperature, and C_i , which can feed back on the canopy microenvironment of [CO_2], air temperature, and vapor pressure resulting in a tightly coupled system that requires the simultaneous solutions of energy, moisture, and carbon balances throughout the canopy. Once a solution is found, aggregating the shaded and sunlit photosynthesis at each layer and summing over the canopy determine canopy-scale photosynthesis:

$$A'_c = \sum_{i=1}^N A_{i,sun} L_{i,sun} + A_{i,shade} L_{i,shade} \quad (6)$$

where “ i ” represents a canopy layer, N is the number of canopy layers, $A_{i,sun(shade)}$ is sunlit(shaded) leaf photosynthesis ($\mu\text{mol m}^{-2} \text{s}^{-1}$), and $L_{i,sun(shade)}$ is the sunlit(shaded) LAI ($\text{m}^2 \text{m}^{-2}$) of canopy layer i .

In MLCan net leaf carbon assimilation (A_n) and stomatal conductance (g_s) were linked with the Ball-Berry equation [Ball and Berry, 1987]:

$$g_s = f_{sv} \cdot m \frac{A_n \cdot h_s}{C_s} + b \quad (7)$$

where the slope (m) and intercept (b) are parameters specific to soybean, f_{sv} is the stomatal sensitivity to leaf water potential (ψ_l), h_s is the leaf surface relative humidity, and C_s is leaf surface [CO_2]. Despite the Ball-Berry model's empirical origin, it has been shown to accurately represent the response of g_s to environmental conditions. In the 385-HOT and 585-HOT treatment scenarios in this study g_s at the top of the canopy decreased on average by 18% and 36%, respectively, which was similar in magnitude to experimental results from Ruiz-Vera *et al.* [2013] and indicates that g_s was responding to environmental conditions in a manner consistent with observations. With zero representing total loss of stomatal conductance when ψ_l reaches critical water potential [Tuzet *et al.*, 2003], f_{sv} can range from 0 to 1. The formulation for f_{sv} in MLCan depends on soy-specific reference potential (ψ_r) and sensitivity parameter (s_r):

$$f_{sv} = \frac{1 + \exp[s_r \cdot \Psi_f]}{1 + \exp[s_r (\Psi_f - \Psi_l)]} \quad (8)$$

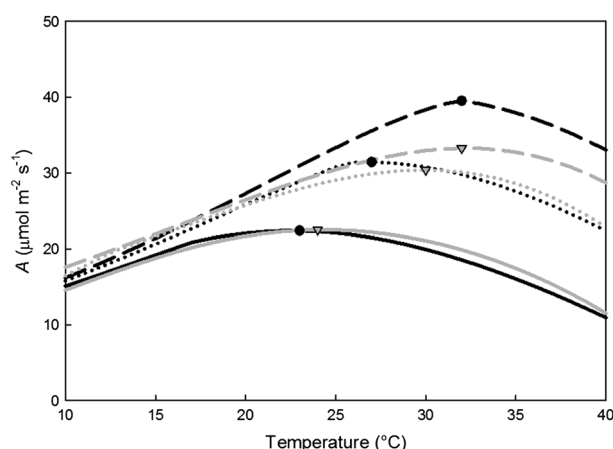


Figure 1. Modeled temperature response of photosynthesis for leaves simulated at 400 (solid line), 600 (dotted line), and 800 (dashed line) $\mu\text{mol mol}^{-1}$ CO_2 using the model parameters derived from *Bernacchi et al.* [2001, 2003] (black lines) and from *Long* [1991] (grey lines). Shown also are photosynthesis temperature optimums based on model parameters from *Bernacchi et al.* [2001, 2003] (closed circles) and *Long* [1991] (open triangles).

MLCan simulated canopy photosynthesis in 30 min steps using meteorological data from the Bondville, Illinois, Ameriflux site for 2009 and 2011. These data included 2 m air temperature, vapor pressure, downwelling shortwave radiation, wind speed, and precipitation. The LAI was specified from observations taken at SoyFACE interpolated to daily values for both the 2009 and 2011 growing seasons using methods described previously [Dermody *et al.*, 2006]. The simulation period for each year was defined as the days when the observed LAI was greater than $3.5 \text{ m}^2 \text{ m}^{-2}$ for the 385-CON plots. The canopy height was assumed to be 1 m during these simulation periods. Further details of the parameters used in MLCan can be found in *Drewry et al.* [2010a, 2010b]. Finally, as described below we simulated several scenarios with combinations of increased atmospheric

$[\text{CO}_2]$ and temperature (Table 1). In the increased $[\text{CO}_2]$ simulations, the atmospheric $[\text{CO}_2]$ concentration was constant, with a value of $585 \mu\text{mol mol}^{-1}$, and for standard atmospheric $[\text{CO}_2]$ simulations the ambient $[\text{CO}_2]$ was $385 \mu\text{mol mol}^{-1}$. These values did not change with season or time of day. For the increased temperature simulations (HOT scenarios in Table 1), the observed ambient 2 m air temperature was uniformly increased by 3.5°C during the growing season. This occurred every hour of the day. Specific humidity was assumed to remain constant during all simulations.

3. Results and Discussion

3.1. Temperature Responses of Model Parameters

The leaf photosynthesis model [Farquhar *et al.*, 1980] utilizes a biochemical approach based on Michaelis-Menton enzyme kinetics to represent Rubisco-limited photosynthesis. The temperature functions integrated into the model represent changes in key biochemical parameters based on *in vitro* measurements collected from a range of different studies [Long, 1991]. Many of the parameters used in Long [1991] appear relatively similar in their temperature sensitivity to the temperature functions derived from *in vivo* measurements (Figure S1 in the supporting information). Notable differences include the lack of a significant temperature function of K_o and a more rapid increase in R_d for the previous parameters [Long, 1991] relative to the parameters used here (supporting information Figure S1). The temperature response of J_{max} is relatively similar between Long [1991] and *Bernacchi et al.* [2003], with approximately 10% differences between these temperature functions at the higher and lower temperature extremes.

3.2. Temperature Response of Leaf-Level Photosynthesis

Leaf photosynthesis was modeled at $[\text{CO}_2]$ of 400, 600, and $800 \mu\text{mol mol}^{-1}$ using the current [Bernacchi *et al.*, 2001, 2003] and previous [Long, 1991] temperature functions (Figure 1). As expected, the kinetics of Rubisco increasingly favored oxygenation over carboxylation as temperature rose, as indicated by the more rapid increase in K_c relative to K_o (supporting information Figure S1). This, coupled with a rapid increase in R_d with temperature (supporting information Figure S1), resulted in temperature optimum for current $[\text{CO}_2]$ (approximately $400 \mu\text{mol mol}^{-1}$) lower than leaf temperatures that often occur under natural settings (Figure 1). With increases in $[\text{CO}_2]$ beyond current levels, the model predicted a higher photosynthetic temperature optimum. This model analysis showed that under current $[\text{CO}_2]$ the thermal optimum of photosynthesis is $\sim 23^\circ\text{C}$ increasing to 27°C at $600 \mu\text{mol mol}^{-1}$ $[\text{CO}_2]$ and 32°C at $800 \mu\text{mol mol}^{-1}$ $[\text{CO}_2]$ (Figure 1).

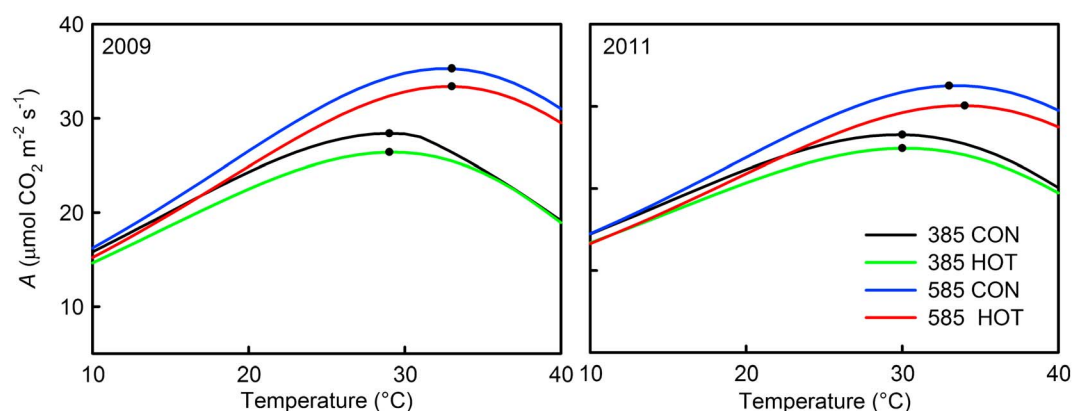


Figure 2. The effect of acclimation to elevated $[\text{CO}_2]$ and/or elevated temperature on the response of photosynthesis to temperature. Parameters used to model A versus T relationship are season means for 2009 and 2011 as given in Table 1 and reflect acclimation to season long growth at elevated temperature and/or elevated $[\text{CO}_2]$ [Rosenthal *et al.*, 2014, Table 1]. Circles represent thermal optima.

Coupled with the increase in the thermal optimum was a significant interacting effect of temperature and $[\text{CO}_2]$ on photosynthetic rates. The modeled photosynthetic rates at $400 \mu\text{mol mol}^{-1}$ $[\text{CO}_2]$ are quite similar between the parameterization used in Long [1991] and the one used here (Figure 1). At $[\text{CO}_2]$ above at $400 \mu\text{mol mol}^{-1}$, the outcomes of the alternative parameterizations begin to diverge both in absolute rate of A as well as thermal optimum. Despite these differences, the theory behind the interacting effects of temperature and $[\text{CO}_2]$ originally presented by Long [1991] is shown with both parameterizations.

3.3. Photosynthetic Acclimation Results in Lower Leaf Photosynthesis

The above modeling exercises were conducted using the same photosynthetic parameterization for all three $[\text{CO}_2]$ levels. Different acclimation scenarios were originally conducted based on percentage decreases in $V_{c,\text{max}}$ but at the time there was a lack of data focusing on acclimation to both $[\text{CO}_2]$ and temperature [Long, 1991]. More recent research has provided a wide range of acclimation information for a number of C3 species grown in a variety of growth conditions [Medlyn *et al.*, 2002; Bernacchi *et al.*, 2005; Ainsworth and Rogers, 2007; Wang *et al.*, 2012]. A characterization of photosynthetic acclimation responses for $V_{c,\text{max}}$ and J_{max} ($\mu\text{mol m}^{-2} \text{s}^{-1}$) of soybean grown in the SoyFACE T-FACE facility was performed in 2009 and 2011 (Table 1) (also see Rosenthal *et al.* [2014, Figure 2]) and used in the modeling exercise here.

Accounting for the measured acclimation responses of $V_{c,\text{max}}$ and J_{max} to $[\text{CO}_2]$ and temperature individually did not remove the cooperative influence of temperature and $[\text{CO}_2]$ on photosynthesis (Figure 2). Elevated

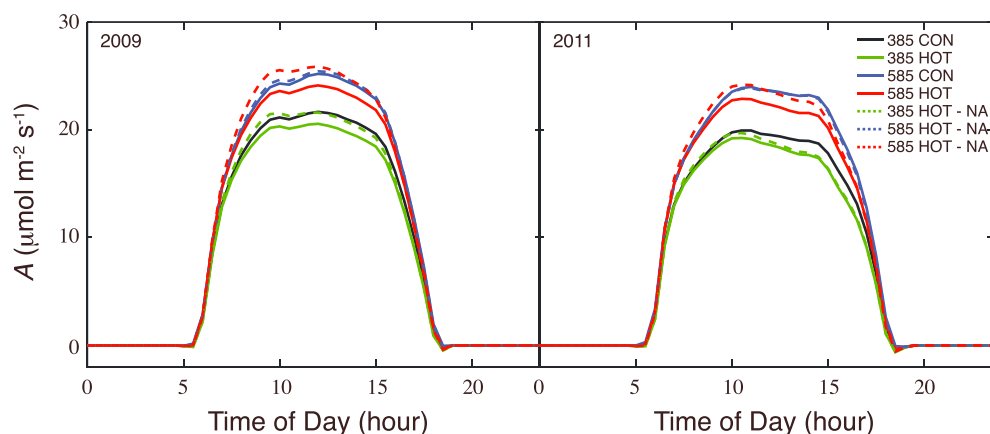


Figure 3. Diurnal photosynthetic rates modeled for control, elevated $[\text{CO}_2]$, elevated temperature, and the combined elevated $[\text{CO}_2]$ and elevated temperature (red line). Treatment abbreviations are as in Table 1. Simulations used seasonally varying $V_{c,\text{max}}$ and J_{max} from Rosenthal *et al.* [2014].

Table 2. Calculated Daily Integrated Carbon Assimilation (A' ; $\text{mol m}^{-2} \text{s}^{-1}$) and Season-Integrated Canopy Assimilation (A_c' ; $\text{mol m}^{-2} \text{d}^{-1}$) for Two Growing Seasons Using Seasonally Varying $V_{c,\text{max}}$ and J_{max} ^a

	A'	%	A_c'	%
2009				
385-CON	0.744	0.0%	59.28	0.0%
385-HOT	0.705	−5.2%	55.24	−6.8%
585-CON	0.860	15.6%	70.15	18.3%
585-HOT	0.828	11.3%	66.95	12.9%
385-HOT = NA	0.739	−0.6%	57.74	−2.6%
585-CON = NA	0.867	16.5%	69.43	17.1%
585-HOT = NA	0.877	17.9%	69.99	18.1%
2011				
385-CON	0.695	0.0%	59.59	0.0%
385-HOT	0.656	−5.6%	54.20	−9.1%
585-CON	0.837	20.4%	72.68	22.0%
585-HOT	0.791	13.8%	67.28	12.9%
385-HOT = NA	0.668	−3.9%	56.50	−5.20%
585-CON = NA	0.831	19.6%	71.50	20.0%
585-HOT = NA	0.824	18.5%	70.42	18.2%

^aThe percentages reflect the change in the treatments relative to the control (385-CON). The treatment abbreviation are as in Table 1; the NA (no acclimation) specifies the model results without considering acclimation of $V_{c,\text{max}}$ or J_{max} .

$[\text{CO}_2]$, even with the acclimation responses incorporated into the model, showed a substantial increase in A to a thermal optimum approaching 35°C for both years, while the control $[\text{CO}_2]$ scenarios reached the optimum around or slightly below 30°C (Figure 2). However, experimentally higher temperatures within a $[\text{CO}_2]$ treatment (e.g., 385-CON versus 385-HOT and 585-CON versus 585-HOT) resulted in lower A at most temperatures, including the thermal optimum, but little to no change in the temperature at which the thermal optimum was reached (Figure 2). These observations are consistent with measured responses from the same experiment [Rosenthal *et al.*, 2014] but contrary to previous studies showing an increase in the thermal optimum with growth at higher temperatures [Kattge and Knorr, 2007]. Our results indicate that acclimation of $V_{c,\text{max}}$ and J_{max} to higher temperatures will not increase the thermal optimum beyond that

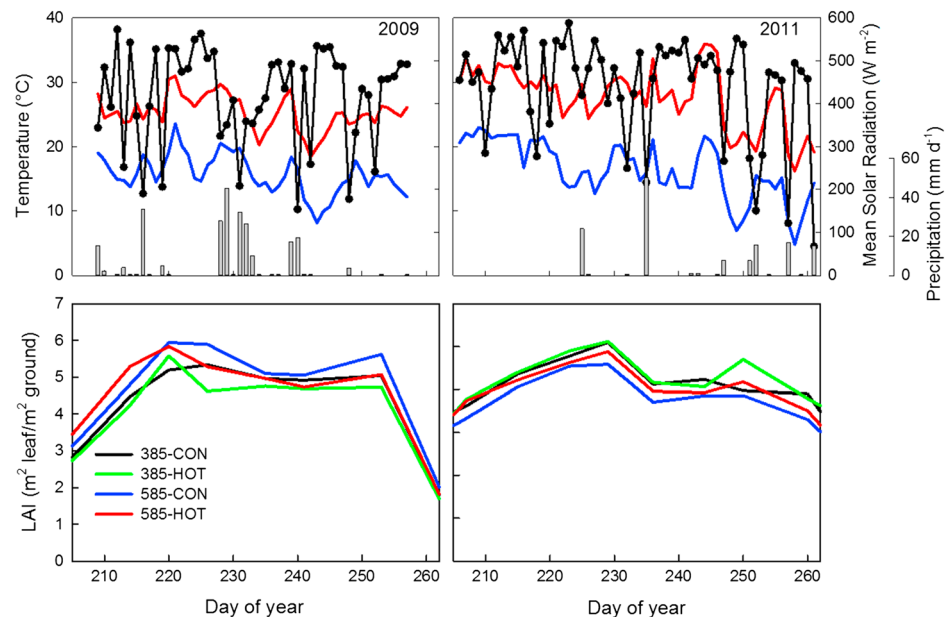


Figure 4. (top row) Meteorological conditions and (bottom row) observed leaf area index measured in (left column) 2009 and (right column) 2011. In Figure 4 (top row) the red lines represent the daily maximum and blue lines daily minimum temperatures, the black line represents the mean daily solar radiation, and the bars represent daily total precipitation.

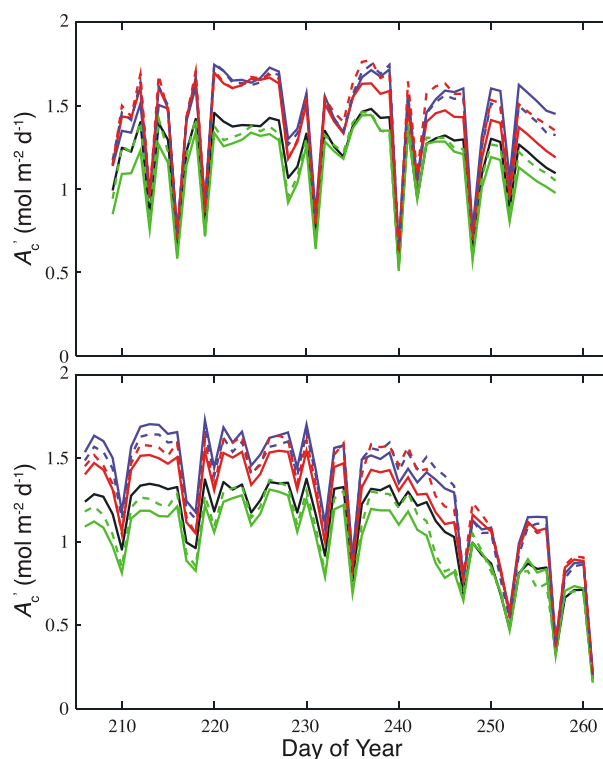


Figure 5. Simulation of the daily total canopy carbon uptake assimilation over the (top) 2009 and (bottom) 2011 growing seasons. Lines are as in Figure 4, and simulations used seasonally varying $V_{c,max}$ and J_{max} from Rosenthal *et al.* [2014].

(585-CON-NA and 585-HOT-NA), the increase would have been higher (Table 2 and Figure 3). Whereas the 585-CON and 585-HOT treatments only differed by ~4% in 2009, in 2011 the difference increased to ~7%. The 2011 growing season was drier and hotter than 2009; thus, it is likely that the warmer temperatures drove A beyond the thermal optimum for much of the growing season (Figure 4). The higher temperatures of 2011 can also explain the greater decreases of A in the 385-HOT treatment versus the control relative to the same comparison in 2009. Acclimation impacted potential carbon uptake of leaf-level A , thereby reducing the A' for all treatments (Table 2), suggesting that neglecting the physiological adjustments associated with photosynthesis in response to these treatments will overestimate leaf photosynthetic rates.

3.4. Scaling to Canopy Photosynthesis

The physiological processes that drive fluxes at the leaf have been shown to scale to the canopy; however, the extent to which the magnitude of leaf responses translate to similar magnitude canopy responses to the treatments is uncertain [Bernacchi *et al.*, 2007; Shimono *et al.*, 2013]. Here the latest generation of mechanistically based canopy photosynthesis model with an integrated mechanistic representation of physiology and biophysical components, MLCan [Drewry *et al.*, 2010a], was parameterized with measured changes in leaf biochemical parameters (Table 1) and canopy properties from the SoyFACE T-FACE experiment. The model was forced by meteorological measurements collected for the 2009 and 2011 growing seasons (Figure 4) as well as measured changes in leaf area index to show the within-season dynamics as well as the total seasonal responses of canopy photosynthesis (A_c' ; $\text{mol m}^{-2} \text{d}^{-1}$).

Compared with the control (385-CON), the impact of the treatments on photosynthesis was increased when scaled from the leaf to the canopy (Figure 5 and Table 2). Whereas A' in the 385-HOT treatment decreased by 5.2% in 2009 and 5.6% in 2011 relative to the control, canopy photosynthesis integrated over the full growing season (A_c') declined by 6.8% and 9.1% for the respective years. For both years, the 585-CON treatment when compared with the control showed a greater percentage increase in A_c' relative to A' (Table 2). The augmented responses when scaling from the leaf to the canopy represent the additive

of $[\text{CO}_2]$ alone, and photosynthetic acclimation to increasing temperatures suppresses A across the range of temperatures likely to be encountered during a growing season.

It is evident from modeled diurnal photosynthetic rates for each growing season that stimulation of A by increased $[\text{CO}_2]$ is greater than the decline associated with warmer temperatures. The analysis also predicts that an increase in $[\text{CO}_2]$ coupled with warmer temperatures, despite acclimation, will lead to higher photosynthetic rates relative to the control. To determine how these responses translate to model predictions over whole growing seasons, diurnal A was modeled and averaged for 2009 and 2011 with and without the influence of the $[\text{CO}_2]$ - and temperature-induced acclimation responses of $V_{c,max}$ and J_{max} (Figure 3). An increase in $[\text{CO}_2]$, regardless of temperature and despite acclimation (585-CON and 585-HOT), resulted in higher daily integral of photosynthesis (A' ; $\text{mol m}^{-2} \text{d}^{-1}$) of between approximately 11% and 14% above control for both years; however, without acclimation responses

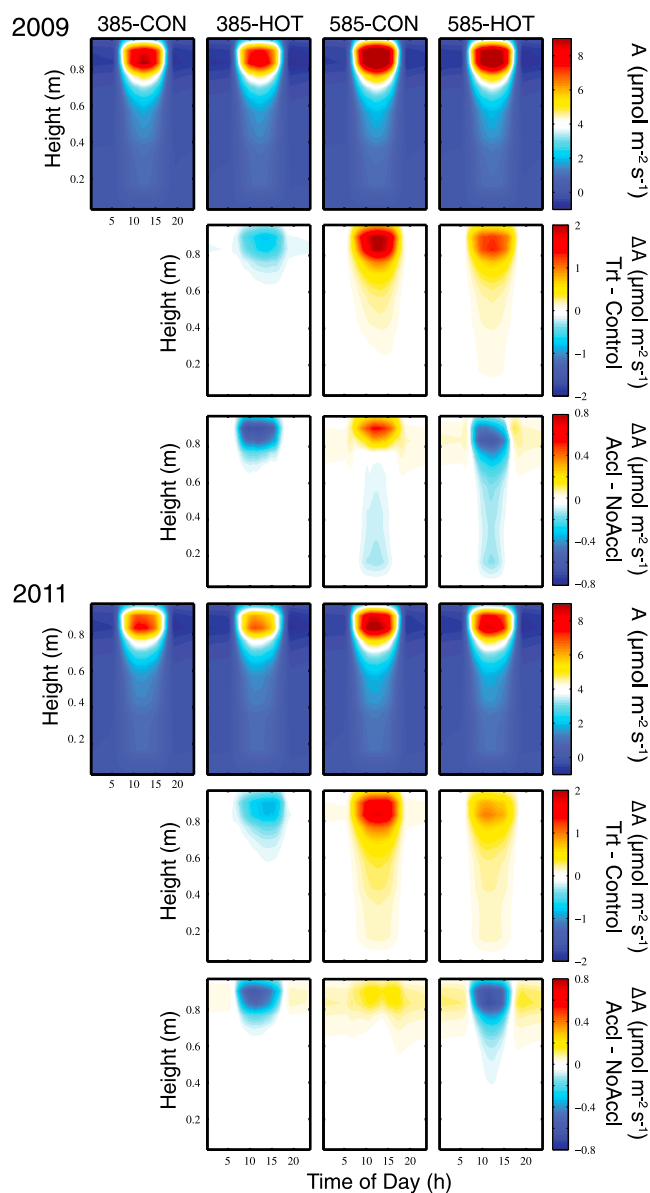


Figure 6. Visual representation of (first row) photosynthesis through the soybean canopy for 2009, (second row) difference plots of the treatment minus control, and (third row) difference plots of acclimated minus nonacclimated for the 2009 growing season. (fourth to sixth rows) Similar plots for the 2011 growing season. Each plot represents A or differences in A (color and intensity) through the vertical canopy profile (Y axis) over the diurnal time course (X axis). Simulations used seasonally varying $V_{c,max}$ and J_{max} from Rosenthal et al. [2014].

effect of leaves at each level in the canopy responding to their microenvironment. Both years showed consistent decreases in A_c' for the 585-HOT relative to the 585-CON treatment. These results indicated that higher temperatures partially offset the benefit of elevated $[CO_2]$ for photosynthesis at the canopy scale and that leaf-level responses of A to these treatments do not scale perfectly to the canopy.

The model was used to determine the role of biochemical ($V_{c,max}$ and J_{max}) and canopy (measured as leaf area index; LAI) acclimation in influencing the rates of A_c . This was done by running the model with and without the measured acclimation responses. In addition to the direct acclimation associated with $V_{c,max}$, J_{max} , and LAI, the model incorporates indirect feedbacks associated with biophysics [Drewry et al., 2010a]. Consistent with previous analysis [Drewry et al., 2010a, 2010b], changes in LAI between treatments had only a small influence on canopy photosynthetic rates (data not shown), and treatment effects on A_c' were dominated by differences in the acclimated versus nonacclimated biochemical parameters. For the 385-HOT and 585-HOT treatments, A_c' was lower in the acclimated scenario compared with the nonacclimated scenario for both years, similar to that observed for A' (Table 2). The decrease in A_c' between the acclimated and nonacclimated circumstances in the 585-CON treatment was negligible; both years showed lower A_c' in the acclimated circumstance which was likely driven by the slightly lower J_{max} similar to that observed using the same model parameterized with

different growing season data [Drewry et al., 2010b]. Consistent with measurements over multiple years at the SoyFACE facility was the decrease in $V_{c,max}$ for plants grown in elevated compared with ambient $[CO_2]$ [e.g., Bernacchi et al., 2005]; this response was also observed for the measurements collected in 2009 and 2011 where $V_{c,max}$ was much lower for the 585-CON relative to the 385-CON treatments (Table 1). Despite the lower $V_{c,max}$ in the 585-CON treatments relative to control, previous work shows that soybean plants are seldom limited by $V_{c,max}$ when grown in elevated $[CO_2]$ [Bernacchi et al., 2005]. Thus, these decreases in $V_{c,max}$ are not predicted, nor are they shown, to influence photosynthesis in elevated $[CO_2]$ (e.g., Figure 5 and Table 2).

The amplification of the leaf-scale responses to the canopy is illustrated using contour plots of photosynthesis through the vertical plant canopy throughout the diel time course (Figure 6). In soybean, the top approximately 20 cm of the plant canopy dominated A_c ; this is where the greatest density of foliage is located and the majority of PAR is absorbed. The influence of higher temperatures in the 385-HOT treatment appears to dominate photosynthetic rates exclusively in this area of high leaf density (Figure 6). While the elevated $[\text{CO}_2]$ treatments (585-CON and 585-HOT) appear to have some attenuation of CO_2 responses even in the less dense subcanopy, the majority of the canopy responses occurred near the top of the canopy (Figure 6).

The role of acclimation in reducing photosynthetic potential is also depicted over the diel time course (Figure 6). It is clear that the role of acclimation was negligible through the canopy for the 585-CON scenario but that the warmed plots saw a large influence at the top of the plant canopy (Figure 6). Consistent with previous reports, this analysis suggests that neglecting biochemical acclimation to elevated $[\text{CO}_2]$ is not likely to have a significant impact on ecosystem-scale models [Drewry *et al.*, 2010b] but neglecting the impact of biochemical acclimation to higher temperature environments, with or without concomitant increases in $[\text{CO}_2]$, are likely to substantially overestimate leaf (Figure 3) and canopy (Figure 5) photosynthesis.

4. Conclusion

The results of this analysis are driven by model output using the MLCan model, which has been validated against a wide range of measurements made at various spatial and temporal scales, including leaf gas exchange, canopy architecture measurements, eddy covariance, and other micrometeorological measurements, for soybean [Drewry *et al.*, 2010a, 2010b]. The parameterization in this study is based on the most intensive measurements made to date on field-grown soybean exposed to elevated $[\text{CO}_2]$ and temperature [Ruiz-Vera *et al.*, 2013; Rosenthal *et al.*, 2014] and the modeled leaf responses of A to temperature match with the measured responses reported previously [Rosenthal *et al.*, 2014]. Thus, these results represent for soybean the most complete model analysis of leaf and canopy photosynthesis to two major components of future climate change. However, important uncertainties remain in this analysis. For example, the measurements of $V_{c,\text{max}}$ and J_{max} were taken at the top of the canopy, and photosynthetic capacity was assumed to decrease through the canopy in a manner identical in all scenarios (equation (5)). Further, the influence of growth temperature effects on g_m is uncertain as is the possibility that the temperature response of J_{max} varies with growth conditions, which may potentially influence the results of this analysis, although previous evidence suggests that adjustment of the J_{max} temperature response to growth temperature is likely to be small with only a 3.5°C difference in growth conditions. Nevertheless, these are potential oversimplifications that additional measurements may clarify. Additionally, to focus on impacts of photosynthetic acclimation by the simulation period in this study is restricted to the time when the canopy is closed. This limits the capability of this study to relate the observed changes in canopy photosynthesis to overall crop yield and total biomass, which would be an important extension. Finally, although the weather conditions in the years represented in this study are distinctly different, they are by no means representative of the full range of potential environmental conditions. As such, significant uncertainty remains of how varying seasonal conditions may influence soybean's physiological response to rising $[\text{CO}_2]$ and temperature. Finally, although the equations underpinning the MLCan model are state of the art, uncertainties and approximations exist and continual advancements are being made to improve the physics of mechanistic crop models. This is particularly relevant when modeling responses to currently atypical environmental conditions.

The theory behind the interactions of $[\text{CO}_2]$ and temperature on photosynthesis is well established. This has contributed to the photosynthesis model developed by Farquhar and colleagues becoming ubiquitous in state-of-the-art ecosystem, agricultural, and global land surface models. However, photosynthetic parameters such as $V_{c,\text{max}}$ and J_{max} are generally derived for broad classes of vegetation and assumed to be invariant in studies of ecosystem productivity under changing global conditions. While this study was focused on soybean, we have shown that photosynthetic acclimation results in a less than predicted increase in productivity with concomitant increases in $[\text{CO}_2]$ and temperature or with rises in temperature alone. Therefore, any ecosystem modeling effort for soybean that neglects biochemical acclimation is, unlike with elevated $[\text{CO}_2]$ alone, likely to overestimate ecosystem productivity. Further, while not all species show similar responses to increases in $[\text{CO}_2]$ and/or temperature, the responses of legumes and crops, particularly related to whether $V_{c,\text{max}}$ or J_{max} are limiting at elevated $[\text{CO}_2]$, may be relatively similar [Ainsworth and Rogers, 2007]. This suggests that the importance of accounting for acclimation of photosynthesis may extend beyond soybean to other major crop species.

Acknowledgments

The MLCan model is openly available at <https://github.com/HydroComplexity/MLCan>, and all data provided in the figures can be acquired via communication with the corresponding author (C.J.B.).

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