ORIGINAL ARTICLE

WILEY Plant, Cell & Environment

Canopy warming accelerates development in soybean and maize, offsetting the delay in soybean reproductive development by elevated CO_2 concentrations

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Funding information

National Institute of Food and Agriculture (NIFA), United States Department of Agriculture (USDA), Grant/Award Number: 2014-67013-21783

Abstract

Increases in atmospheric CO₂ concentrations ([CO₂]) and surface temperature are known to individually have effects on crop development and yield, but their interactive effects have not been adequately investigated under field conditions. We evaluated the impacts of elevated $[CO_2]$ with and without canopy warming as a function of development in soybean and maize using infrared heating arrays nested within free air CO₂ enrichment plots over three growing seasons. Vegetative development accelerated in soybean with temperature plus elevated [CO₂] resulting in higher node number. Reproductive development was delayed in soybean under elevated [CO₂], but warming mitigated this delay. In maize, both vegetative and reproductive developments were accelerated by warming, whereas elevated $[CO_2]$ had no apparent effect on development. Treatment-induced changes in the leaf carbohydrates, dark respiration rate, morphological parameters, and environmental conditions accompanied the changes in plant development. We used two thermal models to investigate their ability to predict the observed development under warming and elevated [CO2]. Whereas the growing degree day model underestimated the thermal threshold to reach each developmental stage, the alternative process-based model used (β function) was able to predict crop development under climate change conditions.

KEYWORDS

carbohydrates, CO2, development, elevated CO2, global warming, heat, respiration, soybean and maize

1 | INTRODUCTION

Global mean surface temperature increased by ~0.94°C from 1880 to 2016 (National Oceanic and Atmospheric Administration, National Centers for Environmental Information, 2017) and is predicted to increase ~4°C above the 2005 global mean temperature by the end of the century if global greenhouse gas emissions continue on the Representative Concentration Pathway (RCP 8.5) scenario (Intergovernmental Panel on Climate Change, 2014). This increase would result in mean summer temperatures that exceed the hottest summers currently on record (Battisti & Naylor, 2009). Environmental warming affects many biological processes that can drive ecosystem changes by altering plant species distribution (Sage & Kubien, 2007) and net ecosystem productivity (Chen et al., 2017; Joo, Zeri, Hussain, DeLucia, & Bernacchi, 2017; Su, Feng, Axmacher, & Sang, 2015). For example, increases in growing season temperature can drive changes in plant growth rates by affecting photosynthesis, photorespiration, and respiration (e.g., Ainsworth & Ort, 2010; Atkin, Bruhn, Hurry, & Tjoelker, 2005; Crafts-Brandner & Salvucci, 2004; Hatfield et al., 2011; Long, 1991; Sage & Kubien, 2007; Sage, Way, & Kubien, 2008; Wall, Kimball, White, & Ottman, 2011). Moreover, growing season temperature can influence the progression of plant vegetative and reproductive developmental stages (e.g., Campbell & Norman, 1998). The significant changes in the global climate system that are looming have instigated investigation of the consequences of global warming on the physiology, growth, and yield of major food crops (e.g., Bishop, Leakey, & Ainsworth, 2014; Hatfield & Prueger, 2015; Mastilović et al., 2017; Obata et al., 2015; Ruiz-Vera et al., 2013; Ruiz-Vera, Siebers, Drag, Ort, & Bernacchi, 2015; Zhao et al., 2016). In-field warming experiments have led to a better understanding of the plant physiological responses to temperature, but impacts of warming under field conditions on the progression through vegetative and reproductive growth stages are less well understood.

The phenology of many plant species is tightly coupled with temperature; thus, the concept of growing degree day (GDD) as an index for thermal time has been widely used to predict the rate at which plants progress through vegetative and reproductive phenological stages (e.g., Baker & Reddy, 2001; Hesketh, Myhre, & Willey, 1973; McMaster & Wilhelm, 1997; Sacks & Kucharik, 2011; Tollenaar, Daynard, & Hunter, 1979). The GDD concept is based on observations that development of poikilotherms is determined by cumulative exposure to heat (e.g., Campbell & Norman, 1998; McMaster & Wilhelm, 1997) with faster development at higher temperatures until temperatures exceed thresholds causing cessation of growth or mortality. The existing GDD models predict that global warming conditions will accelerate development for most plant species. If development is accelerated, reductions in grain crop yields are possible because plants could spend less time in key reproductive stages, even if physiological processes, such as photosynthesis, have not been affected by the increase in temperature (Ainsworth & Ort, 2010). Models other than GDD have also been used to predict maize and soybean development (e.g., Kim et al., 2007; Kumudini et al., 2014; Setiyono et al., 2007; Setiyono et al., 2010). The use of thermal functions classified as process-based functions, like the ß function (Yan & Hunt, 1999; Yin, Kropff, McLaren, & Visperas, 1995), has been shown to better predict vegetative development at supraoptimal conditions; however, predictions of reproductive development at high temperatures are less well developed (Kumudini et al., 2014).

Maize and soybean are the first and the third most important agricultural crops grown globally in terms of economic value, with the United States as the largest producer of both crops (2013 data; Food and Agriculture Organization Corporate Statistical Database, 2017). Combined these crops cover ~69 million ha within the Midwestern United States producing more than ~4 billion bushels (110 million tons) of soybean and ~15 billion bushels (380 million tons) of maize (2016 data; United States Department of Agriculture, National Agricultural Statistics Service, 2017). Because of their agroecological and socio-economic importance, many studies have evaluated the consequences of climate change factors on the growth and yield of soybean and maize (e.g., Ainsworth et al., 2002; Kimball, 2016; Leakey et al., 2006; Lobell, Banziger, Magorokosho, & Vivek, 2011; Lobell & Field, 2007; Morgan, Bollero, Nelson, Dohleman, & Long, 2005; Ruiz-Vera et al., 2013; Ruiz-Vera et al., 2015). There are also many studies focused on the temperature response for development in soybean (Garner & Allard, 1930; Hofstra, 1972; Major, Johson, Tanner, & Anderson, 1975; Pereira-Flores et al., 2016; Piper, Smit, Boote, & Jones, 1996; Setiyono et al., 2007; Sionit, Strain, & Flint, 1975;

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Tremmel & Patterson, 1993) and maize (Hatfield & Prueger, 2015; Kim et al., 2007; Sánchez, Ramussen, & Porter, 2014; Tollenaar et al., 1979). In contrast, only a few studies considered the interactive effect of CO₂ with temperature on development, particularly under field conditions. Chamber-based CO₂ by temperature experiments showed that increased temperature can significantly accelerate the progression of soybean through phenological stages and affect flowering time (e.g., Heinemann, Maia, Dourado-Neto, Ingram, & Hoogenboom, 2006; Hesketh et al., 1973). However, the effect of CO₂ on soybean phenology is more uncertain. CO₂ concentration is reported not to affect trifoliate emergence between mean temperatures from 24 to 30°C (Hesketh et al., 1973), yet other reports indicate that the effects of CO₂ on soybean phenology are temperature dependent (Heinemann et al., 2006). For maize, chamber-based experiments that evaluated the temperature dependence of development under high [CO2] showed a curvilinear response of leaf emergence with growth temperature where the optimum temperature was ~32°C but showed CO2 enrichment did not alter development (Kim et al., 2007).

Growth chambers have significant influence on microclimate (McLeod & Long, 1999), and their artificial lighting regimes are likely to influence reproductive development in crops, such as soybean, that are strongly influenced by photoperiod length (e.g., Kantolic & Slafer, 2001; Kantolic & Slafer, 2007; Piper et al., 1996; Setiyono et al., 2007). Free air CO₂ enrichment (FACE) technology allows for a direct manipulation of CO₂ growth environments under natural photoperiod illumination regimes with nearly natural canopy microenvironments (e.g., Ainsworth, Leakey, Ort, & Long, 2008). Using FACE technology, Castro, Dohleman, Bernacchi, and Long (2009) showed that elevated $[CO_2]$ increased the number of nodes and delayed reproductive development in indeterminant soybean. The CO₂ effect on phenology has not been observed for maize in field FACE experiments. Moreover, there have been no field studies investigating the combined effect of elevated $[CO_2]$ and warming on soybean or on maize development.

The objective of this study was to quantify the effects of increasing temperature with or without the elevation of $[CO_2]$ on the different developmental stages of soybean and maize, in order to detect phenological changes that might impact yield. This research was conducted using temperature by FACE (T-FACE) technology, which relies on infrared heating arrays for controlled increase of canopy temperature above ambient temperatures and on the FACE technology to increase [CO₂] by ~200 µmol mol⁻¹ above ambient. Because rising temperatures allow faster accumulation of GDD, we hypothesized for soybean that (a) the increase of temperature alone and independently of the [CO₂] will accelerate the progression to more advanced vegetative and reproductive developmental stages; (b) the increase in temperature together with elevated [CO2] will result in a higher plant node number than an increase in temperature alone; and (c) the previously detected delay in reproductive development by elevated [CO₂] (Castro et al., 2009) will be offset by the rise in temperature. In the case of maize, we hypothesized that (d) warming will accelerate vegetative and reproductive development, including the tassel stage, independently of [CO₂]. Additionally, some physiological (e.g., dark respiration and leaf carbohydrates) and growth parameters were evaluated to elucidate the causes for any changes observed in

development due to the treatments. Finally, we evaluated the prediction performance of the β thermal model, a process-based model, to see if this model performs better than the GDD model under warming

2 | MATERIALS AND METHODS

and elevated [CO2] conditions.

2.1 | Site description and experimental design

Vegetative and reproductive development data were collected from an indeterminate maturity group III soybean variety (Glycine max (L.) Merr., cv Pioneer 93B15) over two growing seasons (2009 and 2011) and from maize (Zea mays cv. 34b43, Pioneer Hi-Bred International) in one growing season (2010). Plants were grown at the SoyFACE facility located in Urbana, IL, USA (40.04° N, 88.24° W, 217 m above sea level), within the T-FACE in-field heating technology arrays. Details of the site and the agronomic practices associated with SoyFACE can be found in Ainsworth, Rogers, Nelson, and Long (2004), Leakey, Bernacchi, Dohleman, Ort, and Long (2004), Rogers et al. (2004), Bernacchi et al. (2006), and Ruiz-Vera et al. (2013). The experiment was a randomized complete block design with four blocks. In each block, there was one 20-m-wide ambient and one 20-m-wide elevated [CO₂] octagonal plot. The average [CO₂] in the ambient plots was at 385 μ mol mol⁻¹ in 2009 and 390 μ mol mol⁻¹ in 2010 and 2011. The [CO₂] in the elevated [CO₂] plots was set to 585 µmol mol⁻¹ in 2009 and 2010 and 590 µmol mol⁻¹ in 2011, maintained from sunrise to sunset during the full growing season. Heated and nonheated reference plots (3-m diameter) were nested within each larger elevated and reference [CO2] plots (eight in total). The heating arrays consisted of six infrared heaters (Salamander Aluminum Extrusion Reflector Assembly Housing for Ceramic Infrared Heaters; Mor Electric Heating Association Inc., Comstock Park, MI, USA) each containing four infrared heating elements (Mor-FTE 1,000-W, 240-V heaters; Mor Electric Heating Association Inc.). The heaters were situated 1.2 m above the plant canopy in a 3-m-diameter hexagonal pattern (7.1 m²). The heater output (up to 24,000 W of infrared heating power) was regulated by a dimmer system that was controlled by a circuit board (Model LCED-2484, 240 V, 35A; Kalglo Electronics Co., Inc., Bethlehem, PA, USA). A datalogger (CR1000 Micrologger; Campbell Scientific, Inc., Logan, UT, USA) controlled each heated plot using a proportional-integrative-derivative feedback control system. Infrared radiometers (SI-121; Apogee Instruments, Inc., Logan, UT, USA) wired into the datalogger measured the canopy temperature in the heated and reference plots. According to the difference between the heated and reference plots, the voltage output module supplied the 0- to 10-V signal to the dimmer (SDM-CV04; Campbell Scientific Inc.), which in turn regulated the current input to the heaters to maintain ~3.5°C increase over the ambient temperature for 24 hr day⁻¹ throughout the growing seasons. The heated plots were set up after planting and were turned on 12, 11, and 13 days after planting in 2009, 2010, and 2011, respectively. The delay in initiating warming was to allow the plants to become established without excessive temperatures that might potentially desiccate plants prior to establishing deeper roots. The experiment consisted of four treatments: control (ambient $[CO_2]$ and ambient temperature), eT (ambient $[CO_2]$ and heated temperature), eC (elevated $[CO_2]$ and ambient temperature), and eT + eC (elevated $[CO_2]$ and heated temperature).

2.2 | Measurements of the soybean development

Soybean was planted on day of year (DOY) 160 (June 9) in 2009 and DOY 159 (June 8) in 2011. In each plot, six soybean plants chosen at random were marked at the beginning of the season to track their development from emergence to maturity (R7-R8) according to the classification and descriptions in Fehr, Cavines, Burmood, and Pennington (1971) and Ritchie, Hanway, and Benson (1993). In summary, each node formed on the main stem with fully developed leaves represents a vegetative stage, with Vegetative Stage 1 (V1) representing the first node and Vx representing the total number of nodes "x." Reproductive development is divided in eight stages: beginning bloom (R1), full bloom (R2), beginning pod (R3), full pod (R4), beginning seed fill (R5), full seed (R6), beginning maturity (R7), and full maturity (R8). The initiation of reproductive development (R0) is triggered by day length or photoperiod, but this stage cannot be visually determined; thus, RO was not recorded. All other reproductive growth stages (from flowering to maturity) depend on temperature and photoperiod (Setiyono et al., 2007), and they were recorded throughout the growing period. Measurements were made three times a week from emergence to senescence. If damage to a plant occurred, that plant was no longer considered in the data set.

2.3 | Dark respiration, carbohydrate analysis, and growth parameter measurements

Whole leaf dark respiration (respiration for growth and maintenance together; Setiyono et al., 2010) was taken in the field during 4 days (DOY 186, 200, 214, and 242) in the youngest most fully expanded leaf and in old leaves during 2011 (Table S1). In DOY 186, the old leaves were taken from the third node down after the youngest mature leaf node; the leaves from the fifth node down were used the rest of the days. Leaf respiration was measured as a CO₂ efflux from the whole leaf by using customized aluminium leaf chambers, the same chamber used in Gillespie et al. (2012). The leaf chambers were mounted in two open gas exchange systems (LI-6400; LI-COR, Inc., Lincoln, NE, USA) and sealed as specified in Gillespie et al. (2012). Measurements were done in two plants per subplot, from ~9 p.m. to 3 a.m. After a whole leaf was placed inside the chamber, ~10-min acclimation time was allowed before measurements were taken at the treatment temperature. The respiration measurements were normalized by the area of the measured leaves, which were determined by a leaf area meter (LI-COR-3100, LI-COR, Inc.).

Leaf disk samples of ~1.2-cm diameter were collected from two plants per subplot at dusk in the same day respiration measurements were taken and at dawn the following day (Table S1). Samples were kept frozen until the determination of the leaf carbohydrates was done as described in Ruiz-Vera, De Souza, Long, and Ort (2017) and Ainsworth et al. (2007). Total soluble carbohydrate (TSC) is the sum of glucose, fructose, and sucrose. TSC and starch were expressed as glucose equivalents.

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Stem biomass for both years and stem height, basal diameter of the stem, and number of branches for soybean at 2011 were also recorded (Table S1). Details of the harvest methodology can be found in an earlier study by Ruiz-Vera et al. (2013).

2.4 | Measurements of the maize development

Maize was planted on DOY 118 (April 28) in 2010. Eight plants were marked at the beginning of the study in each plot, and their development was recorded every 2 to 3 days throughout the season, following the classification in Ritchie, Hanway, Benson, Herman, and Lupkes (1993). The vegetative stages (V) refers to the number of mature leaves on which collars are visible (from V1 to Vx). Maize is considered in the tassel stage (VT) when the whole tassel is visible. The reproductive developmental stages in maize are silking (R1), blister (R2), milk (R3), dough (R4), dent (R5), and physiological maturity (R6). A plant was deemed senescent when at least 80% of the leaves were dry. The number of senescent plants divided by the total number plants was defined as the "senescence ratio." The senescence data were collected from the same plants tracked for development.

2.5 | Growing degree day calculation

For soybean, the GDD (°Cd) was calculated for each plot following the equations of Campbell and Norman (1998), using the measured canopy temperatures as follows:

If
$$\overline{T_{can}} \leq T_b$$
 or $\overline{T_{can}} \geq T_{supr}$, then $GDD = 0$. (1)

If
$$T_b < \overline{T_{can}} < T_{opt}$$
, then $GDD = \overline{T_{can}} - T_b$. (2)

If
$$T_{opt} \le \overline{T_{can}} < T_{supr}$$
, then $GDD = \frac{T_{supr} - \overline{T_{can}}}{T_{supr} - T_{opt}} (T_{opt} - T_b)$. (3)

Here, $\overline{T_{can}}$ is the daily mean canopy temperature. T_b is base temperature defined as the minimum temperature for growth or development, which is 10°C for soybean (Zhang, Wang, & Hesketh, 1995). The optimum temperature for development (T_{opt}) was set at 30°C for soybean (e.g., Major et al., 1975; Zhang et al., 1995). The upper temperature threshold for development (T_{supr}) was set at 40°C for soybean (Setiyono et al., 2007). During some days in 2011, the maximum temperature in a day exceeded 40°C in the heated treatments (Ruiz-Vera et al., 2013); however, the calculated $\overline{T_{can}}$ for those days was not higher than the T_{supr} .

For maize, GDD was calculated following Equations (1) and (2), where $T_b = 10^{\circ}$ C and $T_{opt} = 30^{\circ}$ C for maize (Hatfield & Prueger, 2015; Nielsen et al., 2002; Stewart, Dwyer, & Carrigan, 1998). Equation (3) was replaced by the one in Lobell et al. (2011); thus,

if
$$\overline{T_{\text{can}}} \ge T_{\text{opt}}$$
, then $GDD = T_{\text{opt}} - T_b$. (4)

The canopy temperature was measured using infrared radiometers (SI-121; Apogee Instruments, Inc., Logan, UT, USA) located in each of the T-FACE plots described above. The canopy temperature was collected in 10-s intervals and averaged for 10-min periods throughout the growing season. In the interval between planting and the beginning of the heat treatment (from planting to DOY 172 in 2009 and 2011 and to DOY 129 in 2010), canopy temperature measurements were not taken. During this interval, GDD was calculated using the hourly air temperature data collected from a meteorological station associated with the Surface Radiation Network (SURFRAD, 40.05° N, 88.37° W, http://www.srrb.noaa.gov/surfrad/index.html), located ~11.5 km from the experimental site. For this calculation, the average daily temperature (T) calculated as $\frac{T_{max} + T_{min}}{2}$ replaced $\overline{T_{can}}$ (see equation 2.9 in Campbell & Norman, 1998), where T_{max} is the daily maximum temperature and T_{min} is the daily minimum temperature.

The accumulated GDD_n (GDD through *n* days) was calculated according to the formula:

$$GDD_n = \sum_{i=1}^n (GDD_i)$$
(5)

until the last heating treatment day, which coincided with the harvest in 2009 (DOY 266) and 2010 (DOY 257) and with R7-R8 stages in 2011 (DOY 264).

2.6 | Development data processing

For both vegetative and reproductive developmental stages (including VT in maize), the DOY when a specific developmental stage was reached (DOYr) was calculated from the daily mean values for each plot. Because measurements were collected three times weekly, there were occurrences when a developmental stage was reached on a day when measurements were not collected. In these situations, extrapolation of DOYr was performed from the measurements immediately preceding and following a specific developmental stage. Because the field data were collected during the progression of a day and not at a specific hour, the DOYr obtained by the extrapolation was rounded up to the nearest whole number. The DOYr values were used to obtain the GDD when a developmental stage was reached (GDDr), and the duration of each developmental stage was defined as number of days in a stage (DIS); DIS was only used for the reproductive data.

2.7 | Temperature response of growth using cardinal temperatures

The β distribution function was used to model temperature response of vegetative growth. This approach is characterized by a unimodal response of growth rate to temperature and has been previously used to describe rate of development and growth in maize and soybean (Setiyono et al., 2007; Yin et al., 1995). The relative growth rate (*r*) is a function of T_b , T_{supr} , and T_{opt} as

$$r(T) = \left(\frac{T_{supr} - T}{T_{supr} - T_{opt}}\right) \left(\frac{T - T_b}{T_{opt} - T_b}\right)^{(T_{opt} - T_b)/(T_{supr} - T_{opt})},$$
(6)

$$R = r(T) \cdot R_{\max},\tag{7}$$

with a maximum value of 1 for days when average daily temperature (*T*) is the same as T_{opt} (Equation (6)). Predicted growth rate (*R*, day⁻¹) is calculated by multiplying *r* and the maximum daily growth rate (R_{max} , day⁻¹) as shown in Equation (7).

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This study used a simplified version of Equation (6), which makes $T_b = 0^{\circ}$ C (Yan & Hunt, 1999). The literature parameters used were $T_{supr} = 43.7$, $T_{opt} = 31.2$, and $R_{max} = 0.53$ for maize (Kumudini et al., 2014) and $T_{supr} = 40$, $T_{opt} = 31$, and $R_{max} = 0.452$ for soybean (Setiyono et al., 2007). For *T*, we used $\overline{T_{can}}$ that was obtained as described above. The observed rates of growth (day⁻¹) were calculated from the field development data. The statistics that evaluated the model performance was the root mean square error (RMSE), and it was calculated as Archontoulis and Miguez (2015):

$$RMSE = \sqrt{\frac{\sum (o_i - p_i)^2}{n - k - 1}},$$
(8)

where *o* is the *i*th observed value of the rate of development (day^{-1}) during vegetative growth phase, *p* is the corresponding predicted value using β distribution function, *n* is the number of observations, and *k* is the number of model parameters. RMSE between observed and predicted rates of growth was calculated (Table 1).

The optimized values for T_{opt} and R_{max} (keeping T_b and T_{supr} fixed) were calculated by minimizing the sum of square of error between observed and predicted rates of growth. For this procedure, the Nelder–Mead method implemented in the R function *optim* (R Core Team, 2018) was used for all the treatments in each year (Table 1). RMSE was also calculated when the optimized values for T_{opt} and R_{max} were applied (Table 1).

2.8 | Statistical analysis

The relationship between the vegetative stages and DOYr and between the vegetative stages and GDDr was fit to a first-order linear regression (PROC REG, SAS System 9.3, SAS Institute, Cary, NC, USA). To test for the statistical significance between the linear regressions, we used the analysis for linear regressions defined in Mead and Curnow (1983). Thus, statistics from the linear regressions from each treatment were compared independently with the statistics from the linear regressions from all treatments combined. The reproductive development data were analysed using a complete block mixed model analysis of variance for repeated measures with the Kenward–Roger

option (PROC MIXED, SAS System 9.3, SAS Institute, Cary, NC, USA). The statistical analysis for DOYr and GDDr was performed up to R7 in soybean and up to R6 in maize. The statistical analysis for DIS was done through the completion of R6 in soybean and through R5 in maize. Because we were testing whether treatment differences exist among the reproductive stages, the fixed effects were [CO₂] (CO₂), temperature (Temp), the reproductive stages (Stage), and their interactions. The random effect was the block. The dark respiration, leaf carbohydrates, stem height, stem basal diameter, number of branches and stem biomass in soybean, tassel stage (VT), and the senescence ratio in maize were analysed as previously specified for reproductive stages. There were no repeated measurements for the stem height, stem basal diameter, number of branches, stem biomass, and VT; their fixed effects were CO₂, Temp, and their interactions. The fixed effects for dark respiration, leaf carbohydrates, and the senescence ratio were CO₂, Temp, DOY, and their interactions. The differences of least square means (t test) were used for the pairwise comparisons between treatments. Statistical significance was set a priori at $P \leq 0.1$.

3 | RESULTS

3.1 | Heating treatments resulted in ~13.5% increase in the rate of growing degree day accumulation across all three growing seasons

The heated treatments (eT and eT + eC) accumulated GDD at a 6.5-18% faster rate than the nonheated treatments (control and eC; Figure 1). At the end of the seasons, the heated treatments accumulated ~253°Cd more GDD in 2009, ~324°Cd more GDD in 2010, and ~160°Cd more GDD in 2011 compared with the nonheated reference plots. The increased rate of GDD accumulation for the heated treatments in each growing season resulted in a large difference in the number of days in which the GDD threshold (maximum GDD achieved in the nonheated treatments throughout the duration of the experiment) was reached. Thus, the heated treatments reached the GDD threshold (~1,100°Cd on DOY 266 in 2009, ~1,700°Cd on

TABLE 1 Treatments means ($\pm SE$) for T_{opt} and R_{max} , and RMSE between observed and predicted values

			Treatment mean			
Year	Crop	Parameter	Control	eT	eC	eT + eC
2009	Soybean	R _{max} T _{opt} RMSE—optimized values RMSE—literature parameters	0.39 ± 0.064 24.99 ± 4.538 0.1979 0.1857	0.45 ± 0.042 29.23 ± 2.457 0.2081 0.1993	0.34 ± 0.006 24.77 ± 3.906 0.1828 0.1887	0.42 ± 0.012 31.63 ± 0.431 0.1646 0.1661
2010	Maize	R _{max} T _{opt} RMSE—optimized values RMSE—literature parameters	0.43 ± 0.014 26.18 ± 1.264 0.1803 0.1876	0.47 ± 0.021 30.42 ± 0.387 0.2037 0.2111	0.46 ± 0.018 30.24 ± 0.442 0.1485 0.1561	0.44 ± 0.013 29.35 ± 1.050 0.1840 0.1945
2011	Soybean	R _{max} T _{opt} RMSE—optimized values RMSE—literature parameters	0.33 ± 0.027 30.25 ± 0.806 0.1023 0.1395	0.30 ± 0.009 26.17 ± 1.502 0.1073 0.1702	0.29 ± 0.009 27.94 ± 0.443 0.0881 0.1380	0.31 ± 0.008 29.19 ± 0.214 0.0962 0.1556

Note. RMSE was calculated with optimized and literature parameters for R_{max} and T_{opt} . These parameters were obtained with the β thermal function (Yin et al., 1995). The treatments are control, increased temperature (eT), elevated CO₂ (eC), and increased temperature and CO₂ (eT + eC). RMSE: root mean square error.



FIGURE 1 Accumulated growing degree days in all four treatments during 2009, 2010, and 2011 growing seasons. The crop planted per year for the experiment is indicated in parentheses. Treatments: control, increased temperature (eT), elevated CO_2 (eC), and increased temperature and CO_2 (eT + eC)

DOY 257 in 2010, and ~1,300°Cd on DOY 264 in 2011) ~24.5 days earlier in 2009, ~24 days earlier in 2010, and ~19.5 days earlier in 2011 (Figure 1). Between the heated treatments, eT compared with eT + eC accumulated ~34°Cd (3 days ahead) more GDD in 2010 and ~24°Cd less GDD (3 days behind) in 2011.

3.2 | Warming and elevated [CO₂] treatments of soybean influenced the rate of progression through vegetative developmental stages

Linear regression analysis of soybean vegetative stages versus DOYr for each treatment revealed that there were significant effects of

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temperature during 2009 (Figure 2a and Table S2). Here, eT + eC developed faster than eC. In 2011, both high temperature and [CO₂] affected vegetative development (Table S2). The pairwise comparisons showed that eT + eC was different from all other treatments, and it was the treatment with the fastest rate of vegetative development (Figure 2b and Table S2). The progression of vegetative development in eC, eT, and control was not different from each other. In addition to the more rapid progression through vegetative developmental stages, the heated treatments accumulated more GDDr than the nonheated treatments in 2009, and eT accumulated more GDDr than the rest of the treatments in 2011 (Figure 2c,d), as observed in the linear regression analyses of vegetative stages versus GDDr (Table S2). High [CO₂] also affected the accumulation of GDDr in 2011; consequently, eT + eC was different from all treatments (Table S2). During the hottest days of the 2011 growing season (approximately DOY 199, Ruiz-Vera et al., 2013), the heated treatments accumulated less GDDr than the nonheated treatments because their $\overline{T_{can}}$ was higher than Topt. Due to the CO2 warming canopy effect (e.g., Bernacchi, Kimball, Quarles, Long, & Ort, 2007), $\overline{T_{can}}$ in eT + eC was higher than in eT, so this treatment presented the least accumulation of GDDr when $\overline{T_{can}} > T_{opt}$ (Figure 2d). Independent of the rate at which higher vegetative stages were achieved, elevated [CO2] treatments (eC and eT + eC) formed more nodes than the control treatment in both years. Thus, eT + eC and eC formed, on average, one additional node per plant in 2009 (Figure 2a). In 2011, eT + eC had two more nodes, and eC and eT had on average one more node relative to control (Figure 2b). Warming decreased stem biomass in both years and stem height, stem diameter at the base, and number of branches in 2011 (Table S1). On the other hand, elevated [CO₂] increased all the same parameters except for number of branches. In 2011, eT + eC was lower than eC in all the morphological parameters and in stem biomass (Table S1).

3.3 | Interannual differences of warming and high [CO₂] on the progression and duration of reproductive development in soybean

Overall, elevated $[CO_2]$ was delayed, and warming accelerated reproductive development in 2009, and these responses were consistent among all reproductive growth stages in that year. From R1 to R7, eC was delayed by ~2.6 days, and eT was accelerated by ~3.7 days when compared with control (Figure 3a).

During 2011, Temperature × CO_2 × Developmental Stage was significant for DOYr, and it was driven by a variable effect of temperature and CO_2 throughout the reproductive stages. Thus, DOYr was accelerated from Stages R1 and R2 and delayed from Stages R3 through R5 by high temperature whereas delayed in R1 and R3 to R5 by elevated [CO_2] (Figure 3b). In R1, eT was ahead of control by 2.8 days, and eC was behind control by 2 days (Figure 3b). From R1 to R2, the opposite effects of higher temperature and elevated [CO_2] offset each other in eT + eC; thus, DOYr in eT + eC was similar to control (Figure 3b). All treatments were delayed from R3 to R5 when compared with control, although eT treatment was much more delayed than eC and eT + eC in R5 (Figure 3b). The DOYr for R6 and R7 was similar in all treatments during 2011.





FIGURE 2 Day of the year (a and b) and growing degree days (c and d) when the vegetative developmental stages were reached (DOYr and GDDr) in all four treatments during 2009 and 2011. Definition of the treatments is as in Figure 1. In the inside tables are the intercept, slope, and R^2 values for the linear regressions that were fitted in each treatment. *SE* is indicated in each panel

In general, DIS showed a significant temperature response for both years and an additional significant temperature by CO_2 response in 2011; these effects were observed in certain reproductive stages (Figure 3c,d). In both years, there were no treatment differences in the number of days that the treatments stayed in R1 (Figure 3c,d). In 2009, the heated treatments resulted in fewer DIS for R4 than the nonheated treatments (average of 3.5 less days; Figure 3c). In 2011, eT and eT + eC had higher DIS during R2 than the nonheated treatments, and eT remained in R2 almost 3 days longer than eT + eC (Figure 3d). In the same year and during R5, control stayed the longest, eT stayed the shortest, and eC and eT + eC stayed the same number of days in this stage. (Figure 3d). The longest soybean reproductive stages were R5 and R6 during 2009 and R2 and R5 during 2011 (Figure 3c,d).

In both years, heated treatments accumulated more GDDr than nonheated treatments during reproductive development. In 2009, the higher accumulation of GDDr due to warming was observed between R2 and R7, whereas during 2011, it was observed from R3 to R7 (Figure 3e,f). Elevated [CO₂] also increased GDDr during 2011 (~24°Cd more GDD to reach a stage; Figure 3f) in most of the reproductive stages (except for R2), as clearly observed in eC versus control (Figure 3f).

3.4 | Dark respiration and leaf carbohydrates increased under elevated [CO₂] but decreased under warming during 2011

Across the season, dark respiration was increased by 15% in the young leaves of high $[CO_2]$ grown and decreased by ~23% as a result of the warming treatment in both young and old leaves. In the young leaves, eT lowered respiration by ~31% compared with both nonheated treatments (control and eC), whereas the combined eT + eC treatment resulted in 19% lower respiration compared with eC (Table S1). In old leaves, respiration in eT and eT + eC was on average 30% lower than in eC (Table S1).

Leaf TSC was increased by 32% at dusk and by 82% at dawn under the eC treatment compared with control (Table S1). The CO_2 effect on TSC during dawn was detected in three of the four sampling days. eT versus control was decreased for TSC by ~25% when measured at both dusk and dawn (Table S1). Similar treatment responses



FIGURE 3 Day of the year when the reproductive developmental stages were reached (DOYr), the duration of the stages in days (DIS), and growing degree day when the reproductive developmental stages were reached (GDDr) for all four treatments during 2009 (a, c, and e) and 2011 (b, d, and f). Definition of the treatments is as in Figure 1. Significant effects for the season are indicated in the upper left corner of each panel. The letters above the bars indicate the statistical difference ($P \le 0.1$) between treatments

as those observed for TSC were also observed for starch. Starch was increased by 70% in eC versus control, whereas it was reduced by 13% in eT versus control at dusk. The percentage changes at dawn were more than three times the changes observed for eC versus control at dusk and similar to the changes observed in eT versus control. The CO₂ × Temperature interaction was significant for starch at dawn such that eT + eC had 43% lower starch than eC.

3.5 | Vegetative and reproductive developments were accelerated by warming in maize

High temperature influenced DOYr by accelerating the vegetative development in maize during 2010 (Figure 4a and Table S2). Thus, eT and eT + eC developed faster than control and eC. Despite the faster vegetative development in the heated treatments, the plants



FIGURE 4 Day of the year (a) and growing degree days (b) when the vegetative developmental stages were reached (DOYr and GDDr) in all four treatments during 2010. Definition of the treatments is as in Figure 1. In the inside tables are the intercept, slope, and R^2 values for the linear regressions that were fitted in each treatment. *SE* is indicated in each panel

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formed the same total number of leaves in all treatments (Figure 4a). Heated treatments accumulated more GDD in each vegetative stage than the nonheated treatments during 2010 (temperature was significant for vegetative stages vs. GDDr; Figure 4b and Table S2).

DOYr was accelerated in all reproductive stages in the heated treatments compared with the nonheated treatment (Figure 5a). The seasonal mean advancement was about 2.6 days. The DIS was not significantly different among the treatments at any reproductive stage (Figure 5b). In all reproductive stages, GDDr was higher in the heated treatments by ~151°Cd compared with nonheated treatments (Figure 5c). Only R2 showed differences in the two temperature treatments where eT + eC accumulated less GDDr than eT. The tassel stage in the heated treatments was reached ~4.1 days earlier and accumulated ~67°Cd more GDD in heated treatments compared with nonheated treatments (Figure 6a,b). Warming also accelerated senescence in maize; thus, by DOY 237, there were 56% and 44% more senescent plants in eT and eT + eC than control, respectively (Figure S1). By DOY 250, 90% or more of the plants were senescing.

3.6 | The β function provided a better fit using optimized parameterization relative to prescribed parameters

Optimized values of T_{opt} and R_{max} were obtained by successfully fitting the observed data to the β distribution function (convergence = zero) under warming and/or elevated [CO₂]. In general, optimized values of T_{opt} and R_{max} (Table 1) resulted in lower RMSE in comparison with when the parameters were taken from the literature. The exceptions were for control and eT during soybean 2009 growing season. RMSE calculated using the cardinal temperatures from the literature was between 0.166–0.199 for 2009, 0.156–0.211 for 2010, and 0.138–0.170 for 2011 (Table 1). The calculated RMSE when optimized R_{max} and T_{opt} was used ranged between 0.165–0.208 for 2009, 0.149–0.204 for 2010, and 0.088–0.107 for 2011 (Table 1).

4 | DISCUSSION

This study tested four predictions: (a) an increase in canopy temperature will accelerate soybean vegetative and reproductive







FIGURE 6 Day of the year when tassel stage was reached (DOYr; a) and growing degree day when tassel stage was reached (GDDr; b) for all four treatments during 2010. Definition of the treatments is as in Figure 1. The letters above the bars indicate the statistical difference ($P \le 0.1$) between treatments

development at both ambient and elevated [CO₂]; (b) higher temperature together with elevated [CO₂] will produce soybean plants with more nodes than plants under only high temperature; (c) a delay in soybean reproductive development by elevated [CO₂] will be offset by the increase in temperature; and (d) an increase in temperature will accelerate maize vegetative and reproductive development at both ambient and elevated [CO₂]. In addition, an alternative thermal model to predict vegetative development in soybean and maize under warming and elevated [CO₂] conditions was evaluated. Our results showed that temperature accelerated soybean vegetative development in eT + eC but not in eT in both years (Figure 2a,b) thus partially consistent with the first hypothesis. Higher temperature had a variable effect in soybean reproductive development, accelerating the progression through the reproductive developmental stages in some cases but delaying in others (Figure 3a,b). Timing of soybean flowering was consistently accelerated by warming during both growing seasons (Figure 3a,b). Under conditions of elevated [CO₂] and high temperature, soybean produced more nodes than under elevated [CO₂] without warming (Figure 2a,b), supporting the second hypothesis. The delay imposed in soybean reproductive development by high [CO₂] was counteracted by the increase of temperature (Figure 3a,b), supporting the third hypothesis. The fourth hypothesis was confirmed for maize because temperature accelerated its vegetative and reproductive development (Figures 4a and 5a) and tassel stage (Figure 6a) at both ambient and elevated [CO₂]. Additionally, we were able to associate changes in development to changes in physiological processes including night respiration and availability of resources as carbohydrates for growth. Finally, our analysis highlighted shortcomings of the GDD method to predict crop development under warming conditions, while providing evidence that the β function can predict vegetative development with global warming.

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Warming plus elevated [CO₂] accelerated soybean vegetative development during both years (eT + eC; Figure 2a,b and Table S2). It was unexpected that eT alone did not significantly accelerate vegetative development during 2009, despite a slightly higher slope in the eT linear regression compared with control (Figure 2a). Lower available assimilates for growth might have explained this lack of acceleration in vegetative development in eT during 2009, but photosynthesis and above-ground biomass data were not different between eT and control during this year (Ruiz-Vera et al., 2013). The cooler conditions in 2009 (Ruiz-Vera et al., 2013), however, may have counteracted the expected acceleration in development. In 2011, which was a warmer and drier year compared with the 30-year mean (Ruiz-Vera et al., 2013), photosynthesis was reduced under the heated conditions leading to reduced growth when compared with control. The reduction of photosynthesis and consequently less carbohydrate accumulation (TSC at dusk; Table S1) and lower dark respiration in young leaves likely explains why eT did not result in accelerated vegetative development. The influence of carbohydrate accumulation, respiration rate, and biomass partitioning may explain the differences in the rate of vegetative development between eT + eC and eC. Despite the fact that eT + eC showed lower assimilates and dark respiration rate than eC (Table S1), vegetative development in eT + eC was faster than eC (Figure 2b and Table S2). eC had highest overall biomass in 2011 (Ruiz-Vera et al., 2013; Table S1), including more branches than eT + eC (Table S1) and consequently more reproductive organs. Thus, additional node formation in eC plants were not limited to the main stem where the number of nodes are what determine progression through vegetative development. Consequently, eC plants spent significant resources in respiration for growth and for maintenance, which was possible due to the high photosynthesis eC had that year (~22% higher than control and ~10.5% higher than eT + eC; Ruiz-Vera et al., 2013). The high respiration rate in eC was observed in both young and old leaves (Table S1), suggesting an overall higher respiration than eT + eC for the whole plant profile. Castro et al. (2009) showed that eC and its associated higher TSC levels drove greater node number than control plants. In a similar way, it is shown here that by season's end, eC had one more node than control; additionally, eT + eC plants had on average one more node than eC.

Overall, heated treatments accumulated more GDD at a faster rate than the nonheated treatments (Figure 1). For 2011, this was apparent around 45 days after planting, which was later than in 2009 (Figure 1). The approximately 1°C higher midday canopy temperature in eT + eC versus eT during 2011 (Ruiz-Vera et al., 2013) allowed a faster rate of GDD accumulation in eT + eC compared with eT (Figure 1). These results suggest that warmer canopy temperatures associated with elevated [CO2] can impact soybean development, more so during hot and dry growing conditions such as those experienced in 2011. In general, we observed that heated treatments required more GDDr when temperatures were not above their T_{opt} (Figure 2c,d). After V4, all treatments in 2011 had a higher GDDr than in 2009 (Figure 2c,d), and this occurred despite a similar amount of time spent in the vegetative stages (Figure 2a,b). Different GDD requirements to achieve certain vegetative stages may indicate that the ability to predict the progression of vegetative development in soybean using a simple GDD model diminishes as temperatures warm.

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Soybean reproductive development was faster in the eT treatment than control during 2009 (Figure 3a). With the exception of the start of flowering (R1) and full bloom (R2), which were faster in eT, the same responses were not observed in 2011 (Figure 3b). Acceleration of R1 in response to high temperature has been reported previously for plants grown in controlled environments (e.g., Baker, Allen Jr, Boote, Jones, & Jones, 1989; Heinemann et al., 2006). Here, eT achieved R1 3.5 days earlier than control in both years, and the time in R2 was prolonged in all the treatments during 2011 compared with 2009 (Figure 3c,d). The longest R2 was for eT, which was ~3 times longer than in 2009 and ~7 days longer than control within the same year (Figure 3c,d). Daily maximum canopy temperature in the heated treatments exceeded the temperature threshold of 40°C (Setiyono et al., 2007) for reproductive development during few days in R2 (Ruiz-Vera et al., 2013). Consequently, $\overline{T_{can}}$ was above T_{opt} , which reduced the rate of development and could have contributed to the prolongation of R2 relative to control. Reproductive development started when vegetative development was around V6, so many of the factors that affected vegetative development also affected reproductive development. As mentioned above, fewer assimilates and lower respiration for growth were observed in eT plants (Table S1). During full bloom, the accumulation of dry matter increased until full seed or R6 (Ritchie, Hanway, & Benson, 1993); thus, a reduction of resources for growth by high temperature could have caused eT to remain in R2 longer. Other factors could have affected the duration of R2 in all the treatments; for example, prolonged flowering may help preserve yield during periods of stress (Ritchie, Hanway, & Benson, 1993) by maintaining pod number.

Elevated [CO₂] has been reported to delay reproductive development from R3 to R7 by up to 3 days (Castro et al., 2009). A similar result was observed here, with eC relative to control showing delayed development for all reproductive stages (R1 to R7) during 2009 and for most stages (R1 and R3-R5) during 2011 (Figure 3a,b). These delays in reproductive development under elevated [CO₂] alone were observed in 2011 despite increases in soybean canopy temperature up to ~1°C during midday when compared with control (Ruiz-Vera et al., 2013), much higher than the canopy temperature increases recorded in Castro et al. (2009; between 0.02 and 0.30°C from 2002 to 2004). Warming applied to plants grown at elevated $[CO_2]$ (eT + eC) counteracted delays in reproductive development that were present under eC alone. This was clear during 2009, when none of the reproductive stages were delayed in eT + eC compared with control (Figure 3a), whereas in 2011, R1 and R2 were delayed, but all subsequent stages were not (Figure 3b). The hottest days in 2011 occurred during R2, which may underlie the prolongation of R2 in all the treatments compared with 2009 (Figure 3c,d). Specifically, the heated treatments lasted the longest in R2; thus, any acceleration in reproductive development due to warming disappeared for the following stages.

By the end of both soybean growing seasons, simple GDD calculations predicted that the heated treatments would be more than 20 days ahead in development than the nonheated treatments (Figure 1). However, the mean acceleration in the heated treatments by R7 was ~3 days in 2009 and none in 2011 (Figure 3a,b). From this experiment, it is clear that warming treatments accumulated more

GDD before reaching reproductive and vegetative developmental stages; however, exceptions can occur such as when the T_{can} is higher than the T_{opt}. The overhead infrared lamps used in this experiment may not have the full effect on GDD than the natural warming perhaps due to a greater temperature gradient through the canopy than the natural situation. Even so, this research suggests that as the climate warms, the current GDD metrics may not accurately predict development because both the GDD metrics and the observed developmental stages become uncoupled. This is not the first time that disparity between the calculated GDD and the observed developmental stages has been observed. Different GDD requirements were observed for development when three different temperatures were compared, at either 400 or 700 $\mu mol\ mol^{-1}$ of [CO₂], which was attributed to a night temperature effect (Heinemann et al., 2006). For example, the start of flowering at day/night temperature of 30/25°C required 50°Cd more than at 20/15°C at both [CO2]. Soybean development under elevated [CO₂] has also shown different GDD requirements. In a soybean FACE experiment (Castro et al., 2009), elevated [CO₂] delayed reproductive development by ~3 days, but the GDD metrics predicted an acceleration of 3 days in development. This predicted acceleration in development was attributed to elevated [CO₂]-induced closure of stomatal conductance causing a warming of the plant canopy (e.g., Bernacchi et al., 2007). These differences were attributed to an independent and opposite effect of elevated [CO₂] in development. Despite the fact that GDD, which is based on air temperature, is a standard method to predict the progression of development in crops, the importance of other parameters might increase under specific conditions. Thus, this study illustrated how net carbon uptake, the amount of assimilates, and dark respiration influenced development. Additionally, the similar photoperiod in all the treatments and during soybean reproductive development could be constraining the rate of development predicted by GDD, especially under warming. Regardless of the mechanism, our research showed that GDD predictions of development did not match observed developmental data.

Our results from dark respiration in soybean appear to be linked to the phenological responses of soybean to increased [CO₂] and warming. Dark respiration in soybean has been studied previously under elevated [CO2] in controlled environments (Bunce, 1995; Bunce & Ziska, 1996; Griffin et al., 2001; Thomas & Griffin, 1994) and in open top chambers (Bunce, 2005), but the results differ among these studies. A field experiment using FACE technology found a 37% increase of dark respiration in soybean under elevated [CO₂] that was associated with a higher respiratory capacity and availability of carbohydrates for respiration (Leakey et al., 2009). A study evaluating the effect of elevated [CO2] and temperature in soybean (Bunce & Ziska, 1996), using growth chambers, found no sensitivity of dark respiration to the increase of temperature. However, this result disagreed with a later open top chamber study (Bunce, 2005) showing 2.5-fold increase in respiration form 18 to 26°C. In our warming and FACE experiment, dark respiration in the younger leaves was reduced under warming conditions and increased under elevated [CO2] resulting in eT + eC having similar respiration rate than control (Table S1). Both responses agree with the leaf carbohydrates trend (Table S1), supporting the idea that

the availability of resources has a major impact in the rate of dark respiration.

Maize development and GDD accumulation required to reach a stage were unaffected by elevated [CO₂] (Figures 4a,b and 5a-e), consistent with developmental records of maize grown in FACE (Leakey et al., 2004; Leakey et al., 2006; Markelz, Strellner, & Leakey, 2011) and growth chambers (e.g., Kim et al., 2007). In contrast to C_3 plants, C₄ plants like maize do not exhibit a higher carbon uptake, biomass, or yield under elevated [CO₂] under adequate moisture conditions (Leakey et al., 2006). Warming accelerated maize development and plant senescence, similar to previous results for vegetative development and senescence (Hatfield & Prueger, 2015). Despite the different rates of development, the same total number of leaves was produced regardless of the heating treatment. Warming accelerated vegetative development by ~5 days (Figure 4a) and resulted in an earlier start of tassel and R1 stages 4 and 3 days earlier, respectively, relative to the nonheated treatments (Figures 5a and 6a). The faster plant senescence at warming (when 80% of leaves were dry; Figure S1) also suggests that leaves started to senesce earlier in the heated plants, but this did not impact grain filling stages (R3-R5) because kernel weight was not affected (Ruiz-Vera et al., 2015). Similar to soybean, there were more GDDs needed to reach a specific developmental stages in maize. These results show that the GDD model associated with significant in-field heating does not predict the progress to developmental stages under warming conditions despite the strong sensitivity of maize to GDD.

The development of soybean and maize has been described using models other than GDD (e.g., Kumudini et al., 2014; Setiyono et al., 2007), which are suggested to better represent developmental responses under warming conditions (Kumudini et al., 2014). One such model, the β function, fits our soybean and maize data at control and warming conditions with or without increases in [CO₂], supporting this model as a good approach to predict crop development under climate change. For both soybean and maize, the RMSE values obtained using optimized R_{max} and T_{opt} were improved in comparison with RMSE values obtained using literature parameters (Table 1). This improvement demonstrates that in comparison with the literature values, optimized R_{max} and T_{opt} better reflected the impact of warming and elevated [CO2] on vegetative development. Additionally, optimized $T_{\rm opt}$ in soybean and maize revealed variability between the treatments. For example, the optimized T_{opt} in maize under warming and/or elevated [CO₂] conditions was more than 3°C higher than T_{opt} in control (Table 1). This difference suggests that thermal development acclimates to the growing conditions, which supports our results that the GDD model does not accurately reflect the progression through development in our treatments as the GDD model is unable to account for acclimation.

5 | CONCLUSIONS

Both atmospheric $[CO_2]$ and temperature are predicted to continue to increase. Our results indicate that vegetative development in soybean will be faster and plants will have more nodes as temperature and $[CO_2]$ (eT + eC) increase. Furthermore, the results showed that

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warming conditions can offset delayed soybean development associated with growth under elevated [CO₂]. The magnitude of the changes in soybean development with warming and/or elevated [CO₂] is also shown to depend on the growing season conditions, on the carbon budget of the plant, on processes like dark respiration, on the interaction among vegetative, reproductive growth, and senescence, and on the specific mechanisms that plants adopt under stress conditions. Compared with soybean, vegetative, reproductive, and tassel developments in maize were not affected by elevated [CO₂], but they were accelerated with warming. Senescence was accelerated with warming in maize but had no major impact on yield. Interestingly, we found that warming with or without elevated [CO₂] increased the GDD threshold needed to advance developmental stages in both soybean and maize, reflecting an inadequacy of the GDD approach to explain the development of these crops as temperature increases. Additionally, we found that the process-based "ß function" model, which uses cardinal temperatures to predict development, was successfully able to model our data at warming and elevated [CO₂] conditions. Despite the wide use of the GDD model, it appears that with global warming, better approaches are needed to predict crop development.

ACKNOWLEDGEMENTS

The authors acknowledge Elizabeth A. Ainsworth for her helpful comments on the manuscript; Joseph C. Castro for his advice on the data analysis; David W. Drag for the maintenance of the experimental set up; Kristen A. Bishop for her help with the carbohydrate analysis; and Marcelo Zeri, Nuria Gomez-Casanovas, George Hickman, C. Vanessa Piattoni, Matt Nantie, Sarah Campbell, and Christina Burke for their indispensable help on the collection of the field measurements. Funding for this research was provided by the National Institute of Food and Agriculture (NIFA), United States Department of Agriculture (USDA) under Award Number 2014-67013-21783.

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How to cite this article: Ruiz-Vera UM, Siebers MH, Jaiswal D, Ort DR, Bernacchi CJ. Canopy warming accelerates development in soybean and maize, offsetting the delay in soybean reproductive development by elevated CO₂ concentrations. *Plant Cell Environ*. 2018;41:2806–2820. <u>https://doi.org/10.1111/pce.13410</u>