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Carbon assimilation in crops at high temperatures

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Abstract

Global temperatures are rising, and higher rates of temperature increase are projected over land areas that encompass the globe's major agricultural regions. In addition to increased growing season temperatures, heat waves are predicted to become more common and severe. High temperatures can inhibit photosynthetic carbon gain of crop plants and thus threaten productivity, the effects of which may interact with other aspects of climate change. Here, we review the current literature assessing temperature effects on photosynthesis in key crops with special attention to field studies using crop canopy heating technology and in combination with other climate variables. We also discuss the biochemical reactions related to carbon fixation that may limit crop photosynthesis under warming temperatures and the current strategies for adaptation. Important progress has been made on several adaptation strategies demonstrating proof-of-concept for translating improved photosynthesis into higher yields. These are now poised to test in important food crops.

KEYWORDS

crop photosynthesis, heat wave, Rubisco

1 | INTRODUCTION

Agricultural production faces numerous global change-related abiotic stresses, including rising temperatures, which pose a threat to global food production and sustainability (Ainsworth & Ort, 2010). Global mean temperatures have risen by approximately 1°C since the Industrial Revolution. If the atmospheric CO_2 concentration increase continues at its current pace (i.e., IPCC RCP8.5 scenario), an additional 1.5°C increase over the 2001 average global temperature will occur by mid-century and 3°C to 5°C by 2100. However, these temperature increases will be spatially heterogeneous, as some areas of the world are predicted to warm more rapidly than others (Ciais et al., 2013; IPCC, 2018; Teixeira, Fischer, Van Velthuizen, Walter, & Ewert, 2013). Temperatures over land are increasing at a faster rate than over water (IPCC, 2018) and will continue to do so, especially at higher latitudes in the Northern Hemisphere (Hoegh-Guldberg et al., 2018), which could experience temperature increases of up to 10°C, whereas 3°C–4°C increases are possible in the tropics (Ciais et al., 2013). Areas of greater warming in the Northern Hemisphere will most likely occur between 40 and 60°N and overlap with major agricultural regions (Bita

& Gerats, 2013; Teixeira et al., 2013). Additionally, heat stress will likely be most detrimental to lower income countries (Deryng, Conway, Ramankutty, Price, & Warren, 2014). Heat waves will present temporal variation in growth temperatures for crops and are predicted to increase in frequency, intensity, and duration over most land areas (Coumou & Robinson, 2013; IPCC, 2013a; Meehl & Tebaldi, 2004; Seneviratne et al., 2012; Wang, Huang, Luo, Yao, & Zhao, 2015).

Warming temperatures have already contributed to global yield losses in wheat (*Triticum aestivum*) and maize (*Zea mays*; Asseng et al., 2015; Lobell & Gourdji, 2012; Lobell, Schlenker, & Costa-Roberts, 2011), and future temperature increases are predicted to negatively affect global yields of key crops, including wheat, maize, rice (*Oryza sativa*), and soybean (*Glycine max*; Zhao et al., 2017). Considering that many of the areas predicted to be most impacted by warming are major growing regions for food crops, adaptation strategies must be sought to sustain productivity, especially with consideration of other changing climate factors. A range of plant processes are affected by heat stress that vary across species, but impacts on photosynthesis are common to virtually all crops (Bita & Gerats, 2013; Hasanuzzaman, Nahar, Alam, Roychowdhury, & Fujita, 2013;

Nadeem et al., 2018). Within photosynthesis, a wide array of component processes are high temperature sensitive. Membrane fluidity increases, and photosynthetic membranes, machinery, and pigments are affected by increased reactive oxygen species generation at above-optimal temperatures. Inactivation of the oxygen evolving complex of photosystem II can also occur in thylakoid membranes at temperatures >42°C (Yamane, Kashino, Koike, & Satoh, 1998). However, research in field crops suggests heat sensitivity of biochemical processes of carbon assimilation is the major cause of photosynthetic inhibition of both C_3 and C_4 photosynthesis, particularly in relation to carboxylation efficiency (Crafts-Brandner, van de Loo, & Salvucci, 1997; Perdomo, Capó-Bauçà, Carmo-Silva, & Galmés, 2017; Perdomo, Carmo-Silva, Hermida-Carrera, Flexas, & Galmés, 2016; Rashid et al., 2018; Salvucci & Crafts-Brandner, 2004). Carboxylation efficiency is largely determined by ribulose-1,5-bisphosphate carboxylate oxygenase (Rubisco) efficiency and activation as well as ribulose-1,5-bisphosphate (RuBP) regeneration. Thus, this review focuses on the effects of rising temperature on these processes in crops, relevant targets for improvement, and recent advances that hold promise to substantially improve crop productivity in higher temperatures.

2 | EFFECTS OF ELEVATED TEMPERATURES AND INTERACTING CLIMATE VARIABLES ON PHOTOSYNTHESIS

Crop photosynthesis varies in response to elevated seasonal growing temperatures. For example, field-grown spring wheat exposed to infrared heating showed no negative effects of elevated temperatures on photosynthesis compared with the control, likely because growth conditions were relatively cool (Table 1; Wall, Kimball, White, & Ottman, 2011). However, in field-grown maize and soybean, 3.5°C increases above ambient seasonal growth temperatures imposed by infrared heaters decreased photosynthesis (Table 1; Ruiz-Vera et al., 2013; Ruiz-Vera, Siebers, Drag, Ort, & Bernacchi, 2015). Photosynthetic acclimation through increased electron transport capacity, differential expression of Rubisco activase isoforms, heat shock protein expression, and reductions in respiration (Yamori, Hikosaka, & Way, 2014) can occur with long-term warming but may still result in lower photosynthetic rates as compared with those at ambient temperature (Way & Yamori, 2014). Acclimation is less likely during heat waves or acute heat stress, which are defined by sudden increases in temperature (Smith and Dukes 2017). These periods of heat stress may therefore have greater effects on daily integrals of photosynthesis, albeit for shorter time spans during crop growth. Indeed, simulated three-day heat waves in field-grown soybean and maize significantly reduced leaf photosynthesis during the duration of the experiment, but recovery of photosynthesis to control levels occurred within 24 hr of the end of the heating period (Table 1; Siebers et al., 2015, 2017). Although simulated heat waves generally led to reductions in yield, the impacts were greater when heating occurred during reproductive stages, suggesting yield reductions were

also affected by direct heat stress on reproductive processes (Siebers et al., 2015, 2017).

The effects of elevated temperature and heat waves on photosynthesis are more complex when occurring in combination with other facets of climate change. The specificity of Rubisco for CO_2 versus O_2 ($S_{C/O}$) declines as temperatures increase, which favors the oxygenation of RuBP and photorespiration over the carboxylation of RuBP and photosynthesis. The ratio of the carboxylation rate (v_c) compared with the oxygenation rate (v_o) of RuBP by Rubisco is determined as

$$v_c/v_o = S_{C/O}\ [CO_2]/[O_2]$$

using the concentrations of CO_2 and O_2 at the site of Rubisco. $S_{C/O}$ in soybean declines from approximately 100 at 25°C to 90 at 30°C (Orr et al., 2016). Thus, an 11% increase in $[CO_2]/[O_2]$ would be required at the site of Rubisco to maintain a similar rate of v_c/v_o with the reduction of $S_{C/O}$. Although atmospheric $[CO_2]$ is predicted to increase by approximately 38% to 550 ppm by the year 2050 (IPCC, 2013b), the increase in $[CO_2]$ at Rubisco in C_3 crops will likely be affected by changes in stomatal and mesophyll conductances and a larger reduction in the solubility of CO_2 as compared with O_2 with warmer temperatures. Therefore, studies describing the effects of elevated temperatures with interacting climate variables on crops, especially in field conditions, are necessary for understanding the complex effects on measured photosynthesis. The results available to date from such studies are described below with open-air field studies summarized in Table 1.

2.1 | Elevated CO_2

Atmospheric CO_2 concentrations are predicted to reach 550 ppm by 2050 (IPCC, 2013b). Elevated CO_2 has the potential to stimulate photosynthesis and biomass in C_3 plants. However, in combination with elevated temperatures, the stimulation of photosynthesis by elevated CO_2 will be affected by warmer growth temperatures favoring oxygenation of RuBP over carboxylation. For example, modeled improvements in soybean CO_2 assimilation with increasing atmospheric CO_2 and growing season temperature will still be hampered by photorespiration by up to 23–48%, depending on the future climate scenario (Walker, VanLoocke, Bernacchi, & Ort, 2016). In field-grown soybean exposed to both Free Air Carbon Enrichment to simulate elevated CO_2 and infrared canopy heating technology to simulate elevated temperatures, the extent of stimulation by elevated CO_2 varied with the growing season. Photosynthetic rates were similarly enhanced by elevated CO_2 at ambient and elevated temperatures in a relatively cool year (2009), but the stimulation by elevated CO_2 in elevated temperatures during a relatively hot year (2011) was substantially smaller than the stimulation by elevated CO_2 alone (Table 1; Ruiz-Vera et al., 2013). In chamber-grown wheat, elevated CO_2 and elevated temperature, when applied separately, negatively affected Rubisco activity. However, elevated temperature reduced the inhibition of Rubisco carboxylation activity by elevated CO_2 (Pérez, Alonso, Zita, Morcuende, & Martínez-Carrasco, 2011). Whereas short-term heat stress reduced

TABLE 1 Summary of crop canopy heating effects (% change) on photosynthesis parameters with and without interacting climate variables. Heating was applied to either simulate elevated temperatures over the growing season or acute heat stress (heat waves lasting either three or five days) during specific growth stages

	Heating above ambient† (°C)	Year(s) of study	Time period of heating	Mean ambient T (°C)	Interacting climate variable‡	Change in A (%)	Type of A_n	Change in g_s (%)	Change in C_i (%)	Control type	Period used to calculate mean values	Source
Elevated temperature												
Soybean	+3.5	2009	GS (A-S)	16.7	--	-5.2	I	-24.4	-4.5	a	7 D over GS	1
	+3.5	2011	GS (A-S)	18.2	--	-14.8	I	-37.7	-15.9	a	6 D over GS	1
	+3.5	2009	GS (A-S)	16.7	CO_2	+13.0	I	-45.8	+34.3	a	7 D over GS	1
	+3.5	2009	GS (A-S)	16.7	CO_2	+19.2	I	-28.2	+40.6	eT	7 D over GS	1
	+3.5	2009	GS (A-S)	16.7	CO_2	+3.0	I	-17.1	-6.1	eC	7 D over GS	1
	+3.5	2011	GS (A-S)	18.2	CO_2	+9.1	I	-53.4	+20.2	a	6 D over GS	1
	+3.5	2011	GS (A-S)	18.2	CO_2	+28.0	I	-25.1	+42.9	eT	6 D over GS	1
	+3.5	2011	GS (A-S)	18.2	CO_2	-10.4	I	-37.1	-17.2	eC	6 D over GS	1
Maize	+2.7	2010	GS (M-A)	22.53	--	-6.0	M	-10.0	-11.5	a	5 D over GS	2
	+2.7	2010	GS (M-A)	22.53	CO_2	-3.6	M	-31.3	+71.3	a	5 D over GS	2
	+2.7	2010	GS (M-A)	22.53	CO_2	+2.8	M	-23.7	+93.5	eT	5 D over GS	2
	+2.7	2010	GS (M-A)	22.53	CO_2	-4.1	M	+3.0	+4.0	eC	5 D over GS	2
Wheat	+1.3/+2.7 (D/N)	2007-9	GS	21.7 (mean daily max)	--	+4.5	M	+2.3	-2.0	a	13 D over GS	3
Heat wave												
Soybean	+7.7/+10.3 (D/N)	2010	V (3 D)	23.6/13.3 (D/N)	--	+19.3	M	+47.2	--	a	D3 of HW	4
	+7.0/+8.0 (D/N)	2010	EP (3 D)	25.6/19.1 (D/N)	--	-25.3	M	-24.3	--	a	D3 of HW	4
	+6.0/+6.2 (D/N)	2010	SF (3 D)	27.8/21.2 (D/N)	--	-58.5	M	-78.3	--	a	D3 of HW	4
	+5.9/+7.3 (D/N)	2011	V (3 D)	27.8/18.1 (D/N)	--	-15.7	M	-40.5	--	a	D3 of HW	4
	+6.2/+9.6 (D/N)	2011	FP (3 D)	25.3/17.6 (D/N)	--	-34.9	M	-56.9	--	a	D3 of HW	4
Soybean	+9.2	2015	FL (5 D)	23.3	--	-19.5	M	--	--	a	D1,3,5 of HW	5
	+9.5	2015	SF (5 D)	22.1	--	-37.9	M	--	--	a	D1,3,5 of HW	5
	+5.3	2016	FL (5 D)	24.4	--	-19.8	M	--	--	a	D1,3,5 of HW	5
	+5.0	2016	SF (5 D)	22.4	--	-21.5	M	--	--	a	D1,5 of HW	5
	+9.2	2015	FL (5 D)	23.3	CO_2	-23.4	M	--	--	a	D1,3,5 of HW	5
	+9.2	2015	FL (5 D)	23.3	CO_2	-4.9	M	--	--	eT	D1,3,5 of HW	5
	+9.2	2015	FL (5 D)	23.3	CO_2	-34.7	M	--	--	eC	D1,3,5 of HW	5
	+9.1	2015	SF (5 D)	22.1	CO_2	-17.2	M	--	--	a	D1,3,5 of HW	5
	+9.1	2015	SF (5 D)	22.1	CO_2	+33.4	M	--	--	eT	D1,3,5 of HW	5
	+9.1	2015	SF (5 D)	22.1	CO_2	-27.4	M	--	--	eC	D1,3,5 of HW	5

(Continues)

TABLE 1 (Continued)

	Heating above ambient† (°C)	Year(s) of study	Time period of heating	Mean ambient T (°C)	Interacting climate variable‡	Change in A (%)	Type of A_n	Change in g_s (%)	Change in C_i (%)	Control type	Period used to calculate mean values	Source
	+5.6	2016	FL (5 D)	24.4	CO_2	+2.0	M	--	--	a	D1,3,5 of HW	5
	+5.6	2016	FL (5 D)	24.4	CO_2	+27.2	M	--	--	eT	D1,3,5 of HW	5
	+5.6	2016	FL (5 D)	24.4	CO_2	-17.1	M	--	--	eC	D1,3,5 of HW	5
	+5.4	2016	SF (5 D)	22.4	CO_2	-16.9	M	--	--	a	D1,5 of HW	5
	+5.4	2016	SF (5 D)	22.4	CO_2	+5.8	M	--	--	eT	D1,5 of HW	5
	+5.4	2016	SF (5 D)	22.4	CO_2	-34.6	M	--	--	eC	D1,5 of HW	5
Maize	+6	2011	V (3 D)	--	--	-19.3	M	+31.2	+90.0	a	D3 of HW	6
	+6	2011	V (3 D)	--	--	-6.2	I	--	--	a	D3 of HW	6
	+6	2011	SI (3 D)	--	--	-9.4	M	-6.6	-37.4	a	D3 of HW	6
	+6	2011	SI (3 D)	--	--	-10.1	I	--	--	a	D3 of HW	6

†Heating above ambient refers to mean increase in temperature above ambient conditions. Actual increases are reported when possible. When not available, targeted increases are listed instead. Study 6 targeted +6°C, but actual temperatures were >6°C above ambient during the vegetative heat wave due to low nighttime temperatures and <6°C during the silking heat wave to avoid 40°C and possible tissue death.

‡In all studies including CO_2 as an interacting climate variable, the targeted elevated CO_2 concentration was 585 μmol mol⁻¹.

Abbreviations: a, ambient temperature and ambient CO_2; A-S, April–September; A_n, net photosynthesis; C_i, intercellular CO_2 concentration; D, day; eC, ambient temperature and elevated CO_2; eT, elevated temperature and ambient CO_2; EP, early pod; FP, full pod; FL, flowering; HW, heat wave; GS, growing season; g_s, stomatal conductance; I, daily integral; M-A, May–August; M, midday level; N, night; SF, seed fill; SI, silking.

photosynthetic parameters in chamber-grown tomato (*Solanum lycopersicum*), elevated CO_2 mitigated most of these effects (Pan, Ahammed, Li, & Shi, 2018). At ambient CO_2, heat waves in field-grown soybean reduced photosynthesis during both flowering and pod-filling stages. Elevated CO_2 conditions often mitigated the effects of higher temperatures compared with elevated temperatures alone, but the interaction substantially decreased photosynthesis compared with either ambient or elevated CO_2 conditions when applied separately (Table 1; Thomey et al., submitted).

In C_4 photosynthesis, CO_2 is concentrated around Rubisco in bundle sheath chloroplasts; thus, stimulation of photosynthesis by elevated CO_2 is minimal. Indeed, field-grown maize photosynthesis declined with elevated temperature regardless of CO_2 conditions (Table 1), and the detrimental effects of elevated temperature on photosynthesis was associated with lower yields at both ambient CO_2 and elevated CO_2 (Ruiz-Vera et al., 2015). Similarly, other studies have also compared thermotolerance with photosynthetic types in elevated CO_2 conditions and found increased thermotolerance in C_3 but not C_4 plants (Wang et al., 2008), except for maize grown at low temperatures (Hamilton, Heckathorn, Joshi, Wang, & Barua, 2008). However, elevated CO_2 does improve water use efficiency of C_4 plants due to the partial stomatal closure it induces (Leakey et al., 2009; Ort & Long, 2014), which can have an increasing important role as temperatures, and thus vapor pressure deficits, rise.

2.2 | Drought

Drought conditions are predicted to become more frequent and severe with rising temperatures (Hoegh-Guldberg et al., 2018). Drought decreases plant transpiration, which limits evaporative cooling of leaves and may exacerbate high temperature stress on leaf photosynthesis caused by decreasing $S_{C/O}$. In addition, drought reduces stomatal conductance, which reduces intercellular CO_2 concentrations and therefore increases oxygenation of RuBP by Rubisco (Feller, 2016), which would increasingly be favored over carboxylation due to the decline in $S_{C/O}$ as temperatures rise. Thus, drought will likely worsen the effects of increasing air temperature on crop photosynthesis. Indeed, the interaction of drought and elevated temperatures led to wheat photosynthetic rates of approximately half that of either factor alone (Perdomo et al., 2016).

3 | RECENT ADVANCES IN CARBON FIXATION

As noted above, the biochemical reactions related to carbon fixation are often most limiting to photosynthesis in major crops. Various limitations to RuBP carboxylation by Rubisco have been identified, along with strategies for potential improvements (Carmo-Silva, Scales, Madgwick, & Parry, 2015; Parry et al., 2013). Rubisco is catalytically slow; thus, plants require large quantities of the enzyme, and Rubisco activation is largely controlled by its accessory protein, Rubisco activase, which is responsible for facilitating the displacement of

inhibitors from the catalytic site of Rubisco. In addition, the oxygenation reaction of Rubisco requires the costly photorespiratory pathway to recycle inhibitory byproducts. Therefore, the major goal of enhancing photosynthetic performance in current and warmer temperatures involves enhancing carboxylation of RuBP by Rubisco. Strategies for doing so (Figure 1) and recent successes are discussed below.

3.1 | More efficient Rubiscos at high temperature

The trade-off between specificity and catalytic activity of Rubisco conceptually hampers efforts to engineer a more efficient enzyme. Although transformation of nuclear genes has had limited success, transformation of genes in the chloroplast has been more successful (Sharwood, 2017). In addition, findings showing transformation of chaperone proteins is also needed may aid in successful introduction of new forms of Rubisco (Whitney, Birch, Kelso, Beck, & Kapralov, 2015). Recent studies, however, are investigating variation in Rubisco, especially in response to higher temperatures. Galmés, Kapralov, Copolovici, Hermida-Carrera, and Niinemets (2015) found variation in the thermal tolerance of Rubisco carboxylase turnover rates across phylogenetic groups. Researchers also identified substantial diversity in Rubisco kinetics among C_3 and C_4 members of the Paniceae family that could improve crop Rubiscos (Sharwood, Ghannoum, Kapralov, Gunn, & Whitney, 2016). Variation in wild relatives of domesticated crops may provide insight into improving Rubisco (Atwell, Wang, & Scafaro, 2014). For example, Prins et al. (2016) found variation in catalytic properties and sequences of Rubisco across Triticeae genotypes that could be useful for improving wheat photosynthesis at high temperature through breeding bread wheat with other close relatives. Alternatively, directed evolution in *Escherichia coli* shows potential for identifying mutations that could improve Rubisco carboxylation rate, efficiency, and specificity (Wilson, Martin-Avila, Conlan, & Whitney, 2018). However, next steps will require efforts to do so in algal and plant chloroplasts. There is also evidence suggesting differential expression of small subunit (SSU) isoforms could lead to Rubisco plasticity with changing environments. Warm-grown Arabidopsis

(*Arabidopsis thaliana*) showed a higher ratio of SSU-B to SSU-1A isoforms, which was associated with higher specificity for CO_2 versus O_2 and greater photosynthetic nitrogen use efficiency (Cavanagh, 2016).

3.2 | Increasing the thermostability of Rubisco activase

Rubisco activity is largely controlled by its accessory protein, Rubisco activase, which is responsible for facilitating the displacement of inhibitors from the catalytic site of Rubisco. In maize, an important C_4 crop in which CO_2 is actively concentrated near Rubisco, Rubisco activase transcript abundance and protein expression correlate with yield (Yin et al., 2014). However, Rubisco activase is sensitive to moderate increases in temperature and therefore limits the proportion of activated Rubisco, and thus photosynthesis, as temperatures increase in both C_3 and C_4 plants (Crafts-Brandner & Salvucci, 2000; Sage, Way, & Kubien, 2008; Salvucci & Crafts-Brandner, 2004). Its role, however, becomes even more important as temperatures rise, and production of catalytic misfire products increases (Bracher, Whitney, Hartl, & Hayer-Hartl, 2017; Carmo-Silva et al., 2015). In Arabidopsis, introduction of more thermotolerant Rubisco activases increases photosynthesis (Kumar, Li, & Portis, 2009; Kurek et al., 2007). Thus, efforts to produce more thermotolerant Rubisco activases in crops is a promising adaptation strategy. As with Rubisco, researchers are looking to wild relatives of common domesticated crops, which can produce different Rubisco activase isoforms with varying levels of thermostability, for more thermotolerant variants with some success. Domesticated rice transformed with a single Rubisco activase gene from a wild relative exhibiting higher Rubisco activase thermostability showed improved crop growth and development at high temperatures. In addition, although transgenic plants did not have higher rates of steady-state photosynthesis, photosynthetic induction was significantly faster in the plants containing wild Rubisco activase at higher growth temperatures (Scafaro et al., 2018). An alternative approach to improving Rubisco activase thermotolerance may be differential expression of
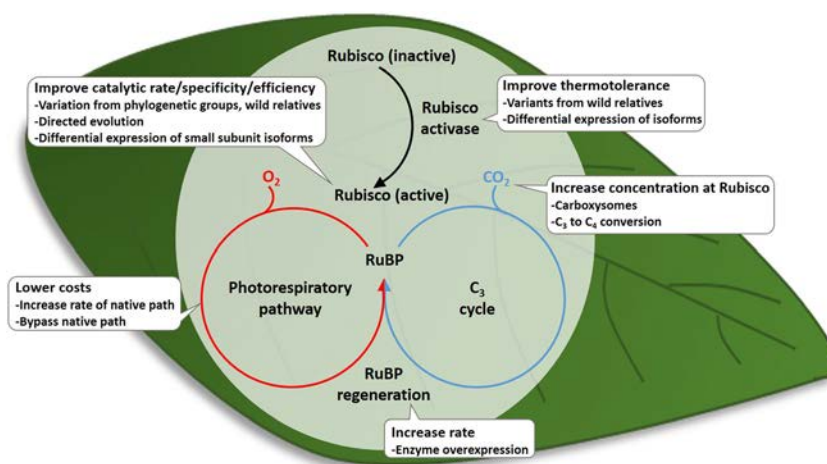

FIGURE 1 Summary of strategies for enhancing carboxylation of ribulose-1,5-bisphosphate by Rubisco and lowering the costs of photorespiration in a C_3 leaf

the two isoforms in a temperature-dependent manner as their sensitivity to heat stress differs in some species (Crafts-Brandner et al., 1997; Law & Crafts-Brandner, 2001; Law, Crafts-Brandner, & Salvucci, 2001).

3.3 | Mitigating increased photorespiratory costs at higher temperature

C_3 plants recycle the inhibitory byproducts of oxygenation by Rubisco through the photorespiratory pathway, but this process costs energy and releases previously fixed carbon and NH_4, which must be refixed at considerable energetic cost. Elevated CO_2 levels should lead to increased CO_2 at the site of Rubisco within plant chloroplasts, but higher temperatures reduce the specificity for CO_2 versus O_2 and also decrease the solubility of CO_2 in solution more rapidly than O_2, resulting in relatively high ratios of O_2/CO_2 near Rubisco. Thus, photorespiration and its associated costs will likely lead to substantial crop yield losses in future climate conditions (Walker et al., 2016). However, recent studies have shown promising results for limiting the costs of photorespiration using several approaches. The first focuses on overexpression of a potentially limiting enzyme within the photorespiratory pathway to accelerate the recycling process. Overexpressing the H-protein of the glycine cleavage system in tobacco (*Nicotiana tabacum*) leaves increased plant biomass when grown in the field (López-Calcagno et al., 2019). However, constitutive overexpression inhibited growth, supporting the need for targeted expression. The second approach inserts enzymes to essentially bypass the multi-organellar pathway. Synthetic glycolate metabolic pathways using enzymes from other organisms in combination with RNAi to limit glycolate flux through the native pathway increased tobacco growth rate, resulting in a >40% increase in biomass at the time of harvest during exponential growth. The alternative pathway also increased light use efficiency of photosynthesis by 17% in the field (South, Cavanagh, Liu, & Ort, 2019). Similarly, an alternative photorespiratory pathway introduced into rice using three rice enzymes improved net photosynthesis by 15–22%, which led to aboveground biomass increases of 14–35% but inconsistent improvements in yield (Shen et al., 2019). A third approach targets concentrating CO_2 at the site of Rubisco for increased fixation of CO_2 versus O_2. One way to achieve this goal involves introducing cyanobacterial carboxysomes into plant chloroplasts. In a recent study, simplified carboxysomes were successfully produced in tobacco chloroplasts using a minimal set of genes (Long et al., 2018). The technique represents a baseline approach to fully functional carboxysome construction and introduction into plant chloroplasts. However, concentrating bicarbonate in the chloroplast and isolating the conversion of bicarbonate to CO_2 solely within the carboxysome are also required for the successful concentration of CO_2 at the site of Rubisco within these specialized structures (Price & Howitt, 2014). Another strategy to increase CO_2 concentrations at Rubisco involves converting C_3 photosynthesis to C_4, which is currently underway in rice (Lin, Coe, Quick, & Bandyopadhyay, 2019; von Caemmerer, Quick, & Furbank, 2012; Wang et al., 2017). Although all of these strategies represent substantial advances in limiting the detrimental costs of photorespiration, further progress is necessary to introduce these techniques into important food crops while realizing consistent benefits to yields.

3.4 | Improving RuBP regeneration

RuBP regeneration will likely become more limiting to photosynthesis under future climate scenarios with rising temperatures and elevated CO_2 (Long, Ainsworth, Rogers, & Ort, 2004). Previous modeling of the carbon reduction cycle (C_3 cycle) has shown limitations to RuBP regeneration by key enzymes, including sedoheptulose-1,7-bisphosphatase (SBP; Zhu, de Sturler, & Long, 2007). Expressing a bifunctional cyanobacterial fructose-1,6-bisphosphatase (FBP)/SBP in soybean grown in the field under both elevated CO_2 and elevated temperature significantly increased carbon assimilation (Köhler et al., 2017; Rosenthal et al., 2011). At ambient CO_2, overexpression of SBP and fructose-1,6-bisphosphate aldolase (FBPA) increased biomass in tobacco grown in the greenhouse (Simkin et al., 2017). A study in Arabidopsis also showed significant increases in photosynthesis and biomass with overexpression of SBP and FBPA, and adding the overexpression of the glycolate H-protein resulted in additive effects on biomass, supporting the use of stacking genes for improving crop production (Simkin et al., 2017), but this remains to be tested in crops.

4 | CONCLUSIONS

Although there have been substantial improvements in the past few years to enhancing carboxylation of RuBP by Rubisco that will lead to increased productivity at higher temperatures, many of these approaches have yet to be realized in food crops with consistent positive impacts on yield. Other strategies may also be necessary to improve productivity in a warming world, such as introducing novel salvage pathways for photorespiratory products, either in parallel or in place of current plant mechanisms (Bar-Even, 2018; Ort et al., 2015).

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