

1 **Transgenic strategies to improve the thermotolerance of photosynthesis**

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14 **Abstract:**

15 Warming driven by the accumulation of greenhouse gases in the atmosphere is irreversible
16 over at least the next century, unless practical technologies are rapidly developed and
17 deployed at scale to remove and sequester carbon dioxide from the atmosphere. Accepting
18 this reality highlights the central importance for crop agriculture to develop adaptation
19 strategies for a warmer future. While nearly all processes in plants are impacted by above
20 optimum temperatures, the impact of heat stress on photosynthetic processes stand out for
21 their centrality. Here we review transgenic strategies that show promise in improving the
22 high temperature tolerance of specific subprocesses of photosynthesis and in some cases
23 have already been shown in proof-of-concept in field experiments to protect yield from high
24 temperature induced losses. We also highlight other manipulations to photosynthetic

25 processes for which full proof-of-concept is still lacking but we contend warrant further
26 attention. Warming that has already occurred over the past several decades has had
27 detrimental impacts on crop production in many parts of the world. Declining productivity
28 presages a rapidly developing global crisis in food security particularly in low income
29 countries. Transgenic manipulation of photosynthesis to engineer greater high temperature
30 resilience holds encouraging promise to help meet this challenge.

31

32 **Keywords:**

33 Temperature stress, Rubisco, photorespiration, Rca, Calvin Benson Cycle, Climate Warming

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42

43 **INTRODUCTION**

44 Agricultural crop production is threatened by numerous global climate change
45 associated abiotic stresses, the most pervasive of which is progressive growing season
46 warming. Global mean temperatures have risen by approximately 1°C since the Industrial
47 Revolution and will increase an additional 1.5°C over the 2001 average global temperature
48 by mid-century (IPCC, 2018). Warming temperatures have already contributed to global

49 yield losses in wheat and maize (Asseng et al., 2015; Lobell & Gourджи, 2012; Lobell,
50 Schlenker, & Costa- Roberts, 2011), and future temperature increases are predicted to
51 further negatively affect global yields of these as well as other key crops including rice and
52 soybean (Zhao et al., 2017).

53 These temperature increases have been and will continue to be spatially
54 heterogeneous, with some areas of the world warming more rapidly than others (Ciais et al.,
55 2013; IPCC, 2018; Teixeira, Fischer, Van Velthuizen, Walter, & Ewert, 2013) and terrestrial
56 temperatures increasing at a faster rate than those over water (IPCC, 2018). Areas of
57 greater warming in the Northern Hemisphere will most likely occur between 40 and 60°N,
58 which overlap with major agricultural regions (Bita & Gerats, 2013; Teixeira et al., 2013).
59 However, a notable exception is the Great Plains of the central United States—the US corn
60 belt. The midwestern US corn belt is one of the few regions globally that has experienced
61 negligible increase in average annual temperature during the last century. The warming that
62 has occurred has been during the cool portion of the year whereas the summer season has
63 not shown a warming trend, in fact there may be a slight cooling trend (Arritt, 2016). The
64 intensive agricultural land use in this region is likely the explanation of this “warming hole”
65 (Alter et al., 2017). The amount of corn harvested annually from this region has increased
66 400% over the past sixty years (National Agricultural Statistics Service, 2016) due to
67 increased acreage under cultivation, along with increased planting densities with more
68 vigorous plants. The increase in photosynthesis that this regional intensification represents
69 is accompanied by a proportional increase in water evaporation from the crop canopy (i.e.,
70 transpiration) causing surface cooling. The subsequent condensation of this water vapor at
71 the top of the troposphere pumps heat away from surface of the earth where crops are, and
72 is consistent with the increase in growing season precipitation that region has experienced.

73 Eastern China, another area of extensive intensification of agriculture, also has not
74 experienced the summer warming characteristic of nearly all other terrestrial regions of
75 similar latitude. This mitigation of warming in the US corn belt and eastern China may not
76 last if intensification of these crops plateaus and greenhouse gas emissions do not abate.

77 Heat stress will likely have its most detrimental outcomes in lower income countries
78 (Deryng *et al.*, 2014). The African continent warrants special attention as many of its
79 countries are already food insecure. Additionally, with >75% of its population below the age
80 of 35, the demographics portend that by mid-century 40% of all the children born globally
81 will be African (UN Department of Economic and Social Affairs Population Facts Dec 2018
82 No. 2019/6) demanding greater output from the African food and agricultural system. The
83 year 2021 was the third warmest year on record for Africa, which has been warming faster
84 than the global average, at a rate of 0.3 °C per decade for the last three decades. In 2021,
85 the temperature across North Africa was 1.2 °C and across West Africa 0.9 °C above the
86 1981-2010 average (State of the Climate of Africa 2021). In addition to the rising average
87 annual temperatures, Africa is also experiencing a rise in the frequency of extremely hot
88 days (State of the Climate of Africa 2021) the hallmark of increasing frequency, intensity and
89 duration of heat waves (Coumou & Robinson, 2013; Meehl & Tebaldi, 2004; Wang, Huang,
90 Luo, Yao, & Zhao, 2015). For the decade beginning in 1980, there were 24 days in which the
91 mean temperature was in the warmest 1% of record range, whereas in the last ten years
92 there were 109 days in the warmest 1% (State of the Climate of Africa 2021). Increased
93 temperature is a leading cause of the 34% decrease in agricultural productivity growth in
94 Africa since 1961. Whereas the growth in productivity has stagnated globally this decrease
95 in Africa is greater than any other region and is expected to decline further in the future. It
96 is projected that additional warming of 1.5 °C would drive nearly a 10% decrease in maize

97 productivity in West Africa and a 20-60% in the wheat harvest in Southern and North Africa.
98 Perhaps no region in the world has been affected as much as the African Sahel¹ region,
99 which is experiencing rapid 2.8% per year population growth in an environment with
100 depleted natural resources and where temperature increases are projected to be 1.5 times
101 higher than in the rest of the world (State of the Climate in Africa 2019). Agriculture is
102 critical to Africa's economy, accounting for the majority of lifework across the continent
103 where IPCC projections suggest that warming scenarios portend debilitating effects on crop
104 production and food security. For countries across the Sahel, modelled shifts to midcentury
105 temperatures represent novel climates not currently observed for any crop on the
106 continent, limiting adaptation strategies (Burke et al. 2009). Whereas millet and sorghum
107 have greater resilience to heat-stress conditions than other African crops, 5-8% yield losses
108 are projected even in these crops by mid-century (State of the Climate in Africa 2019).

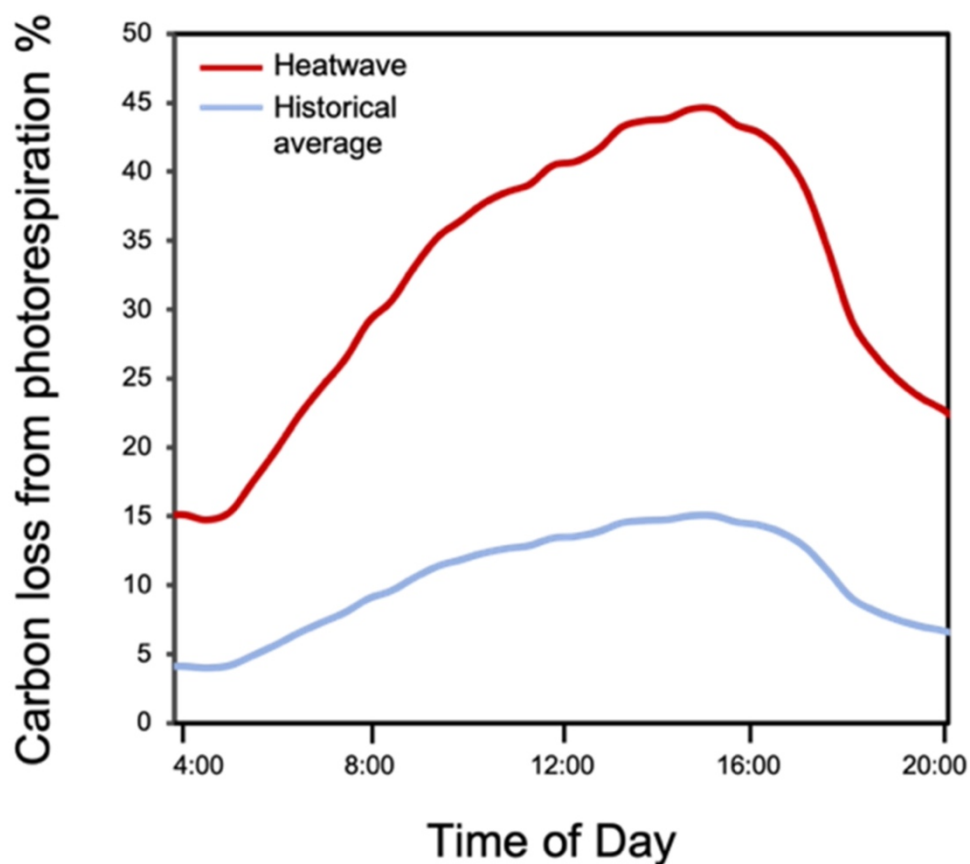
109 The recent and ongoing rise in global average temperature near Earth's surface is
110 caused primarily by the accumulation of greenhouse gases in the atmosphere. In 2021
111 anthropogenic activities released an estimated 10.9 Gt C into the atmosphere, surpassing
112 terrestrial and marine sinks (net uptake of $\sim 6.4 \text{ Gt C yr}^{-1}$) and resulting in an estimated
113 increase of 5.2 Gt C in the form of higher CO₂ (*i.e.* in increase in atmospheric CO₂
114 concentration by $\sim 2.5 \text{ ppm}$; Friedlingstein et al., 2022). This accumulation of CO₂ in the
115 atmosphere drives radiative forcing by absorbing a greater fraction of outgoing radiation,
116 such that incoming radiation exceeds outgoing radiation, resulting in tropospheric warming.
117 Apart from CO₂, methane and nitrous oxide are even more potent greenhouse gases than
118 CO₂ (>30 and 300 times greater radiative forcing potential, respectively). However, the
119 increase in atmospheric concentration is relatively short, 12 years for methane and 114
120 years for nitrous oxide compared to 300-1,000 years for CO₂ (Forster et al., 2007). The scope

121 of the threat to agriculture is revealed by the fact that atmospheric temperature increase
122 caused by increasing atmospheric CO₂ will not decrease appreciably even if zero carbon
123 emissions is achieved (Solomon et al., 2009). Warming caused by atmospheric CO₂
124 accumulation is persistent and will remain irreversible on a millennium time scale unless
125 countered by still to be developed negative carbon technologies.

126 Unless practical technologies can be rapidly developed and deployed at scale to
127 remove and sequester carbon dioxide from the atmosphere, anthropogenic atmospheric
128 warming is irreversible over at least the next 10 generations. Accepting this reality,
129 highlights the paramount importance for crop agriculture to develop adaptation strategies
130 for a warmer future. For many crops, high temperature stress during their reproductive
131 phase results in yield losses more detrimental than those incurred during periods of
132 vegetative heat stress (Hedhley et al., 2008; Hatfield et al., 2011; Jagadish 2020). However,
133 the magnitude of these losses will depend on the timing of heat-stress, which may vary on
134 an annual basis. Temperature-sensitive vegetative processes, like photosynthesis, will be
135 impacted by warming throughout the growing season, thus strategies to enhance their
136 resilience could provide broad scope for improvement. There have been numerous
137 authoritative reviews synthesizing the effect of rising temperature on plant carbon
138 metabolism (Dusenge et al. 2019; Ferguson et al. 2021) and crop photosynthetic
139 performance (Slattery and Ort 2019; Moore et al. 2021; Ainsworth and Ort 2010).
140 Concurrently, there is a renewed focus surrounding the potential to engineer
141 photosynthesis for increased yield (recently reviewed in: Long et al. 2015; Bailey-Serres et
142 al. 2019; Burgess et al. 2023; Garcia et al. 2023). Here, we expand these to focus this review
143 on transgenic adaptation strategies for the effects of a warming climate on photosynthesis
144 and photorespiration.

145 Net photosynthetic carbon assimilation (A_n) in C3 plants is well explained by the
146 proportion of Rubisco in the active state and ribulose biphosphate (RuBP) regeneration
147 capacity (Farquhar et al., 1980). Under current atmospheric [CO_2] and saturating light, the
148 temperature dependence of photosynthesis is well described by Rubisco biochemistry,
149 though a decline in electron transport rates at high temperatures can also limit CO_2 fixation
150 (Sage and Kubien 2007; Schrader et al. 2004; Busch and Sage 2017). Rubisco is regulated by
151 a heat-labile chaperone protein Rubisco activase (Rca), which is essential for removing
152 inhibitory sugar phosphate inhibitors from the catalytic sites of Rubisco, and maintaining
153 photosynthetic carboxylation capacity (Carmo-Silva et al. 2015; Qu et al. 2022). Rubisco is a
154 dual function enzyme, and its substrate specificity declines with increased temperature,
155 which increases the oxygenation, rather than carboxylation of RuBP and promotes CO_2
156 release via photorespiration (Badger and Andrews 1974; Ogren 1984). Photorespiration
157 salvages one molecule of 3-phosphoglycerate (3-PGA) from two molecules of the
158 oxygenation product 2-phosphoglycolate (2-PG) with the release of one molecule of CO_2 via
159 a series of enzymatic conversions and transport steps spanning the chloroplast, peroxisome,
160 and mitochondria (Peterhansel et al. 2010). The photorespiratory pathway is energetically
161 costly, requiring 3.5 ATP and 2 NADPH equivalents to recover RuBP from 2-PG and 3-PGA,
162 and releases NH_3 and 25% of the previously fixed CO_2 in the mitochondria. This can result in
163 a dramatic yield drag in C3 crops, with modelled wheat yield losses of 20% across the US
164 annually, and yield reductions of 50% or more observed in warmer growing regions (Walker
165 et al. 2016). Though photorespiratory losses are less pronounced in cool growing regions,
166 modelling the impact of heatwaves similar to those experienced in the UK in July 2022
167 reveals daily carbon losses associated with photorespiration of >40% for a typical C3 crop
168 (Figure 1). Models of photorespiratory losses in wheat and soybean under future climate

169 scenarios suggest that yield penalties of 8-20% would persist at atmospheric CO₂
170 concentrations of 1000 ppm when accompanied by a 3.7 °C temperature increase across the
171 US (Walker et al., 2016). As a result of the direct impacts of temperature on Rubisco
172 biochemistry, transgenic strategies aimed at improving Rubisco carboxylation or lowering
173 the cost of photorespiration have been targets for improvement of photosynthetic thermal
174 tolerance.



175 **Figure 1:** Modelled losses in daily canopy carbon gain attributed to photorespiration
176 associated with the UK 2022 July heatwave using weather data recorded at NIAB Cambridge
177 on 19 July 2022 (red) compared to the historical average July temperatures (1990-2020;
178 blue) assuming CO₂ concentrations at 400 ppm. Model parameters and assumptions follow
179 Walker et al., 2016.

180

181 **Improving Rubisco carboxylation above the thermal optima**

182 Improving Rubisco substrate specificity, particularly at higher temperatures, is a
183 long-standing aspiration of photosynthesis research. Direct replacement of a crop Rubisco
184 with a higher-specificity version has been proposed to achieve this (McGrath and Long

185 2014), but this is complicated by inter-specific assembly incompatibility due to the
186 specialized assembly requirements of Rubisco (Aigner *et al.*, 2017). Despite this,
187 bioengineering efforts have replaced tobacco and potato Rubisco with faster but less CO₂
188 specific versions of Rubisco from the proteobacterium *Rhodospirillum rubrum* (Whitney and
189 Andrews 2003; Manning *et al.* 2023) and *Halothiobacillus neapolitanus* (Chen *et al.* 2022),
190 the cyanobacterium *Synechococcus elongatus* (Lin *et al.* 2014; Occhialini *et al.* 2016), the
191 purple bacteria *Rhodobacter sphaeroides* (Gunn *et al.* 2020), as well as plant Rubiscos from
192 closely related species (Martin-Avila *et al.* 2020). However, attempts have yet to overcome
193 the growth impairment that results from reduced Rubisco specificity and content compared
194 to the untransformed controls.

195 Improving Rubisco to enhance photosynthetic carbon assimilation above the thermal
196 optima can also be achieved through means other than direct engineering of its catalytic
197 properties. The nuclear encoded Rubisco small subunit (*rbcS*) enhances Rubisco CO₂
198 specificity (Schulz *et al.* 2022), and has been demonstrated to vary in response to growth
199 temperature in *Arabidopsis* (Cavanagh *et al.* 2023), highlighting the potential for future
200 engineering efforts to identify a more efficient Rubisco isoform (Mao *et al.* 2022). Rubisco
201 activation is mediated by Rca, which removes inhibitory sugar phosphates from inactive and
202 inhibited Rubisco. Transgenic rice plants overexpressing a rice isoform of both Rca and *rbcS*
203 maintain higher rates of A_n at elevated (i.e., 36°C) temperatures, likely due to their
204 increased proportion of active Rubisco (Suganami *et al.* 2020). Similarly, rice overexpressing
205 *rbcS* and a maize Rca maintain higher rates of A_n at ambient and elevated temperatures
206 showing increases in maximum carboxylation rate (V_{cmax}) at 40°C, relating to their increased
207 proportion of activated Rubisco (Qu *et al.* 2021). This increase in photosynthesis at elevated
208 temperatures resulted in a 26% increase in dry-weight biomass relative to WT under growth

209 in controlled conditions at 40°C (Qu et al. 2021). Although these transgenic targets remain
210 to be tested in field settings, rice overexpressing Rubisco was reported to have 16-28%
211 increased yields with improved nitrogen-use-efficiency in sufficiently fertilized (*i.e.* > 10 g N
212 m⁻²) paddy conditions (Yoon et al. 2020). Over the four years of field plantings, yields were
213 highest in seasons with relatively high vegetative growth phase temperatures (Yoon et al,
214 2020), suggesting that co-expressing Rca with Rubisco could drive further improvements
215 under climate-warming scenarios.

216 **Improving thermal stability of Rca**

217 Rubisco itself remains active at temperatures above 50°C, though most isoforms of
218 Rca inactivate around 40°C (Crafts-Brandner and Salvucci 2000). Thus, the observed *in vivo*
219 deactivation of Rubisco at higher temperatures can be attributed to the heat sensitivity of
220 Rubisco activase, which in turn leads to photosynthetic inhibition and subsequent yield loss
221 (Carmo-Silva et al. 2015; Qu et al. 2022). *Arabidopsis* plants expressing a thermostable Rca
222 isoform exhibit higher photosynthesis and recovery after a short-term high temperature
223 exposure (Kumar et al. 2009) and increased biomass and seed yield compared to WT plants
224 (Kumar et al. 2009) or those expressing unaltered isoforms (Kurek et al. 2007) when grown
225 at elevated temperature. Although overexpression of Rca alone can result in lower Rubisco
226 content and impaired growth at ambient temperatures (Fukayama et al. 2012; Fukayama et
227 al. 2018), overexpressing a thermotolerant isoform from a rice wild relative is reported to
228 improve both photosynthesis and yield above a threshold leaf temperature in the range of
229 38–42°C (Scafaro et al. 2016; Scafaro et al. 2018). Given the additive benefit of co-
230 overexpressing Rubisco and Rca discussed above, combining this strategy with a
231 thermostable superior Rca may drive a growth benefit under optimal as well as heat stress
232 conditions.

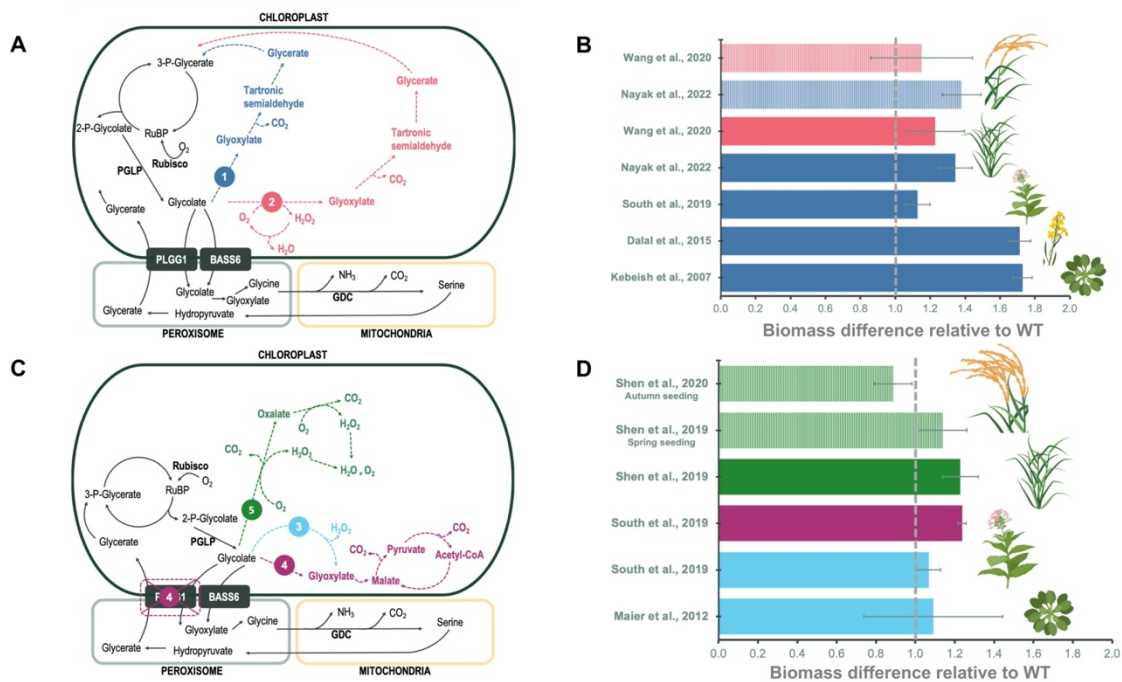
233 Many species have multiple isoforms of Rca with differing heat sensitivity (Crafts-
234 Brandner and Salvucci 2000; Crafts-Brandner et al. 1997; Law and Crafts-Brandner 2001;
235 Carmo-Silva et al. 2015; Scafaro et al. 2019; Kim et al. 2021). In wheat, increased
236 temperatures induce the expression of a more thermostable, but less efficient Rca (Scafaro
237 et al. 2019; Degen et al. 2020). This trade-off can be overcome via mutagenesis and is the
238 result of a single amino acid substitution (Degen et al., 2020). Further, the trade-off
239 between high-temperature stability and activity is not present in the highly active CAM
240 isoform found to be 10°C more thermostable than both rice and Arabidopsis Rca (Shivhare
241 and Mueller-Cajar 2017), indicating that engineering Rca for enhanced performance and
242 thermostability is possible.

243 Because in C4 plants CO₂ is concentrated around Rubisco in bundle sheath
244 chloroplasts suppressing the oxygenation reaction, the stimulation of photorespiration by
245 elevated temperatures is minimal or absent. As a consequence, photosynthesis of C4 plants
246 generally has a higher temperature optimum than in C3 plants (Sage and Kubien, 2007). PEP
247 carboxylase (PEPC) is the primary carboxylase in C4 plants, which fixes bicarbonate rather
248 than CO₂. Thus C4 photosynthesis at low CO₂ levels is co-limited by CO₂ diffusion as well as
249 by the activities of carbonic anhydrase and PEPC. In high CO₂ environments, Rubisco activity
250 and RuBP regeneration become important regulators of C4 photosynthesis (von Caemmerer
251 & Furbank, 2016). At high temperature, electron transport rate and RuBP regeneration have
252 been reported as limitations to C4 photosynthesis (Dwyer et al., 2007; Kubien et al., 2003;
253 Pittermann & Sage, 2001; Sage, 2002). Using RNAi transgenics to reduce Rca content in the
254 C4 dicot *Flaveria bidentis* confirmed the requirement for Rca, but demonstrated that losses
255 in Rubisco activation state and activity above the thermal optimum are not related to Rca
256 content, indicating that other factors regulate Rubisco activation at high temperatures in C4

257 species (Hendrickson et al., 2008). Yet another report concluded that heat sensitivity of Rca
258 function is linked with decreased Rubisco activation in C4 grasses (Perdomo et al., 2017). C4
259 grass species, such as sorghum have separate α and β genes as do many other species but in
260 these grass species the Rca- α form is expressed only under heat stress ($> 42\text{ }^{\circ}\text{C}$). Kim *et al.*
261 (2021) found that the induction profile of Rca- α protein paralleled the recovery profile of
262 both A_n and Rubisco activation from a $42\text{ }^{\circ}\text{C}$ heat treatment. This correlation between Rca- α
263 isoform protein accumulation and the maintenance of Rubisco activation suggests that
264 manipulating the regulation of Rca- α isoform expression could be a promising strategy to
265 increase the temperature tolerance of this group of C4 grasses.

266 **Manipulating photorespiration to improve thermotolerance**

267 To lower the cost of photorespiration, synthetic pathways have been designed to
268 metabolize glycolate and release CO_2 in the chloroplast stroma, where it can be immediately
269 re-fixed by Rubisco (Figure 2; recently reviewed in: Eisenhut et al. 2019). These
270 “photorespiratory bypass” approaches have primarily relied on transgenic technologies to
271 introduce metabolic pathways in plant chloroplasts to either convert glycolate to glycerate
272 (Figure 2A-B; Kebeish et al. 2007; Dalal et al. 2015; Wang et al. 2020; Nayak et al. 2022) or
273 fully decarboxylate glycolate to release CO_2 in the chloroplast (Figure 2C-D; Shen et al. 2019;
274 Maier et al. 2012; South et al. 2019).



275 **Figure 2:** Chloroplastic photorespiratory bypass pathways tested in plants. (a) Pathway 1
 276 (dark blue) converts glycolate to glycerate using five genes from the *E. coli* glycolate
 277 pathway encoding the enzymes glycolate dehydrogenase, glyoxylate carboligase, and
 278 tartronic semialdehyde reductase. Pathway 2 (pink) achieves this using *Oryza*
 279 *sativa* glycolate oxidase and *E. coli* catalase (to remove the hydrogen peroxide generated by
 280 glycolate oxidase), glyoxylate carboligase, and tartronic semialdehyde reductase. Major
 281 native photorespiratory flux through the chloroplast, peroxisome, (grey, solid lines) are also
 282 shown, including steps catalyzed by phosphoglycolate phosphatase (PGLP) and the glycine
 283 decarboxylase cleavage (GDC) system. (b) Differences in above ground biomass (solid) and
 284 grain yield (dashed) for various species expressing pathway 1 (dark blue) or pathway 2 (pink)
 285 relative to unmodified controls. Values greater than 1 indicate an increase relative to WT
 286 controls. (c) Glycolate oxidation pathways release CO₂ in the chloroplast. Pathway 3 (light
 287 blue) introduces genes encoding glycolate oxidase, malate synthase, and catalase. Pathway 4
 288 (purple; AP-3) uses *Chlamydomonas reinhardtii* glycolate dehydrogenase (eliminating the
 289 need for catalase) and malate synthase, and downregulates the native glycolate-glycerate
 290 exchange transporter PLGG1 via RNAi suppression to increase metabolic flux through the
 291 alternative metabolic pathway. Pathway 5 (green) uses glycolate oxidase, oxalate oxidase,
 292 and catalase for the consecutive decarboxylation of glycolate with production of CO₂. (d)
 293 Differences in above ground biomass (solid) and grain yield (dashed) for various species
 294 expressing pathway 3 (light blue), pathway 4 (purple, AP-3) or pathway 5 (green) relative to
 295 unmodified controls. Values greater than 1 indicate an increase relative to WT controls.
 296 Values reported are aggregate means from original study, and error is the coefficient of
 297 variation. Created with BioRender.com

298

299 Expression of glycolate oxidase in the chloroplast intended to fully decarboxylate
 300 glycolate releasing CO₂ within the chloroplast has demonstrated a growth and yield
 301 advantage in field-grown model and agronomic crops (South et al. 2019; Shen et al. 2019;

302 Wang et al. 2020). South et al., (2019) modified the original glycolate oxidation pathway
303 proposed by Maier et al., (2012) to overexpress *Chlamydomonas reinhardtii* glycolate
304 dehydrogenase to remove the need for catalase, and repressed glycolate transport from the
305 chloroplast through suppression of the glycolate/glycerate antiporter PLGG1 in tobacco.
306 This pathway (named AP-3) led to 5-8% increases in the daily integral of photosynthetic
307 carbon assimilation (A') and drove 19-37% increases in biomass in field-grown tobacco
308 relative to a WT control (South et al. 2019). Field-grown rice plants overexpressing an
309 alternative full decarboxylation strategy combining chloroplast-localized glycolate oxidase,
310 oxalate oxidase and catalase (the GOC pathway) again demonstrate a photosynthetic and
311 biomass advantage over WT controls in agriculturally relevant settings (Shen et al., 2019).
312 When the reported diurnal measurements of photosynthesis are converted to A' (following:
313 Bernacchi et al. 2006), the transgenic rice plants fixed 15-25% more daily carbon, driving a
314 14-35% increase in biomass over multiple growing seasons, though grain yield increases
315 were unstable over growing seasons (Shen et al., 2019). Further modification of this
316 pathway in rice to return inputs to the Calvin-Benson cycle displays stable yield
317 enhancement (Wang 2020).

318 In rice and tobacco, the overexpression of the glycolate oxidation pathways in
319 chloroplasts appear to benefit photosynthesis through increased chloroplast CO_2
320 concentration, suggesting that synthetic glycolate metabolism could mitigate the impact of
321 warming on photosynthetic carbon fixation and growth at elevated temperatures. This
322 hypothesis was confirmed by comparing the cost of growth at elevated temperature
323 between AP-3 and WT tobacco plants under canopy-warming conditions in the field
324 (Cavanagh et al. 2022). Following a short-term shift to elevated temperature, plants with
325 engineered photorespiration maintain higher rates of net assimilation compared to WT

326 controls. Measured over two field plantings, transgenic plants maintained ~16% greater A_n
327 relative to WT plants under heated conditions (i.e., canopy warmed 5°C relative to
328 ambient). Transgenic plants sustained 19% less biomass loss under heated
329 conditions compared to control plants, having produced 26% more total biomass than WT
330 plants under heated conditions, compared to 11% under ambient conditions (Cavanagh et
331 al. 2022). Overall, this argues against the suggestion that alternative pathways could be
332 maladaptive under adverse conditions (Burgess et al. 2023) and provides strong proof-of-
333 concept for targeting photorespiration to improve the high temperature resilience of
334 photosynthesis.

335 **Increasing RuBP Regeneration**

336 As temperatures increase and exceed the optimum for photosynthesis, it is predicted that
337 the rate of RuBP regeneration will become limiting (Sage and Kubien 2007). Rising $[CO_2]$ will
338 also shift control away from Rubisco toward RuBP regeneration in C3 crops (Bernacchi et al.
339 2005; Sage and Kubien 2007). Therefore, transgenic strategies enhancing RuBP
340 regeneration, such as the overexpression of the Calvin Cycle enzyme sedoheptulose-1,7-
341 bisphosphatase (SBPase) (Raines 2003), should confer an advantage to C3 photosynthesis at
342 elevated temperatures, particularly when combined with increased $[CO_2]$ treatments.
343 Transgenic rice overexpressing SBPase maintain higher rates of A_n (measured at 25°C) than
344 WT and untransformed control plants following a 2h temperature stress at all temperatures
345 above 35°C (Feng et al. 2007). Transgenic plants also maintained a higher growth rate over
346 the three days following heat exposure (between 35-45°C) (Feng et al., 2007). A progressive
347 decline in the activation state of both Rubisco and phosphoribulokinase (PRK) was
348 associated with temperature treatments, but SBPase overexpressing lines maintained
349 higher rates of activation of both enzymes at all temperatures above 35°C. High

350 temperatures also caused Rca to form a greater association with the thylakoid membranes
351 in WT but not transgenic plants (Feng et al., 2007), suggesting an unresolved link between
352 SBPase activity, RuBP regeneration, and Rubisco activation state at elevated temperatures.
353 While these results indicate that overexpression of SBPase could be a transgenic target to
354 improve photosynthetic thermal tolerance, they have not demonstrated a benefit over
355 sustained heat treatment. To explore the full benefit of this manipulation, field-grown
356 transgenic soybean overexpressing the cyanobacterial bifunctional FBP/SBPase was
357 simultaneously exposed to elevated [CO₂] and elevated temperature (+2.7°C) (Köhler et al.
358 2016). Transgenic plants maintained higher photosynthetic carbon assimilation, and
359 maximal rates of carboxylation, and RuBP regeneration than controls across all treatments.
360 Under ambient [CO₂] (400 ppm) conditions, canopy heating resulted in yield declines across
361 all genotypes. However, under elevated [CO₂] (600 ppm), overexpression of the bifunctional
362 FBP/SBPase was thermoprotective and heated plants maintained the same yield as
363 unheated plants, while WT showed yield reductions of 11-22% (Köhler et al. 2016). Thus,
364 there is strong and continually accumulating evidence that accelerating the rate of RuBP
365 regeneration is a viable strategy for simultaneously adapting C3 photosynthesis to two
366 components of climate change; increasing atmospheric [CO₂] and increasing growing season
367 temperatures. That it appears this adaptation could be achieved by the upregulation of
368 single native genes (e.g., SBPase) indicates the proof of concept achieved by transgenic
369 manipulation might be possible by screening for genetic variation in a natural, wild, or
370 mutagenized populations.

371 **Other Promising targets not yet directly tested**

372 Transgenic overexpression of photorespiration enzymes

373 Theory suggests that C3 plants overinvest in photorespiration enzymes for optimal growth
374 in current and future atmospheres (Zhu et al. 2007). However, antisense knockdowns of the
375 enzymes involved in the mitochondrial glycine decarboxylase cleavage (GDC) system, which
376 plays a central role in regulating photorespiratory flux (Hagemann and Bauwe 2016; Timm
377 and Bauwe 2013; Fu et al. 2023), result in poor photosynthesis and growth rates in potato
378 (Heineke et al. 2001) and rice (Xu et al. 2009). Conversely, overexpression the GDC-H and
379 GDC-L proteins separately improve photosynthesis and plant growth in *Arabidopsis* (Timm
380 et al. 2012; Timm et al. 2015; Simkin et al. 2017) and tobacco (López-Calcano et al. 2019).
381 This effect is perhaps realized through minimizing the inhibitory accumulation of 2PG in the
382 chloroplast while also boosting RuBP regeneration by increasing the rate of return of 3-PGA
383 to the C3 cycle (Betti et al. 2016; Peterhansel et al. 2013; Flügel et al. 2017).

384 Boosting the capacity of the photorespiratory pathway will likely drive a benefit
385 under heat stress, when the rate of Rubisco oxygenation increases. *Arabidopsis*
386 overexpressing the stromal protein phosphoglycolate phosphatase (PGLP) maintain higher
387 photosynthetic rates after short and long-term exposure to a 10°C temperature increase
388 than do control plants (Timm et al. 2019), supporting the suggestion that a faster
389 photorespiratory metabolism improves thermotolerance. However, no growth impacts are
390 reported for the plants overexpressing phosphoglycolate phosphatase under heat stress.
391 Further, no other single photorespiratory enzyme overexpressing line has been directly
392 tested under heat stress conditions, though field-grown tobacco GDC-H overexpression lines
393 have a greater growth benefit than greenhouse-grown plants (26-47% compared to 13-38%;
394 Lopez Calcagno et al 2019), suggesting that this modification can confer resilience under
395 higher photorespiratory conditions in the field (high light and temperatures). Given the
396 increases in thermotolerance conferred by alternative photorespiration (Cavanagh et al.,

397 2022), future experiments are required to know if enhancing photorespiratory capacity can
398 directly boost photosynthetic thermotolerance.

399 Other photorespiration transgenic targets remain to be explored. For example,
400 catalase mutants have an increased stoichiometry of CO₂ release from photorespiration,
401 due to increased non-enzymatic decarboxylation of pyruvate in the peroxisome (Bao et al.
402 2021). Though the full contribution of non-enzymatic decarboxylation on photorespiratory
403 CO₂ release remains to be resolved, Bao et al (2021) do note that the activity of glycolate
404 oxidase increases more rapidly with temperature than that of catalase in *Beta vulgaris*,
405 which could potentially drive non-enzymatic CO₂ degradation at elevated temperatures
406 (Grodzinski and Butt 1976). These findings support preliminary work on variation in
407 photorespiration (Zelitch 1989). Therefore, the transgenic overexpression of peroxisomal
408 catalase, or of a more thermotolerant version of the enzyme, might improve the efficiency
409 of photorespiration under elevated temperatures.

410 Increasing canopy albedo by reducing leaf chlorophyll level.

411 Enhanced reflectance of incident solar radiation by leaves (i.e., increased albedo) can result
412 in reduced canopy temperature and transpiration, which would be expected to be
413 adaptative by mitigating the increase in temperature, drought and vapor pressure deficit
414 that global change forecasts. Field experiments with a pale-green soybean mutant showed
415 that short wavelength radiative forcing was lower by $4.1 \pm 0.6 \text{ W m}^{-2}$ during the growing
416 season and by $1 \pm 0.1 \text{ W m}^{-2}$ across the full year (Genesio et al., 2020). Moreover, modeling
417 by Singarayer et al. (2009) predicted that an increase in canopy albedo of 0.04 could have a
418 regionally and seasonally specific cooling as much as $\sim 1^\circ\text{C}$. Thus, designing higher albedo
419 canopies is considered a plausible mitigation strategy for global warming (Genesio et al.,
420 2020).

421 Because reduced absorption of solar radiation that accompanies increased
422 reflectance (i.e., increased albedo) also lowers leaf temperature, higher albedo canopies
423 should increase net CO₂ assimilation (A_n) by mitigating negative heat stress effects
424 (Ainsworth and Ort, 2010) and in turn also improve water use efficiency (WUE). Cooler
425 soybean canopies lower vapor pressure deficit, resulting in higher WUE, which was reported
426 for alfalfa with reduced chlorophyll content compared to the full green control (Estill et al.,
427 1991). Albedo is measured on a scale from zero for a perfectly black surface to 1 for a
428 perfect reflecting white surface. Considerable natural genetic variation in albedo exists
429 within and between important crop species such as wheat, barley, corn, oats, rye, soybean
430 and sunflower with values varying from 0.02 to 0.1 (Breuer et al. 2003). Differences in
431 albedo can be driven by differing thickness and types of leaf waxes (Uddin and Marshall,
432 1988), leaf hairiness as well as the arrangement of the leaves in the canopy (Hatfield and
433 Carlson, 1979) but differences in chlorophyll content maybe the most predictable and least
434 pleiotropic way to engineer albedo (Slattery and Ort, 2021). For example, it was shown that
435 under field conditions, a soybean mutant containing half of the chlorophyll of the near
436 isogenic wild type had lower leaf temperatures throughout the growing season (Slattery et
437 al., 2017). It is evident that increasing crop canopy albedo has the potential to be
438 thermoprotective to photosynthesis and productivity at the crop level as well as decrease
439 radiative forcing on a regional scale if higher albedo crops are adopted at large scale. While
440 there is the legitimate worry that reducing absorption of a crop canopy will reduce canopy
441 carbon gain and thereby yield it has been well documented that this does not happen for
442 select low chlorophyll mutants. Because so much of the light absorbed at the top of dense
443 crop canopies exceeds the capacity of photosynthesis to utilize, leaf chlorophyll can be
444 reduced as much as 70% with no or little penalty on carbon gain or yield (Slattery et al.,

445 2017; Walker et al., 2018). But the direct experimental validation of the hypothesis that
446 lower leaf temperature of low chlorophyll content crops has not yet been accomplished.

447

448 **Concluding thoughts**

449 Almost every biological process in a plant from phenology to reproduction to water
450 relations is affected by high temperature stress. As mentioned above, high temperature
451 stress during the reproductive phase of many crops has the largest impact on season long
452 yield (Hatfield et al., 2011). Integrating the impact of temperature on both carbon
453 metabolism and reproduction is crucial to reveal potential cross-talk between pathways
454 (Ferguson et al., 2021). For example, Siebers et al. (2015) measured reductions in mid-day
455 photosynthesis ranging between 15-58% in field-grown soybean exposed to a 6°C heatwave
456 when temperatures warmed to above the thermal optimum, regardless of the
457 developmental stage of the crop. However, a 10% reduction in end of season yield was only
458 observed when heat waves were applied during early pod developmental stages. Heat
459 waves imposed during vegetative growth had no lasting impacts on yield, indicating that the
460 yield loss was not only due to direct impacts of the heat waves on photosynthesis but that
461 effects on reproductive process also played a major role. Thomey et al. (2019) extended this
462 work to investigate interactions of high temperature with elevated [CO₂] showing that the
463 stimulation of yield by [CO₂] fertilization was reduced when the temperature optimum of
464 soybean was surpassed further implicating temperature sensitivity of reproduction in heat
465 induced yield loss. Thus, it is evident that in order to get the full benefit of improving the
466 resilience of photosynthesis to warming temperatures a commensurate improvement in the
467 resilience of reproduction processes will be needed.

468 There can be no doubt that adapting crops to higher temperatures is nowhere more
469 important or more urgent than in Africa. Our focus in this review has been on transgenic
470 strategies to improve thermotolerance in crop photosynthesis and this may seem a
471 particularly difficult route toward adaptation in Africa. While that may be true, the
472 development and the recently approved release of Bt containing Pod Borer Resistant (PBR)
473 Cowpea for commercial production in Nigeria is a path setting demonstration that
474 transgenic adaptation in Africa may be possible. Moreover, transgenic technologies can also
475 be valuable in providing proof-of-concept research that an adaptation concept is
476 worthwhile before investing in searching for useful genetic variation in a natural or
477 mutagenized populations and then introducing the trait into target food crops by
478 introgressive hybridization.

479

480 ¹ The Sahel is a transitional region between the wooded Sudanian savanna to the south and
481 the Sahara to the north. It spans ~6000 km from the Atlantic Ocean on the west coast of
482 Africa to the Red Sea in the east. The Sahel belt from west to east includes parts of
483 northern Senegal, southern Mauritania, central Mali, northern Burkina Faso, the extreme
484 south of Algeria, Niger, the extreme north of Nigeria, Cameroon and Central African
485 Republic, central Chad, central and southern Sudan, the extreme north of South Sudan,
486 Eritrea and Ethiopia. (https://en.wikipedia.org/wiki/Sahel#cite_note-2)

487

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