



Kent Academic Repository

Simkin, Andrew J., López-Calcano, Patricia E. and Raines, Christine A. (2019) *Feeding the world: improving photosynthetic efficiency for sustainable crop production*. Journal of Experimental Botany, 70 (4). pp. 1119-1140. ISSN 0022-0957.

Downloaded from

<https://kar.kent.ac.uk/93865/> The University of Kent's Academic Repository KAR

The version of record is available from

<https://doi.org/10.1093/jxb/ery445>

This document version

Publisher pdf

DOI for this version

Licence for this version

CC BY (Attribution)

Additional information

Versions of research works

Versions of Record

If this version is the version of record, it is the same as the published version available on the publisher's web site. Cite as the published version.

Author Accepted Manuscripts

If this document is identified as the Author Accepted Manuscript it is the version after peer review but before type setting, copy editing or publisher branding. Cite as Surname, Initial. (Year) 'Title of article'. To be published in *Title of Journal*, Volume and issue numbers [peer-reviewed accepted version]. Available at: DOI or URL (Accessed: date).

Enquiries

If you have questions about this document contact ResearchSupport@kent.ac.uk. Please include the URL of the record in KAR. If you believe that your, or a third party's rights have been compromised through this document please see our [Take Down policy](#) (available from <https://www.kent.ac.uk/guides/kar-the-kent-academic-repository#policies>).



REVIEW PAPER

Feeding the world: improving photosynthetic efficiency for sustainable crop production

Andrew J. Simkin^{1,2,*}, Patricia E. López-Calcano² and Christine A. Raines^{2,*}

¹ NIAB EMR, New Road, East Malling, Kent ME19 6BJ, UK

² School of Biological Sciences, Wivenhoe Park, University of Essex, Colchester CO4 3SQ, UK

* Correspondence: andrew.simkin@emr.ac.uk or rainc@essex.ac.uk

Received 5 September 2018; Editorial decision 27 November 2018; Accepted 21 January 2019

Editor: John E. Lunn, MPI of Molecular Plant Physiology, Germany

Abstract

A number of recent studies have provided strong support demonstrating that improving the photosynthetic processes through genetic engineering can provide an avenue to improve yield potential. The major focus of this review is on improvement of the Calvin–Benson cycle and electron transport. Consideration is also given to how altering regulatory process may provide an additional route to increase photosynthetic efficiency. Here we summarize some of the recent successes that have been observed through genetic manipulation of photosynthesis, showing that, in both the glasshouse and the field, yield can be increased by >40%. These results provide a clear demonstration of the potential for increasing yield through improvements in photosynthesis. In the final section, we consider the need to stack improvement in photosynthetic traits with traits that target the yield gap in order to provide robust germplasm for different crops across the globe.

Keywords: Calvin–Benson cycle, sink capacity, synthetic biology, yield potential.

Introduction

Over the past 50 years, agricultural yields of our major crops have risen, in keeping with demand. For the most part, these increases came about due to advances in agronomic approaches and classical breeding that have maximized plant architecture and light capture, resulting in higher yielding varieties. However, the year on year increase in yields of the major crops in many parts of the world have plateaued, and new technological solutions must be explored to develop higher yielding varieties, to maintain the supply of food required to meet the needs of the growing population (Fischer and Edmeades, 2010; Ray *et al.*, 2013; Long *et al.*, 2015; Ort *et al.*, 2015). It has been estimated that by 2050 the global population will increase from its current 7.6 billion to 9.7 billion, requiring between a 70% and a 100% increase in the yield of the major food crops due to

increases in living standards, an increase in the requirements for plant-based proteins for animal feed (increased meat consumption), and an increase in the requirements for plant-based fuels (WorldBank, 2008; RSOL, 2009; Tilman *et al.*, 2011; Tilman and Clark, 2015; FAO, 2017). Clearing new land to bring it into use for crop production is not a feasible option as there is little quality land available and therefore this approach would require an increase in the use of nutrient and water inputs in order to deliver the yields needed. This would also have negative impacts on marine, freshwater, and terrestrial ecosystems, leading to damage to unique habitats and a decrease in biodiversity (Vitousek *et al.*, 1997; Dirzo and Raven, 2003; Godfray *et al.*, 2010; GOFS, 2011; Godfray, 2014). Furthermore, approximately one-third of all greenhouse gas emissions can

be attributed to crop production and additional land clearance for agriculture (Burney *et al.*, 2010). To mitigate environmental damage caused by extensive agriculture and land clearance, it will be necessary to meet global food demands without increasing the amount of cultivatable land, emphasizing the need to improve crop yields. Moreover, such yield improvements will need to be managed in conjunction with global climate change, where atmospheric [CO₂] levels are expected to increase from 409 ppm to 550 ppm by 2050 (Solomon, 2007; Le Quere *et al.*, 2009).

Our aim is to provide an overview of the current work to improve photosynthetic efficiency. This review explores the impacts of manipulating the Calvin–Benson (CB) cycle, photorespiration, and electron transport on biomass and seed yield, and also reports on some of the unexpected outcomes where negative effects were observed. In the last section, we explore the future opportunities including combining multigene manipulation of photosynthetic carbon assimilation to improve yield potential with traits that target the yield gap.

Photosynthesis and crop yield

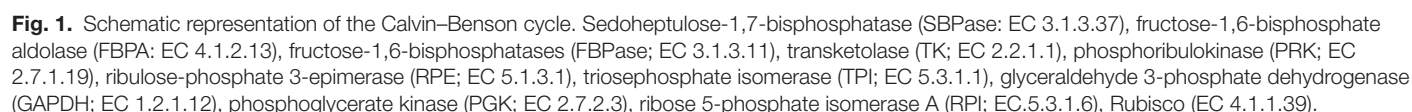
Photosynthesis is the primary determinant of crop yield, and the efficiency by which a crop captures light and converts it into biomass over the growing season is a key determinant of final yield, be that biomass or grain (Long *et al.*, 2006). The maximum yield attainable from a crop has been termed yield potential and can be defined as the maximum yield attainable when the best adapted crop variety is grown, in optimal conditions with no biotic or abiotic stress (Evans and Fischer, 1999). Determinants of yield potential are light availability, light capture, energy conversion, and plant architecture. For our major crops, rice, wheat, and maize, the only one of these four components contributing to yield that is below the potential maximum is energy conversion, which is determined by photosynthetic efficiency (Long *et al.*, 2006; Zhu *et al.*, 2010). However, the efficiency of this conversion of energy to harvestable biomass, given that as much as 50% of fixed carbon is lost to photorespiration under certain conditions, has yet to be adequately explored.

Supporting evidence that increased yields can be obtained by increasing photosynthetic CO₂ assimilation comes from CO₂ enrichment studies, which have consistently shown compelling evidence that yields can be increased through improved CO₂ uptake (Lilley *et al.*, 2001; Miglietta *et al.*, 2001; Calfapietra *et al.*, 2003; Ainsworth and Long, 2005; Gielen *et al.*, 2005; Leakey *et al.*, 2009; Weigel and Manderscheid, 2012). Although a number of studies showed that there was a negative correlation between leaf area photosynthesis and yield (Evans, 1993, 1998), in the case of wheat, a positive relationship between photosynthetic rates and biomass (Kruger and Volin, 2006) and yield (Fischer *et al.*, 1998) has been observed.

Direct manipulation of the CB cycle in a variety of species between 1992 and 2015 has demonstrated that even small decreases in a limited number of CB cycle enzymes could

have a negative impact on carbon assimilation and growth. For example, reductions in enzymes such as sedoheptulose-1,7-bisphosphatase (SBPase; EC 3.1.3.37; Harrison *et al.*, 1998, 2001; Lawson *et al.*, 2006), the chloroplastic fructose-1,6-bisphosphatases (FBPase; EC 3.1.3.11; Koßmann *et al.*, 1992; Sahrawy *et al.*, 2004; Rojas-González *et al.*, 2015), or fructose-1,6-bisphosphate aldolase (FBPA; EC 4.1.2.13; Haake *et al.*, 1998, 1999) resulted in slower growth and a decrease in final biomass yield. Furthermore, a decrease in the activity of the plastid transketolase (TK; EC 2.2.1.1) by 20–40% in antisense tobacco plants was also shown to inhibit ribulose-1,5-bisphosphate (RuBP) regeneration and photosynthesis (Henkes *et al.*, 2001); as light levels increase, the inhibition of photosynthesis became more pronounced with the maximum rate of photosynthesis limited under both saturating light and saturating CO₂. In TK antisense cucumber, a decrease in growth, net photosynthetic rate, stomatal conductance, transpiration rate, and the number of female flowers per plant was observed (Bi *et al.*, 2015). Taken together, these transgenic studies revealed that there is no single limiting step in photosynthetic carbon assimilation, and that control of flow of CO₂ in the CB cycle is shared between all of the enzymes. Furthermore, this work also demonstrated that this share of control between enzymes is not equal and that the control exercised by any individual enzyme is dependent on environmental conditions and development stage. The hypothesis from this is that improvements in photosynthesis could be achieved through manipulation of more than one individual step in the CB cycle (Stitt and Schulze, 1994; Raines, 2003).

In plants that fix atmospheric CO₂ using the CB cycle (Fig. 1) enzyme Rubisco, the theoretical maximum energy conversion efficiency attainable is 4.6% for C₃ plants (Zhu *et al.*, 2010) but, in the field, efficiencies of <50% of this are realized. Modelling studies developed using ordinary differential equations have been used to describe photosynthetic carbon assimilation by the CB cycle and have identified enzymes with the greatest influence on CB cycle CO₂ assimilation (Laisk *et al.*, 1989; Pettersson and Ryde-Pettersson, 1988; Poolman *et al.*, 2000). The output from the model of Poolman *et al.* (2000) provided evidence that the control of flux in the CB cycle is shared mainly between SBPase and Rubisco, dependent on the environmental conditions in which the plants are grown. Building on these early models, more recent studies have included sucrose/starch biosynthesis and photorespiration leading to the development of a more dynamic model of carbon metabolism (Zhu *et al.*, 2007). The work of Zhu *et al.* (2007) used an evolutionary algorithm together with a model using existing kinetic data and constraining the amount of nitrogen. Based on this, it was proposed that increasing SBPase, FBPA, and ADP-glucose pyrophosphorylase (AGPase; EC 2.7.7.27) in the same plant, together with a modest reduction in photorespiration, could lead to an increase in the efficiency of photosynthetic carbon assimilation. The importance of this model is that it highlighted the fact that more than one target is likely to be needed and that modelling has the potential to allow the most promising combination of targets to be identified. This model remains to be fully tested experimentally.



Early work to improve photosynthetic efficiency through transgenic manipulation focused on the overexpression of a single individual enzyme in the CB cycle (Table 1). The overexpression of SBPase, for example, in *Arabidopsis thaliana* (Arabidopsis) (Simkin *et al.*, 2017a), tobacco (Lefebvre *et al.*, 2005; Simkin *et al.*, 2015), and tomato (Ding *et al.*, 2016) has shown that an increase in SBPase enzyme activity results in an increase in both photosynthetic carbon assimilation and biomass yield. Lefebvre *et al.* (2005) showed in tobacco that the photosynthetic CO₂ assimilation rates increased in young expanding leaves, and both sucrose and starch accumulated, resulting in a 30% increase in biomass. However, no significant increase in photosynthetic rates was observed in the fully expanded leaves of these same plants (Lefebvre *et al.*, 2005). The results observed by Lefebvre *et al.* were confirmed in follow-up experiments showing that these increases were conserved across generations,

10 years apart, and when grown under both high and low light (Simkin *et al.*, 2015). Subsequently, increased SBPase activity in tobacco was shown to increase biomass yield substantially in field-grown tobacco under an open-air elevation of CO₂ (Rosenthal *et al.*, 2011). Further support for these results also comes from work on *Arabidopsis* where a 42% increase in biomass, increased CO₂ assimilation, and accelerated development were observed (Simkin *et al.*, 2017a); and in tomato, where biomass, sucrose, and starch all accumulated (Ding *et al.*, 2016), demonstrating that SBPase is one of the enzymes that can exert control over the flow of carbon in the CB cycle in a number of different species. Although the simplest explanation for the positive effect of increasing SBPase activity is a direct consequence of improving CO₂ assimilation, an interesting alternative hypothesis is that changes in metabolites caused by increasing SBPase activity may act as a signal that alters plant growth and development. The metabolic changes that occur in response to changing SBPase activity have not been elucidated, but it is interesting to note the changes in development

Table 1. Summary of single targeted manipulations of Calvin–Benson cycle enzymes and their biological outcomes

Manipulation	Transgene expressed	Plant	Functional description	Biomass and yield	References
Calvin–Benson cycle	SBPase	Arabidopsis	Tissue-specific expression. 37–85% increase in SBPase, activity, 37% increase in CO ₂ assimilation	42% increase in dry weight and a 53% increase in seed yield	Simkin <i>et al.</i> (2017a) ^a
		Tobacco	Constitutive expression. 90–110% average increase in SBPase activities, increase in photosynthetic rates, increases in sucrose and starch	30–34% increase in dry weight	Lefebvre <i>et al.</i> (2005); Simkin <i>et al.</i> (2015) ^b
		Tomato	Constitutive expression. 55–139% increase in SBPase activity, ~25% increase in CO ₂ assimilation, increases in sucrose and starch	Up to 39% increase in dry weight in best lines. Tomato plants found to be more chilling tolerant	Ding <i>et al.</i> (2016) ^b
		Wheat	Constitutive expression. Up to 90% increase in SBPase activities in some lines, increase in CO ₂ assimilation	Up to 40% increase in grain yield	Driever <i>et al.</i> (2017) ^b
		Rice	Constitutive expression. Up to 200% increase in SBPase activities in some lines, increased CO ₂ assimilation rates under elevated temperature	Higher growth rates under elevated temperature	Feng <i>et al.</i> (2007) ^b
	Cyanobacterial SBPase	Tobacco	Tissue-specific expression. More than 20% increase in the rate of photosynthetic CO ₂ fixation	50% increase in final dry weight	Tamoi <i>et al.</i> (2006) ^a
	Cyanobacterial FBPase	Tobacco	Tissue-specific expression. 15% increase in CO ₂ fixation rates in some lines	30% increase in dry weight	Tamoi <i>et al.</i> (2006) ^a
	FBPaldolase	Arabidopsis	Tissue specific expression. 46–80% increase in FBPaldolase activity, 31% increase in CO ₂ assimilation	32% increase in dry weight, 35% increase in seed yield	Simkin <i>et al.</i> (2017a) ^a
		Tobacco	Tissue-specific expression. 40–90% increase in FBPaldolase activities, 19% increase in photosynthetic CO ₂ fixation	10–30% increase in dry weight at ambient CO ₂ with a 70–120% increase in high CO ₂	Uematsu <i>et al.</i> (2012) ^a
	Transketolase	Tobacco	Constitutive expression. 76–150% increase in transketolase activity, no increase in photosynthesis	Negative effect on plant growth resulting in leaf chlorosis	Khozaei <i>et al.</i> (2015) ^b
		Rice	Tissue-specific expression. 80–94% increase in transketolase content, no effect on photosynthesis	No changes to biomass, plant height, or tiller number. Chlorosis NOT observed	Suzuki <i>et al.</i> (2017) ^a
	Cyanobacterial SBP/ FBPase	Tobacco	Tissue-specific expression. 70% increase in FBPase activity, 130% increase in SBPase activity, 20% increase in photosynthetic CO ₂ fixation	Increase in biomass of 40–50%	Miyagawa <i>et al.</i> (2001) ^a
		Lettuce	Tissue-specific expression. Photosynthetic capacity was increased by 30–60%	60% increase in fresh weight	Ichikawa <i>et al.</i> (2010) ^a
	Cyanobacterial SBP/ FBPase	Soybean	Constitutive expression. 4–14% increase in CO ₂ fixation rates in some lines	Under ambient CO ₂ , elevated temperature led to reductions in seed yield. Under elevated CO ₂ and elevated temperature, seed yield was maintained while the WT showed 11% and 22% reductions	Köhler <i>et al.</i> (2017) ^c

Transgenes were under the control of either photosynthetic tissue-specific promoters or a constitutive promoter. Growth conditions are indicated: ^a controlled environmental conditions; ^b greenhouse; ^c field experiments.

which occurred in the SBPase antisense plants and in response to manipulation of other metabolic pathways (Lawson *et al.*, 2006; Raines and Paul, 2006).

More recently it was shown that by increasing SBPase activity in wheat, significant increases in photosynthetic rates can be achieved (Driever *et al.*, 2017). Importantly, these increases in

SBPase activity resulted in an increase in grain yield (+30–40%) as well as biomass yield. To confirm these results, Driever *et al.* (2017) grew these plants under two different growth regimes. In one experiment, plants were grown at high density where tillering is limited and, in another, at lower density where tillering was encouraged. Under the higher growing density, plants

had fewer tillers with an increase in seed number per ear and, at the lower growing density, plants produced more ears with no significant increase in the number of seeds per ear. In the lines with the highest SBPase activity, total seed weight, seed number, and whole-plant biomass were shown to be increased in both experiments, demonstrating that increasing SBPase activity can have a positive effect regardless of planting density (Driever *et al.*, 2017).

The results obtained by overexpression of plant enzymes are supported by parallel research, in which cyanobacterial enzymes SBPase (cySBPase), FBPase (cyFBPase), or the bifunctional fructose-1,6-bisphosphatases/sedoheptulose-1,7-bisphosphatase (cyFBP/SBPase) were expressed in higher plants. In tobacco, Tamoi *et al.* (2006) demonstrated that plants expressing cySBPase showed an increase of >20% in the rate of photosynthetic CO₂ fixation and in their growth rate, with a 1.5-fold increase in final biomass. Furthermore, some plants expressing cyFBPase were also shown to accumulate a larger amount of biomass (+1.3-fold) compared with controls, with a 15% increase in CO₂ fixation rates in some lines. These results suggest that both SBPase and FBPase enzyme activities exert some level of control over the flow of carbon through the CB cycle. Moreover, Miyagawa *et al.* (2001) expressed the cyanobacterial cyFBP/SBPase in tobacco cv. Xanthi. These authors showed that the expression of this bifunctional enzyme (FBPase activity increased by as much as 1.7-fold and SBPase activities by 2.3-fold) in plants enhances photosynthesis by ~1.20-fold, increasing biomass by 40–50% (Table 1). These results are supported first by the expression of cyFBP/SBPase in lettuce which resulted in a 1.3-fold increase in photosynthetic capacity and a 1.6-fold increase in fresh weight (Ichikawa *et al.*, 2010) and, secondly in soybean, which showed that plants had significantly higher rates of carbon assimilation (4–14%) compared with controls (Köhler *et al.*, 2017).

In 2012, the overexpression of the CB cycle enzyme FBPA in tobacco also resulted in an increase in photosynthesis and growth, under elevated CO₂ (700 ppm) (Uematsu *et al.*, 2012). Under these conditions, Uematsu *et al.* saw a 1.4- to 1.9-fold increase in aldolase activities, a 1.5-fold elevation of photosynthetic CO₂ fixation, and an increase in biomass of 70–120%. However, these effects were much less when plants were grown in ambient CO₂ where increases in biomass ranged from 10% to 30% compared with the wild type (Uematsu *et al.*, 2012).

These individual gene manipulations have demonstrated that increases in the activity of enzymes of the CB cycle can increase photosynthetic carbon assimilation, enhance growth, and lead to significant increases in vegetative biomass under controlled conditions.

Photorespiration

In addition to the carboxylation reaction carried out by Rubisco, in which CO₂ is added to RuBP resulting in flow of carbon through the CB cycle, a competing reaction of the Rubisco enzyme results in the fixation of O₂. This oxygenase activity of Rubisco competes with the fixation of CO₂ at the active site (see Fig. 2) and, in ~25% of the reactions, oxygen

is added to RuBP instead of CO₂, leading to the formation of a molecule of 3-phosphoglycerate (3PGA) and a molecule of 2-phosphoglycolate (2PG) at the cost of one ATP and one NAD(P)H. The metabolite 2PG is not used in the CB cycle and needs to be recycled at a high energy cost, thereby reducing the efficiency of CO₂ assimilation and impacting significantly on yield (Anderson, 1971; Bowes *et al.*, 1971; Ludwig and Canvin, 1971; Sharkey, 1988; Tolbert, 1997; Zhu *et al.*, 2010; Busch, 2013; Walker *et al.*, 2016a, b).

In the photorespiratory pathway, 2PG is recycled into 3PGA in a process which takes place in three organelles (chloroplast, peroxisome, and mitochondria) and in the cytosol. This pathway is able to recover 75% of the carbon, with the remaining 25% being released as CO₂ in the mitochondria (Bauwe and Kolukisaoglu, 2003; Peterhansel *et al.*, 2010). Although photorespiration prevents the accumulation of 2PG and the concomitant inhibition of CB by this metabolite, it does so at a high energetic cost. This process also generates one molecule each of hydrogen peroxide (H₂O₂) and ammonia (NH₃) for two oxygenation events for all steps leading to glycine production (Tolbert, 1979). H₂O₂ and NH₃ have been shown to function as signaling molecules with important roles in plant fitness, including disease resistance and nitrogen assimilation (Rachmilevitch *et al.*, 2004; Taler *et al.*, 2004; Rojas *et al.*, 2012); however, both of these molecules can be toxic if they accumulate to high levels (Peterhansel *et al.*, 2010) and the re-assimilation of NH₃ via glutamine synthetase and glutamine 2-oxoglutarate aminotransferase also adds to the energetic costs (Wallsgrove *et al.*, 1980; Keys, 2006; Masclaux-Daubresse *et al.*, 2010; Moroney *et al.*, 2013; Huma *et al.*, 2018). For these reasons, photorespiration has been a long-standing target in attempts to improve photosynthesis. As reviewed recently, there has been an array of approaches aimed at engineering photorespiration with the goal of increasing crop productivity (South *et al.*, 2018). Here, we will not discuss approaches aiming to introduce a bypass to photorespiration and will only summarize manipulations in the levels of the endogenous proteins involved in this process, some of which have led to an increase in plant productivity. Two successive reactions taking place in the mitochondria have received a particular amount of attention. First, the oxidative decarboxylation of glycine to methylene tetrahydrofolate (THF) by the glycine cleavage system (GCS), which in turn is used by serine hydroxymethyltransferase (SHMT) to form serine from a second glycine (Foyer *et al.*, 2009; Bauwe *et al.*, 2010). First discovered in bacteria by Sagers and Gunsalus (1961), the reversible conversion of glycine to serine is crucial to the majority of organisms so far characterized, including cyanobacteria, green microalgae, and plants (Kisaki and Tolbert, 1970; Kisaki *et al.*, 1971; Eisenhut *et al.*, 2008; Kikuchi *et al.*, 2008; Zelitch *et al.*, 2009; Hackenberg *et al.*, 2011). These reactions involve three different enzymes: the pyridoxalphosphate-dependent enzyme glycine decarboxylase (P-protein; EC 1.4.4.2), the THF-dependent enzyme aminomethyltransferase (T-protein; EC 2.1.2.10), and the NAD⁺-dependent enzyme dihydrolipoyl dehydrogenase (L-protein; EC 1.8.1.4). A fourth protein involved in this process is the lipoic acid-containing H-protein, which acts as a hydrogen carrier and interacts with the P-, T-, and L-proteins,

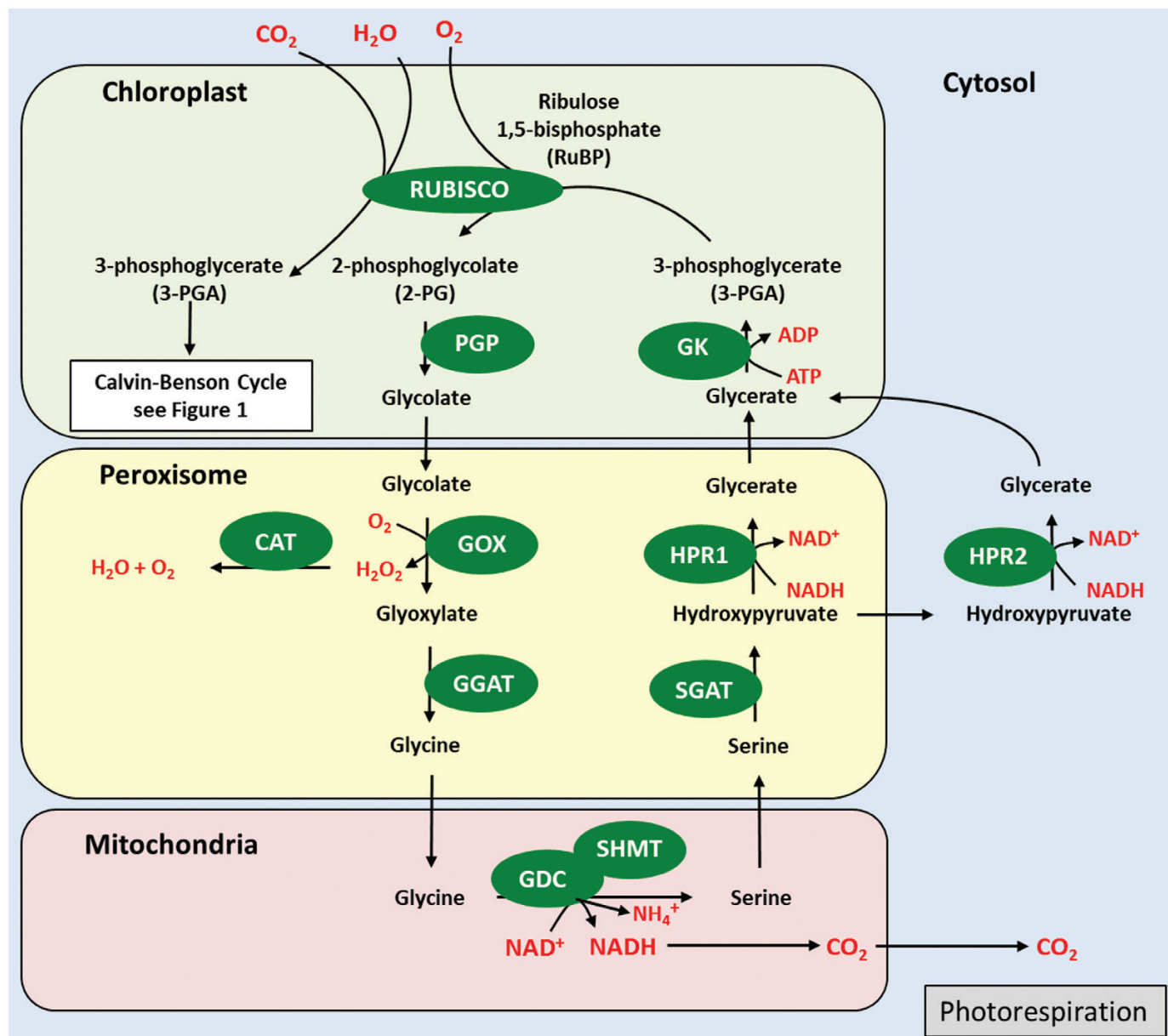


Fig. 2. Schematic representation of photorespiration. Glycolate oxidase (GOX; EC 1.1.3.1), 2-phosphoglycerate phosphatase (PGP; EC 3.1.3.13), serine-glyoxylate transaminase (SGAT; EC 2.6.1.45), glycine:2-oxoglutarate aminotransferase (GGAT; EC 2.6.1.4), glycerate-3-kinase (GK; EC 2.7.1.31), hydroxypyruvate reductase (HPR; EC 1.11.81), glycine decarboxylase (GDC), catalase (CAT; EC 1.11.16), serine hydroxymethyltransferase (SHMT; EC 2.1.2.1), Rubisco (EC 4.1.1.39).

to transfer intermediates successively between the enzymes and finally to NAD^+ (Oliver *et al.*, 1990; Oliver, 1994; Faure *et al.*, 2000; Douce *et al.*, 2001; Foyer *et al.*, 2009; Bauwe *et al.*, 2010).

Modelling studies indicated that in environments where few stresses are likely, a modest reduction in the levels of the photorespiratory proteins could lead to a better nitrogen distribution, which would in turn lead to higher CO_2 assimilation (Zhu *et al.*, 2007). However, previous studies had shown that reductions in the flux through the photorespiratory pathway under high photorespiratory conditions (i.e. high temperature or water stress) leads to a decrease in photosynthetic efficiency. For example, knockdown of the GCS P-protein in potato and H-protein in rice was shown to lead to reductions in flux through the photorespiratory cycle, a reduction in the rate

at which mitochondria oxidize glycine (~70%), and a reduction in photosynthesis and growth rates (Heineke *et al.*, 2001; Bykova *et al.*, 2005; Zhou *et al.*, 2013; Lin *et al.*, 2016). Antisense P-protein potato plants [containing 30–40% of wild-type (WT) levels] accumulated >100-fold higher levels of glycine and displayed a significant reduction in the rate of glycine oxidation (Heineke *et al.*, 2001; Bykova *et al.*, 2005); and deletion of the GCS P-protein in Arabidopsis was shown to be lethal under non-photorespiratory conditions (Engel *et al.*, 2007). Furthermore, in rice under ambient CO_2 , knockdown of the H-protein also resulted in chlorophyll loss, protein degradation, lipid peroxidation, and an accumulation of reactive oxygen species (ROS), leading to ROS-induced senescence (Zhou *et al.*, 2013). Moreover, a T-protein insertion mutant had very

high leaf glycine and glyoxylate levels (Engel *et al.*, 2008) and a T-protein knockout was shown to be lethal even in a non-photorespiratory environment on growth medium; however, a T-protein knockdown (containing ~5% of WT protein levels) was able to grow in normal air, although at a lower growth rate with a lower photosynthetic performance, and accumulated a moderate amount of glycine (Peterhansel *et al.*, 2013b). These results are consistent with earlier studies by Winkler *et al.* (1997) who identified a heterozygous barley mutant with a 50% reduction in the levels of the GCS H-protein. When grown in air, no significant difference in metabolites content of photosynthesis was observed in these plants. However, under low CO₂ and high light where photorespiration is enhanced, photosynthetic rates decreased and glycine accumulated. These plants also showed a 2-fold increase in glycine content and had lower CO₂ assimilation rates under drought stress (Winkler *et al.*, 1997; Shimada *et al.*, 2008).

Given that a reduction in activity of the enzymes of the photorespiratory pathway resulted in negative effects, the overexpression of components of the GCS has been explored as a strategy to increase photorespiration flow and decrease accumulation of photorespiratory intermediates. In Arabidopsis, overexpression of the H-protein or L-protein resulted in an improvement in photosynthesis and an increased vegetative biomass (Timm *et al.*, 2012, 2015, 2016; Simkin *et al.*, 2017a) (Table 2). Furthermore, recent work in tobacco has also shown that the mesophyll-specific overexpression of the H-protein results in enhanced growth and increased biomass both in the greenhouse and when grown in the field (up to 47%) (López-Calcano *et al.*, 2018). In contrast, overexpression of the T-protein did not alter photosynthetic CO₂ uptake or improve plant growth in Arabidopsis (Timm *et al.*, 2018). Interestingly, L-protein overexpressors were also shown to have high sucrose (and fructose and maltose) contents (Timm *et al.*, 2015). Timm *et al.* (2015) proposed that the enhanced photorespiratory metabolic capacity of L-protein overexpression alters carbon flow through the tricarboxylic acid (TCA) cycle. Interestingly, the overexpression of one or other of the GCS proteins did not lead to an increase in the other three GCS proteins (Timm *et al.*, 2012, 2015; Peterhansel *et al.*, 2013a; López-Calcano *et al.*, 2018). These results reveal that the biosynthesis of the four GCS proteins is independently regulated and may only be linked by factors such as light or developmental stage. This is consistent with the idea that the GCS proteins do not form a true protein-associated complex (Table 2).

It has been demonstrated previously that 2PG is toxic as it has been shown to inhibit two CB cycle enzymes, triosephosphate isomerase (TPI) in pea (Anderson, 1971), which plays important roles in both the CB cycle and starch synthesis, and PRK in spinach (Kelly and Latzko, 1976). Recent work supporting this hypothesis has demonstrated that 2PG also inhibits the CB cycle enzymes TPI and SBPase, slowing down starch synthesis in Arabidopsis (Flügel *et al.*, 2017). Additionally, glyoxylate has been shown to inhibit Rubisco activation in isolated chloroplasts and *in vivo* (Chastain and Ogren, 1989; Campbell and Ogren, 1990; Hausler *et al.*, 1996). These authors have proposed that the additional stimulation of GCS activity results in a reduction in the levels of these photorespiratory

metabolites, reducing the possibility of CB cycle inhibition (see Fig. 2) (Anderson, 1971; Kelly and Latzko, 1976; Cook *et al.*, 1985; Chastain and Ogren, 1989; Campbell and Ogren, 1990; Eisenhut *et al.*, 2007; Timm *et al.*, 2012, 2015; Lu *et al.*, 2014; Simkin *et al.*, 2017a).

Given the results obtained from both the down-regulation and up-regulation of proteins in the photorespiratory pathway, reducing photorespiration by decreasing the activities of the GCS enzymes has largely been abandoned. To date, the most heavily studied and most promising approaches to enhancing productivity by limiting photorespiration come from the introduction of alternative routes to metabolize 2PG, liberating CO₂ for use in the CB cycle (Kebeish *et al.*, 2007; Khan, 2007; Carvalho *et al.*, 2011; Maier *et al.*, 2012; Peterhansel *et al.*, 2013a, b; Nölke *et al.*, 2014; Dalal *et al.*, 2015; Xin *et al.*, 2015; South and Ort, 2017; South *et al.*, 2018).

Electron transport

Manipulation of the photosynthetic electron transport chain is another potential option for improving photosynthetic carbon assimilation and yield (see Fig. 3). The first demonstration that increases in electron transport can drive improvements in plant growth came from Chida *et al.* (2007). These authors showed that the expression of the algal (*Porphyra yezoensis*) cytochrome (Cyt) *c*₆ in the chloroplasts of Arabidopsis leads to an increase in chlorophyll and starch content as well as an increase in ATP and NADPH. These changes were accompanied by an increase in CO₂ assimilation, efficiency of photosynthetic electron transport, and biomass (Chida *et al.*, 2007). In cyanobacteria and green algae, Cyt *c*₆ has been shown to replace plastocyanin as an electron transporter in response to copper deficiency (Merchant and Bogorad, 1987). Chida *et al.* (2007) also demonstrated that algal Cyt *c*₆ can transfer electrons from the Cyt *b*₆*f* complex to Arabidopsis PSI *in vivo* and at a faster rate than Arabidopsis's native plastocyanin (Table 2). Similar results were also observed when the Cyt *c*₆ from *Ulva fasciata* was overexpressed in tobacco (Yadav *et al.*, 2018). These authors observed an increase in photosynthetic rates, improved water use efficiency, and increased growth compared with controls (Table 2).

The cytochrome *b*₆*f* complex

The Cyt *b*₆*f* complex is a central component of photosynthetic electron transport and is located in the thylakoid membrane where it acts in both cyclic and linear electron transport mediating electron flow between PSII and PSI, providing ATP and NADPH for photosynthetic carbon fixation by oxidizing PQH₂, and reducing plastocyanin (Kurusu *et al.*, 2003; Cramer *et al.*, 2006, 2011; Tikhonov, 2014). The complex is composed of eight different subunits, two encoded in the nucleus [PetC (Rieske FeS) and PetM] and the remaining six [PetA (Cyt *f*), PetB (Cyt *b*₆), PetD, PetG, PetL, and PetN] in the chloroplast genome (Willey and Gray, 1988; Anderson, 1992; Hurry *et al.*, 1996; Knight *et al.*, 2002; Cramer and Zhang, 2006; Cramer *et al.*, 2006; Baniulis *et al.*, 2009; Schöttler *et al.*, 2015). This protein complex also

Table 2. Summary of single targeted manipulations of photorespiration, electron transport, and putative carbon transport and their biological outcomes

Manipulation	Transgene expressed	Plant	Functional description	Biomass and yield	References
Photorespiration	Glycine decarboxylase H-protein	Arabidopsis	Tissue-specific expression. 19% increase in CO ₂ assimilation and elevated photosynthetic electron transport rates compared with controls	50% increase in dry weight, no increase in seed yield	Simkin et al. (2017a), ^a Timm et al. (2012) ^a
		Tobacco	Tissue-specific expression. Increase in GDC-H protein content. Photosynthetic CO ₂ assimilation rates are increased. Damage to PSII by photorespiratory stress is reduced	13–38% increase in dry weight	López-Calcano et al. (2018) ^{b,c}
		Tobacco	Constitutive expression. Protein accumulated to 3.6- to 7-fold higher in constitutively expressing plants compared with tissue-specific expression	Over 50% reduction in leaf area throughout the early growth phase	López-Calcano et al. (2018) ^b
	Glycine decarboxylase L-protein Glycine decarboxylase T-protein	Arabidopsis	Tissue specific expression. Have high sucrose fructose and maltose contents. Increased rates of photorespiration and CO ₂ were observed	19–47% increase in dry weight	Timm et al. (2015) ^a
		Arabidopsis	No alterations in photosynthetic CO ₂ uptake	No increase in plant growth	Timm et al. (2018) ^a
Electron transport	Algal Cyt c ₆	Arabidopsis	Constitutive expression. 31% increase in CO ₂ assimilation rates	30% increase in plant size	Chida et al. (2007) ^a
		Tobacco	Constitutive expression. Higher photosynthetic/ electron transport rates and improved water use efficiency. Significant increases in chlorophyll and carotenoid content	Increased biomass	Yadav et al. (2018) ^a
	Rieske FeS	Arabidopsis	Constitutive expression. Up to 30% increase in CO ₂ assimilation, elevated photosynthetic electron transport rates compared with controls. Significant increases in chlorophyll and carotenoid content	29–72% increase in dry weight and up to 51% increase in seeds yield in some lines	Simkin et al. (2017b) ^a
Carbon transport	Cyanobacterial inorganic carbon transporter B	Arabidopsis	Constitutive expression. Significantly higher photosynthetic rates	Approximately 23% increase in biomass at low humidity	Lieman-Hurwitz et al. (2003, 2005) ^a
		Tobacco	Constitutive expression. 20–28% increase in CO ₂ assimilation rates	71% increase in biomass	Simkin et al. (2015) ^b
		Rice	Constitutive expression. 18% increase in CO ₂ assimilation	17.9% increase in biomass and increased plant height	Gong et al. (2015) ^c
		Soybean	Constitutive expression. Approximately 7–20% increases in photosynthetic CO ₂ uptake	In ambient CO ₂ , a 30% increase in dry weight and a 30% increase in seed yield, Up to 35% increase in dry weight and 6% increase in seed mass in elevated CO ₂	Hay et al. (2017) ^{b,c}

Transgenes were under the control of either photosynthetic tissue-specific promoters or a constitutive promoter. Growth conditions are indicated: ^a controlled environmental conditions; ^b greenhouse; ^c field experiments.

functions as a dimer, enhancing its complexity. The trans-membrane domains of the cyt *b₆* and Rieske FeS proteins are involved in the monomer–monomer interaction of the complex, and the PetD gene product functions as a scaffold, giving these three proteins an important role in the stability of the complex (Hager et al., 1999; Cramer et al., 2006; Schwenkert et al., 2007; Hojka et al., 2014). The PetG, PetN, and PetM subunits have also been shown to have essential roles in both the assembly and stability of the Cyt *b₆f* complex, with the *PetL* gene product assigned a minor role in its stability (Bruce and Malkin, 1991; Kuras and Wollman, 1994; Hager et al., 1999; Hojka et al., 2014; Monde et al., 2000; Schöttler et al., 2007; Schwenkert et al., 2007).

Previous studies have shown that by reducing the accumulation of the Rieske FeS protein, it is possible to manipulate the levels of the Cyt *b₆f* complex (Price et al., 1998; Yamori et al., 2011b). First, Cyt *b₆f* inhibitors were used (Kirchhoff et al., 2000), and then antisense studies suppressing the Rieske FeS protein (PetC) have shown that the Cyt *b₆f* complex is a key determinant of the electron transport rate (Price et al., 1995, 1998; Hurry et al., 1996; Anderson et al., 1997; Ruuska et al., 2000; Yamori et al., 2011a, b). Antisense studies have shown

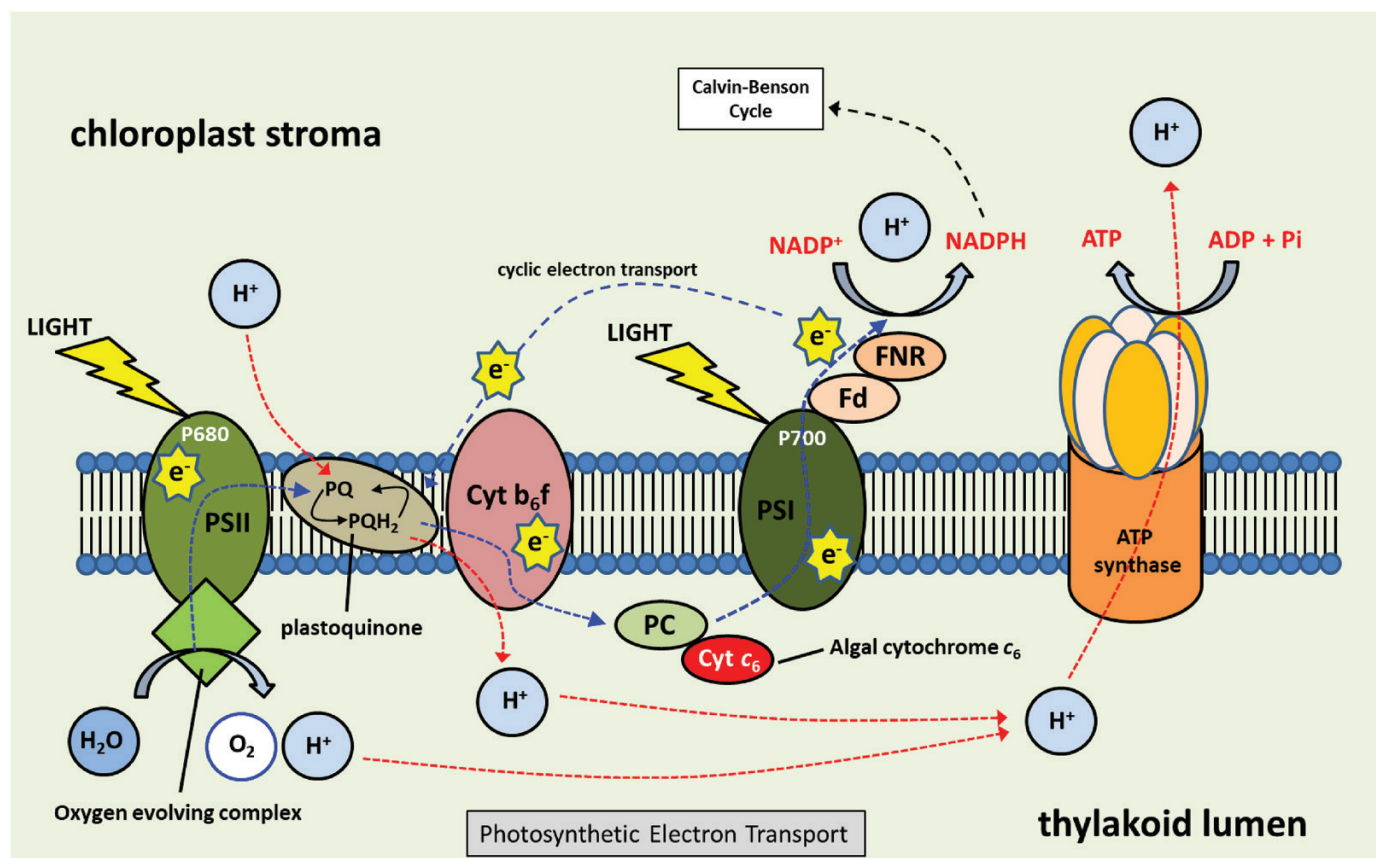


Fig. 3. Schematic representation of photosynthetic electron transport. Ferredoxin (Fd), ferredoxin-NADP reductase (FNR), cytochrome *b₆f* complex (Cyt *b₆f*), plastocyanin (PC), cytochrome *c₆* (Cyt *c₆*).

that a decrease in the accumulation of the Rieske FeS protein results in a decrease in photosynthetic electron transport and a reduction in biomass and seed yield (Price *et al.*, 1998; Yamori *et al.*, 2011b, 2016). Plants with reduced levels of the Rieske FeS protein were also shown to have a lower Chl *a/b* ratio (Hurry *et al.*, 1996; Price *et al.*, 1998), reduced levels of the ATP synthase complex, and a reduction in the transthylakoid pH gradient (Price *et al.*, 1995; Ruuska *et al.*, 2000).

These findings suggested that the electron transport chain, and specifically the Cyt *b₆f* complex, is a limiting step in photosynthetic carbon assimilation and that increasing electron transport could increase photosynthesis and yields. Recognized as a potential target for increasing photosynthetic electron transport, the feasibility of manipulating a membrane-located multiprotein complex has been questioned. In addition to structural complexity of the Cyt *b₆f* complex, the Rieske FeS protein has been shown to be one of the subunits needed for stable assembly of the Cyt *b₆f* complex (Miles, 1982; Metz *et al.*, 1983; Barkan *et al.*, 1986; Anderson *et al.*, 1997), therefore the overexpression of the Rieske FeS protein is a potential route for improving photosynthetic electron flow through the Cyt *b₆f* complex. This was demonstrated by the overexpression of the Rieske FeS protein in *Arabidopsis* where it was shown to lead to substantial increases in CO₂ assimilation and relative electron transport rates, and, importantly, to contribute to a 27–72% increase in biomass and up to a 51% increase in seed yield (Simkin *et al.*, 2017b) (Table 2). These authors

demonstrated using chlorophyll fluorescence imaging and dual-PAM measurements that overexpression of the Rieske FeS protein resulted in an increase in the potential quantum yield of PSII and PSI photochemistry (Genty *et al.*, 1989, 1992; Baker, 2008) from the early stages of development; and that final increases in leaf area evident in mature plants are probably due to a combination of increased photosynthesis and an increase in light capture due to the greater leaf area (Simkin *et al.*, 2017b). These data also showed an increase in the fraction of PSII centres available for photochemistry due to observed increases in *q_L* and a lower 1–*q_p* (Baker *et al.*, 2007). The overexpression of Rieske FeS protein led to an increase in the levels of the two core proteins of the Cyt *b₆f* complex, Cyt *b₆* and Cyt *f*, as well as an increase in proteins associated with PSI (LhcaI, PsaA) and PSII (PsbA, PsbD) and the ATP synthase delta subunit (AtpD). Interestingly, a recent study using *Arabidopsis* reported increases in Cyt *b₆f* complex proteins in plants grown under square wave light compared with plants grown under fluctuating light. These increases in Rieske FeS, Cyt *b₆*, and Cyt *f* proteins were also accompanied by increases in PSI/PSII proteins LhcaI, PsaA, PsbA, PsbD, and AtpD (Violet-Chabrand *et al.*, 2017). Furthermore, the *hcf* mutant, in which the biogenesis of the Cyt *b₆f* is reduced, was shown to have a decrease in components of both PSI and PSII (Lennartz *et al.*, 2001). HCF164 encodes a thioredoxin (Trx)-like protein, anchored to the luminal side of the thylakoid membrane where it functions as a disulphide oxidoreductase. These studies

imply that some as yet unknown mechanism ties changes in electron transport proteins to changes in PSI and PSII proteins. A chloroplast-localized RNA-binding protein (PBR1) has been shown recently to play a role in co-ordinating the biogenesis of the PSI, Cyt *b₆f*, and the NDH complexes (Yang *et al.*, 2016), providing further support for this hypothesis. This co-ordination of regulation requires further study to elucidate the mechanism behind it.

Multitarget manipulation of photosynthetic carbon assimilation

It has been shown previously that increasing the activity of SBPase and FBPA in transgenic tobacco resulted in an increase in carbon assimilation and biomass yield (Lefebvre *et al.*, 2005; Uematsu *et al.*, 2012; Simkin *et al.*, 2015). More recently, Simkin *et al.* (2015) demonstrated that the simultaneous overexpression of SBPase and FBPA in tobacco resulted in a cumulative increase in biomass (+62% compared with +34% in SBPase alone). This was the first demonstration that multigene manipulation of the C_3 pathway can lead to greater increases in yield compared with single manipulations. However, in a parallel study in Arabidopsis, no such cumulative impact was observed when SBPase and FBPA were co-expressed (Simkin *et al.*, 2017a). These differing results between tobacco and Arabidopsis show that manipulation of the C_3 pathway may be species dependent, and specific targeted manipulations may need to be identified for different crop plants.

Simultaneous manipulation of the Calvin–Benson cycle and expression of ictB

It has also been shown that combining the overexpression of CB enzymes (SBPase and FBPA) with the expression of the putative inorganic carbon transporter B (ictB:YP399376) from cyanobacterium *Synechococcus* sp. PCC 7942 (Bonfil *et al.*, 1998; Kaplan and Reinhold, 1999) resulted in a cumulative increase in biomass yield as compared with SBPase, FBPA, or ictB alone. The ictB protein was originally proposed to be involved in HCO_3^- accumulation; however, subsequent work demonstrated that ictB is not a HCO_3^- transporter and its true function remains unknown (Xu *et al.*, 2008; Price *et al.*, 2013). Interestingly, the transformation of ictB into Arabidopsis and tobacco has resulted in significantly faster photosynthetic rates at limiting CO_2 levels (Kaplan *et al.*, 2001; Lieman-Hurwitz *et al.*, 2003, 2005). Arabidopsis plants expressing ictB from *Anabaena* sp. PCC 7120 showed a similar phenotype (Lieman-Hurwitz *et al.*, 2005), further demonstrating that ictB could significantly alter carbon assimilation rates. Growth experiments further demonstrated that plants expressing ictB grew significantly faster than wild-type plants under low humidity. Lieman-Hurwitz and colleagues proposed that ictB enhances photosynthesis and growth in transgenic Arabidopsis plants due to a higher internal CO_2 concentration around Rubisco resulting in higher enzyme activity (Lieman-Hurwitz *et al.*, 2003). In rice, the expression of ictB resulted in an 18.4% increase in photosynthetic carbon assimilation and enhanced mesophyll

conductance; however, no significant increases in biomass, tiller number, grain number, or grain weight were observed (Gong *et al.*, 2015). The expression of ictB in soybean (*Glycine max* cv. Thorne) was also shown to increase photosynthetic CO_2 assimilation significantly in both greenhouse and field trials. Plants also showed an increase in biomass production under drought conditions (Hay *et al.*, 2017). Although the function of ictB has not been shown *in planta*, Simkin *et al.* (2015) further demonstrated that the expression of ictB in greenhouse-grown tobacco could result in increases in the maximum rate of CO_2 assimilation, Rubisco carboxylation ($V_{c_{max}}$), electron transport (J_{max}), and biomass yield (+71%) compared with controls grown under the same conditions. The analysis of the expression of ictB showed no evidence to support the hypothesis that the stimulation of the carboxylation reaction of Rubisco was the sole cause of the observed increases in photosynthetic rates given that transgenic plants with increased levels of FBPA and SBPase had similar A/C_i curves to ictB-expressing lines (Simkin *et al.*, 2015).

Although the cumulative effect of the co-expression of ictB with either SBPase or SBPase+FBPA was clear in the biomass data set, no cumulative enhancement of photosynthesis was detected in these plants (Simkin *et al.*, 2015). It should be noted that the analysis of photosynthetic rates in these plants was carried out at a single time point and that the speed of changes during a diurnal period, or at specific times of day, may be greater and cumulative over time in plants expressing multiple transgenes compared with plants expressing ictB alone. This, however, remains to be investigated. The combined expression of ictB with the bifunctional cyFBP/SBPase in rice also resulted in a cumulative increase in photosynthetic rates, tiller number, grain number, or grain weight compared with plants expressing either ictB or cyFBP/SBPase alone (Gong *et al.*, 2015).

Simultaneous manipulation of the Calvin–Benson cycle and photorespiration

In response to the positive impact of increasing photorespiration in photosynthetic tissue on plant growth in Arabidopsis and tobacco, Simkin *et al.* (2017a) explored the possibility that simultaneously increasing photorespiration by overexpression of the GCS H-protein and increasing the activity of two enzymes from the CB cycle (SBPase and FBPA) could have a cumulative impact on photosynthetic efficiency and yield (Simkin *et al.*, 2017a). In this work, plants expressing SBPase, FBPA, and GCS H-protein either alone or in combination were evaluated. This study revealed that the simultaneous manipulation of photorespiration and the CB cycle results in a synergistic positive impact on biomass yield under low and high light (Simkin *et al.*, 2017a). Interestingly, manipulation of the photorespiratory pathway alone resulted in an increase in biomass yield, but in these plants no increase in seed yield was evident. This is in contrast to results obtained in plants overexpressing CB enzymes where an increase in both biomass and seed yield (+20–39%) was observed. Moreover, simultaneous manipulation of the CB cycle and photorespiratory pathways resulted in a synergistic increase in seed yield (+62%)

compared with plants overexpressing CB enzymes alone (Simkin *et al.*, 2017a). The reasons for these differential effects on seeds yield are unclear given that plants were grown under the same conditions in a randomized grouping. However, it has been suggested that changes in carbon source/sink allocation lead to changes in starch and sucrose levels observed in GCS H-protein-overexpressing lines (Timm *et al.*, 2012; Simkin *et al.*, 2017a). These results further highlight the need to evaluate independent and multitargeted manipulations in different plant species to identify the specific targets to improve crop yields.

Unexpected outcomes of targeted manipulations

Although this review highlights a number of successes in improving photosynthesis, it should also be noted that not all manipulations have led to beneficial or desired outcomes. Recent work in tobacco carried out by Khozaei *et al.* (2015) showed that constitutive overexpression of the CB cycle enzyme TK led to a negative effect on plant growth and resulted in leaf chlorosis (Table 1). Plants overexpressing both TK and SBPase also demonstrated a mottled phenotype and restricted growth, indicating that overexpressing SBPase in conjunction with TK is not sufficient to overcome the phenotype observed in TK-overexpressing lines (CAR, unpublished data). Furthermore, the overexpression of TK in rice (+80 to 94%), either alone or in combination with the overexpression of Rubisco, did not lead to an increase in photosynthesis or an increase in biomass (Suzuki *et al.*, 2017). The results obtained here have also been observed in cyanobacteria (Liang and Lindblad, 2016). In cyanobacteria, increasing SBPase and FBPase activity has been shown to increase biomass, whilst the overexpression of TK resulted in a chlorotic phenotype, consistent with the observations in tobacco (Liang and Lindblad, 2016). Another example of unexpected outcomes is the constitutive overexpression of the GCS H-protein. In three previous studies, it was demonstrated that the tissue-specific overexpression of the GCS H-protein resulted in an increase in photosynthetic efficiency and in biomass (Timm *et al.*, 2012; Simkin *et al.*, 2017a; López-Calcano *et al.*, 2018). However, López-Calcano *et al.* (2018) also demonstrated that the constitutive overexpression of the H-protein resulted in a reduction in growth and biomass, with young plants displaying a >50% decrease in leaf area (Table 2). Constitutive overexpression of the GCS H-protein also resulted in a significant decrease in glucose, sucrose, and fructose (59, 24, and 25%, respectively) and a significant increase in starch (39%). Finally, the expression of the bifunctional cyFBP/SBPase in soya led to a significant decrease in seed yield under ambient CO₂ and elevated temperature compared with the WT (Table 1; Köhler *et al.*, 2017). However, in this instance, under elevated CO₂ and elevated temperature, seed yield was maintained whilst the WT showed an 11–22% decrease, indicating that the manipulation of photosynthesis can result in both positive and negative impacts depending on growth conditions.

Improving the efficiency of responses to the fluctuating light environment

In nature, plants must be able to respond to fluctuations in light intensity that take place over time periods ranging from seconds to minutes. In the short term, these changes are modulated by a series of regulatory processes, which must allow for a rapid shift from a low to a high photosynthetic rate (Athanasίου *et al.*, 2010; Alter *et al.*, 2012; Kono and Terashima, 2014; Kaiser *et al.*, 2016, 2018a; Yamori, 2016; Violet-Chabrand *et al.*, 2017; Matthews *et al.*, 2018). It has been shown that under fluctuating light conditions, photosynthesis can be limited during transitions from low to high light and from high to low light. The time taken for photosynthesis to reach steady state following a change in light availability can be between a few minutes and >30 min, dependent on the duration and magnitude of the change regardless of whether there were increases or reductions in light level. Therefore, manipulating electron transport and the CB cycle to enable a rapid response to fluctuations in light availability has the potential to improve crop yield (Lawson *et al.*, 2012; Violet-Chabrand *et al.*, 2017; Kaiser *et al.*, 2018b; Slattery *et al.*, 2018). Two regulatory processes known to impact on responses to fluctuating light are down-regulation of electron transport and light activation of the enzymes of the CB cycle. Below we present some of the current evidence, which highlights the potential of manipulating these processes to increase photosynthetic efficiency.

The dissipation of excess energy through non-photochemical quenching

Non-photochemical quenching (NPQ), or the dissipation of excess energy in the form of heat, is an important strategy for photoprotection. When the levels of light absorbed by a leaf exceed the leaf's assimilatory capacity, there is a decrease in the proton conductance of the chloroplast ATPase that rapidly results in a significant decrease in thylakoid lumen pH (Kanazawa and Kramer, 2002; Takizawa *et al.*, 2008). This change in pH activates qE (Horton *et al.*, 1996; Müller *et al.*, 2001), which is able to protect the photosynthetic apparatus over short-term fluctuations in light intensity by dissipating the excess absorbed light energy as heat (Grasses *et al.*, 2002; Külheim *et al.*, 2002; Li *et al.*, 2002). The process of NPQ involves the activation of the xanthophyll cycle, which is dependent on the activities of the enzymes violaxanthin de-epoxidase (VDE) and zeaxanthin epoxidase (ZEP) (Demmig-Adams and Adams, 1996), together with sensing of changes in the lumen pH by PsbS, a PSII protein. This process of induction occurs over a time scale of seconds to minutes and is independent of changes in gene expression (Li *et al.*, 2002, 2004). Although changes in NPQ are relatively rapid, they are not instantaneous. This is particularly noticeable in the rate of NPQ relaxation, which can lead to loss of potential photosynthetic capacity, as down-regulation of PSII continues even when light levels have returned to non-stress levels (Pérez-Bueno *et al.*, 2008). Recently, Kromdijk *et al.* (2016) modified both components of the NPQ system; increasing the amount of PsbS for pH sensing and the amount of ZEP and VDE for more rapid xanthophyll cycle kinetics.

These plants displayed a faster relaxation of NPQ and recovery of CO₂ fixation rate, and potentially higher photoprotection under excessive light conditions. This manipulation showed that without directly changing photosynthetic capacity, maximum carboxylation capacity ($V_{c_{max}}$), or ribulose biphosphate regeneration capacity (J_{max}), the overall CO₂ fixation of plants exposed to fluctuating light conditions could be improved. Furthermore, plants in these experiments showed a 14–20% increase in biomass under both glasshouse and field conditions (Kromdijk *et al.*, 2016).

Redox regulation of photosynthesis

The CB cycle is dependent on ATP and NADPH produced by the photosynthetic electron transport chain. It is thus of crucial importance that these two processes, the CB cycle and production of ATP and NADPH, are closely regulated in order to balance CO₂ fixation with the availability of energy from the light reactions to drive the CB cycle. One of the most important mechanisms to link these processes relies on a group of redox-sensitive molecules, the Trxs. In plants, Trxs were first identified during the 1970s (Wolosiuk and Buchanan, 1977; Buchanan *et al.*, 1979; Wolosiuk *et al.*, 1979; Buchanan, 1980, 1991), and the mechanisms of action of these molecules have been well characterized along with the enzymatic activities they modulate, which includes the CB cycle, the malate valve, and photorespiration (Buchanan and Balmer, 2005; Balsera *et al.*, 2014; Knesting and Scheibe, 2018; Nikkanen and Rintamäki, 2014; Schürmann, 2003; Schürmann and Buchanan, 2008; Yoshida and Hisabori, 2017). Four types of typical Trxs are reported for chloroplasts, Trx *f*, *m*, *x*, and *y*. Trxs function by transmitting the redox signal from ferredoxin thioredoxin reductase (FTR) to target enzymes. It has been well described that Trx *f* and *m* reductively activate the CB cycle enzymes phosphoribulokinase (PRK), NADP-glyceraldehyde-3-phosphate dehydrogenase (GAPDH), FBPase, and SBPase (Buchanan, 1980; Laing *et al.*, 1981; Wirtz *et al.*, 1982; Crawford *et al.*, 1989; Scheibe, 1991; Geiger and Servaites, 1994; Hutchison *et al.*, 2000; Schürmann and Jacquot, 2000; Howard *et al.*, 2008; Schürmann and Buchanan, 2008; Michelet *et al.*, 2013; Naranjo *et al.*, 2016). The mechanism of dark deactivation of these enzymes on the other hand is not yet well understood, and has not been exploited for improving photosynthesis. Nevertheless, a recently published study suggests that a stroma-localized atypical Trx from Arabidopsis, designated Trx-like2 (TrxL2), could be responsible for oxidatively deactivating the CB enzymes. This might be a novel target to explore if manipulation of this process can impact photosynthetic efficiency (Yoshida *et al.*, 2018).

A chloroplast NADPH-dependent thioredoxin reductase (NTRC) has also been described as an important player in stress and oxidative damage responses (Serrato *et al.*, 2004; Pérez-Ruiz *et al.*, 2006). Like Trxs, the NTRC can interact with a number of enzymes in the chloroplast including CB cycle enzymes; additionally, it can interact with 2-Cys peroxiredoxins and Trxs, and is activated by both light and NADPH produced in the oxidative pentose phosphate pathway. Given their similarities, it is not surprising that Trx and NTRC have been proposed

to have some overlapping functions (Thormählen *et al.*, 2015; Nikkanen *et al.*, 2016).

Although these regulatory mechanisms enable the light activation of the CB cycle, they also impose a limitation as the activation process of Rubisco and the other enzymes of the CB cycle is slower than the change in environmental conditions. Reducing the time it takes to reach maximum steady-state photosynthesis could have a significant impact on the CO₂ assimilated over the life of every leaf, particularly when considering how dynamic light incidence can be in plant canopies in field settings (Chazdon and Pearcy, 1986a, b; Krall *et al.*, 1995; Tinoco-Janguren and Pearcy, 1995; Lawson *et al.*, 2012; Taylor and Long, 2017).

Limitations imposed by the rate of Rubisco activation are of particular importance in photosynthetic induction (Sage *et al.*, 1987; Hammond *et al.*, 1998; Soleh *et al.*, 2016); a large number of studies have focused on understanding Rubisco and its activation by Rubisco activase (Rca) (Portis and Parry, 2007; Portis *et al.*, 2008; Carmo-Silva *et al.*, 2015). Full activation of Rubisco can take up to 30 min when plants are transferred from the dark into light and, although activation of the remaining CB cycle enzymes via the Trx system occurs more rapidly than for Rubisco, it can still take between 1 min and 10 min. The consequences of these delays in activation of the CB cycle enzymes is that they cause a lag in the time taken for photosynthesis to reach maximum steady-state levels. The impact of this will depend on the magnitude and duration of shade flecks in the natural light environment.

More recently, the consequences of this delay in activation have been shown *in vivo* during sun transitions, where Rubisco activation could limit photosynthesis resulting in a reduction of 20% in carbon assimilation, which over the season could impact substantially on yield (Taylor and Long, 2017). This light activation of Rubisco is in part mediated by the action of activase, and evidence to suggest that this may provide a target to improve this response has come from overexpression studies, which have led to a more rapid Rubisco activation (Table 3) (Fukayama *et al.*, 2012; Yamori *et al.*, 2012). Additionally, enhancing the thermostability of Rca in Arabidopsis has been shown to improve CO₂ assimilation rates and plant growth under heat stress (Kurek *et al.*, 2007; Kumar *et al.*, 2009). It is possible that optimizing Rca in both amount and regulation has the potential to decrease the limitations in photosynthesis due to Rubisco activation under a fluctuating light environment.

A relatively unexplored strategy for increasing photosynthetic carbon assimilation is by directly targeting Trx with the aim of modulating the redox regulation of the Trx-regulated enzymes more rapidly. As reviewed recently by Nikkanen *et al.* (2017), overexpression of Trx *f* or NTRC (Table 3) has been suggested as a viable strategy for increasing productivity. Increased levels of TRX *f* in tobacco have been shown to lead to increases in specific leaf weight, starch, and sugars under both ambient and increased CO₂ conditions (Sanz-Barrio *et al.*, 2013; Farran *et al.*, 2014; Aranjuelo *et al.*, 2015). Under glasshouse conditions, overexpression of Trx *f* has led to an increase of 1.7-fold in biomass and up to 5.5 times the amount of fermentable carbohydrates, specifically seven times the amount of

Table 3. Summary of manipulations in Calvin–Benson cycle regulatory mechanisms

Manipulation	Gene targeted	Plant	Manipulation detail	Phenotype	References
Regulatory proteins	Rca ^d	Rice	Tissue-specific expression of the barley Rca	Reduction in Rubisco amount Reduction in CO ₂ assimilation Increased rate of photosynthetic induction by light	Fukayama <i>et al.</i> (2012) ^b
		Rice	Tissue-specific expression of the maize Rca	Increased rate of photosynthetic induction by light Increased rate of Rubisco activation at high temperature (40 °C)	Yamori <i>et al.</i> (2012) ^a
		Arabidopsis	Constitutive expression of a thermostable Rca isoform	Increased rate of Rubisco activation Increased CO ₂ assimilation, biomass, and seed yield at high temperature	Kurek <i>et al.</i> (2007) ^a
		Arabidopsis	Tissue-specific expression of chimeric Rca	Increased rate of Rubisco activation Increased CO ₂ assimilation, biomass, and seed yield at high temperature	Kumar <i>et al.</i> (2009) ^a
	CP12	Tobacco	Antisense down-regulation of CP12 gene family	Reductions in PRK and GAPDH activity Reduced photosynthetic CO ₂ assimilation Reductions in biomass	Howard <i>et al.</i> , 2011a, c) ^b
		Arabidopsis	KO of <i>cp12-1</i> and <i>cp12-3</i> plus reductions of expression of <i>cp12-2</i> below 20% of WT levels	80% reductions in PRK levels Reduced photosynthetic CO ₂ assimilation Over 50% reductions in biomass	Lopez-Calcano <i>et al.</i> (2017) ^a
		Aublet	Constitutive expression of CP12	Increased biomass, photosynthetic rates, GAPDH, and PRK activities Increased survival, and reduced ion leakage after chilling treatment	Li <i>et al.</i> (2018) ^b
		Aublet	Reduced CP12 expression	Reduced biomass, photosynthetic rates, GAPDH, and PRK activities Reduced survival, and increased ion leakage after chilling treatment	Li <i>et al.</i> (2018) ^b
	Trx <i>f</i>	Tobacco	Plastidial expression of Trx <i>f</i>	Up to 21% increase in specific leaf weight Up to 5.5-fold increase in fermentable carbohydrates per unit dry weight Lower photorespiration rate	Sanz-Barrio <i>et al.</i> (2013) ^a ; Farran <i>et al.</i> (2014) ^c ; Aranjuelo <i>et al.</i> (2015) ^a
				42–263% increase in dry weight Increased starch Increased photosynthesis Enhanced tolerance to photo-oxidative and drought stresses	Toivola <i>et al.</i> (2013) ^a ; Nikkanen <i>et al.</i> (2016) ^a ; Kim <i>et al.</i> (2017) ^a
	NTRC	Arabidopsis	Constitutive expression of NTRC	90% reductions in growth	Toivola <i>et al.</i> (2013) ^a
			Null mutant		

Transgenes were under the control of either photosynthetic tissue-specific promoters or a constitutive promoter.

Growth conditions are indicated: ^a controlled environmental conditions; ^b greenhouse; ^c field experiments.

^d For an exhaustive list of manipulations of Rca *in vivo*, see Carmo-Silva *et al.* (2015).

starch and twice as much sucrose is present in the WT at the end of the growth cycle (Sanz-Barrio *et al.*, 2013). The accumulation of these carbohydrates provides an opportunity to use these plants for production of biofuel. Enzymatic hydrolysis that co-hydrolyse both starch and structural carbohydrates were carried out using both the WT and TRX *f* overexpressors and significant increases in glucose and fructose were found in the Trx plants which, if used for bio-ethanol production, would lead to estimated ethanol yields of almost 10-fold that of WT plants (Sanz-Barrio *et al.*, 2013). Contrastingly, increases in biomass were not reported for field-grown plants, although

Trx *f*-overexpressing plants still displayed increased specific leaf weight (>20% compared with the WT), and increases in both starch and soluble sugars of up to 3.6- and 1.7-fold, respectively (Farran *et al.*, 2014). The increase in starch level was also maintained under high CO₂ conditions (Aranjuelo *et al.*, 2015). Despite these changes, this manipulation did not lead to detectable increases in photosynthetic rates under current CO₂ levels, and a decrease in *J*_{max} was reported under elevated CO₂. This may suggest that the changes in carbohydrate accumulation was due to altered allocation rather than an increase in total carbon captured.

Overexpression of NTRC has also been shown to be beneficial for productivity, leading to increases in starch, photosynthesis, and biomass in Arabidopsis. Photosynthetic quantum yield of CO₂ assimilation under light intensities limiting photosynthesis and light-saturated CO₂ fixation rate were ~20% higher in NTRC overexpressors. The biomass increases in the NTRC-overexpressing Arabidopsis plants was between 2- and 2.5-fold in plants grown in long and short days, respectively, under 600 $\mu\text{mol m}^{-2} \text{s}^{-1}$ light (no significant difference in biomass was observed when plants were grown at 130 $\mu\text{mol m}^{-2} \text{s}^{-1}$ light) (Toivola *et al.*, 2013; Nikkanen *et al.*, 2016). Additionally, overexpression of NTRC has been reported to enhance tolerance to oxidative and drought stresses, which are traits of great importance when improving crops for field conditions (Kim *et al.*, 2017).

Another mechanism for redox regulation of the CB cycle is the activation and deactivation of the enzymes PRK and GAPDH through the formation and breakdown of the GAPDH/CP12/PRK complex (Pohlmeyer *et al.*, 1996; Wedel *et al.*, 1997; Scheibe *et al.*, 2002; Graciet *et al.*, 2003, 2004; Boggetto *et al.*, 2007; Carmo-Silva *et al.*, 2011; Howard *et al.*, 2011b), which is also dependent on Trxs (Trost *et al.*, 2006; Marri *et al.*, 2009). This complex has been studied extensively *in vitro* (Avilan *et al.*, 2000; Marri *et al.*, 2005, 2009, 2010) and has also been shown to operate *in vivo* as a response to changes in light availability, modulating the deactivation and activation of PRK and GAPDH enzymes more rapidly than by the sole action of Trxs in higher plants (Howard *et al.*, 2008). This mechanism is so effective that studies have proposed that cyanophages have sequestered it and used it to inhibit the CB cycle and redirect carbon flux from this pathway into the pentose phosphate pathway by expressing a CP12 gene in its host (Thompson *et al.*, 2011). Antisense and mutant studies in higher plants have shown that loss of this protein results in lower photosynthetic rates, slow growth, low GAPDH, PRK, and NADP-MDH, activities and reduced levels of PRK protein (Table 3) (Howard *et al.*, 2011a, c; López-Calcano *et al.*, 2017). *In vitro* and *in vivo* studies have proposed CP12 as a potential chaperone for GAPDH and PRK, preventing heat-induced aggregation and deactivation, and providing protecting against oxidative stress and degradation (Erales *et al.*, 2009; Marri *et al.*, 2014; López-Calcano *et al.*, 2017). Additionally, it was recently reported that CP12 expression might be linked to increased chilling tolerance (Li *et al.*, 2018). This growing body of evidence indicates that the CP12 protein might have other important roles in regulation and maintenance of photosynthesis or even wider metabolism. If regulation of photosynthetic carbon assimilation is to be fully understood, special attention should be paid to this small unstructured protein (Gontero and Maberly, 2012; López-Calcano *et al.*, 2014). Moreover, studies have shown how the enzymes of the CB cycle are also targets of nitrosylation and glutathionylation, two redox post-translational mechanisms (PTMs) whose importance in signalling and regulation has begun to be recognized in the last decade (Meyer *et al.*, 2008; Zaffagnini *et al.*, 2012; Michelet *et al.*, 2013; Rouhier *et al.*, 2015).

Although the regulation of photosynthesis has received attention (Heyneke and Fernie, 2018), it has not been thoroughly

exploited for the realization of increased yield potential, and there is still a gap in the knowledge of the fine detail and speed of Trx-mediated redox regulation of photosynthesis. Nevertheless, given the results observed with overexpression of Trx*f* and NTRC, it would be interesting to investigate whether it would be possible to optimize some of these other redox regulatory mechanisms for increased yield under modern agricultural conditions. One aspect to keep in mind though, given the high diversity and heterogeneity described between CP12, PRK, and GAPDH interactions (Howard *et al.*, 2011b), is that it will be important to test these strategies on a species-specific basis as evidence would suggest that the regulatory mechanisms to which the CB proteins are subjected, vary in significance between species, and successful strategies in one species might not necessarily work on another.

Conclusions and further opportunities

Although the potential for improving yield through single and multigene manipulation of different processes in photosynthesis has been clearly demonstrated, it is unlikely that these alone will provide the large increases in yield under all conditions and in all crops species needed to provide for our growing population in the changing global environment. Going forward, what additional approaches will be required to achieve the increase in yield needed to sustain the growing human population? In addition to the targets discussed in this review, it is likely that it will be necessary to stack a number of different traits targeting photosynthesis. This would include, for example, speeding up relaxation of NPQ and reducing photorespiratory losses by introducing new biosynthetic routes to short-circuit this process. The focus of this review has been on photosynthesis, which provides an increase in source capacity, but it is also likely that it will be essential to consider the sink status of the plants where the source capacity has been increased. The source/sink balance has been the subject of two recent papers, and the potential for combining improvements in both source and sink capacities was highlighted (Chang *et al.*, 2017; Sonnewald and Fernie, 2018). Improving photosynthesis is an approach which targets increasing yield potential, but it will also be necessary to close the yield gap in order to provide resilience, and this will need improvement in water use efficiency (WUE), nitrogen use efficiency (NUE), and response to biotic and abiotic stresses. Some advances are also happening in these areas. One example is the recently published work showing how changes in the amount of PsbS protein result in changes in the redox state of Q_A (Glowacka *et al.*, 2018). Changes in the oxidation state of the plastoquinone pool have been proposed to be able to control stomatal movement (Busch, 2014), and the PsbS transgenics experiments showed a linear relationship between stomatal conductance and Q_A redox values, decreasing stomatal opening in response to light and increasing WUE. Furthermore, attempts to improve NUE via the overexpression of glutamine synthetase, which resulted in increased biomass and grain yield, in a number of different plants including tobacco, wheat, and rice have been reported (Wallsgrove *et al.*, 1980; Hoshida *et al.*, 2000; Migge *et al.*, 2000; Fuentes *et al.*, 2001; Habash *et al.*,

2001; Oliveira *et al.*, 2002). A number of in-depth reviews of plant nitrogen cost of photosynthesis, nitrogen uptake, and remobilization have been published (Masclaux-Daubresse *et al.*, 2010; Evans and Clarke, 2018).

In order to achieve the ambitious goals required to feed the growing population, new approaches and technologies will be required including new breeding techniques such as genome editing approaches for endogenous genes modification (CRISPR/Cas9; Arora and Narula, 2017; Georges and Ray, 2017; Aglawe *et al.*, 2018; Wilson *et al.*, 2019, Preprint) and synthetic biology to produce designer promoters and proteins. The role of modelling in enabling novel targets to be identified will also be crucial given the complexity of the processes involved. To achieve the full potential of these opportunities, the use of new tools, which allow the quick, efficient, and cheap insertion of multiple transgenes into plants, will be paramount (Engler *et al.*, 2008, 2009, 2014; Marillonnet and Werner, 2015; Exposito-Rodriguez *et al.*, 2017), as will be the development of new promoters for use in crop plants, which are currently limited (Mukherjee *et al.*, 2015; Alotaibi *et al.*, 2018). If these opportunities are to be fully exploited, regulations governing the use of genetic modification and genome editing technologies will need to be reviewed.

Acknowledgements

AJS was supported by Realising Increased Photosynthetic Efficiency to Increase Wheat Yields (IWYP, BB/N021045/1) awarded to CAR (University of Essex). AJS and PELC were supported by the Realising Improved Photosynthetic Efficiency (RIPE) initiative awarded to CAR by the University of Illinois, USA. RIPE was possible through support from the Bill & Melinda Gates Foundation, FFAR and UKaid, grant OPP1172157.

Author contributions

AJS and PELC drafted and wrote the manuscript with input from CAR, who also edited the final version.

References

- Aglawe SB, Barbadikar KM, Mangrauthia SK, Madhav MS. 2018. New breeding technique 'genome editing' for crop improvement: applications, potentials and challenges. *3 Biotech* **8**, 336.
- Ainsworth EA, Long SP. 2005. What have we learned from 15 years of free-air CO₂ enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO₂. *New Phytologist* **165**, 351–371.
- Alotaibi SS, Sparks CA, Parry MAJ, Simkin AJ, Raines CA. 2018. Identification of leaf promoters for use in transgenic wheat. *Plants* **7**, 27.
- Alter P, Dreissen A, Luo FL, Matsubara S. 2012. Acclimatory responses of Arabidopsis to fluctuating light environment: comparison of different sunfleck regimes and accessions. *Photosynthesis Research* **113**, 221–237.
- Anderson JM. 1992. Cytochrome *b₆f* complex: dynamic molecular organization, function and acclimation. *Photosynthesis Research* **34**, 341–357.
- Anderson JM, Price GD, Chow WS, Hope AB, Badger MR. 1997. Reduced levels of cytochrome *bf* complex in transgenic tobacco leads to marked photochemical reduction of the plastoquinone pool, without significant change in acclimation to irradiance. *Photosynthesis Research* **53**, 215–227.
- Anderson LE. 1971. Chloroplast and cytoplasmic enzymes. II. Pea leaf triose phosphate isomerases. *Biochimica et Biophysica Acta* **235**, 237–244.
- Aranjuelo I, Tcherkez G, Jauregui I, Gilard F, Ancin M, Millan AFS, Larraya L, Veramendi J, Farran I. 2015. Alteration by thioredoxin f over-expression of primary carbon metabolism and its response to elevated CO₂ in tobacco (*Nicotiana tabacum* L.). *Environmental and Experimental Botany* **118**, 40–48.
- Arora L, Narula A. 2017. Gene editing and crop improvement using CRISPR–Cas9 system. *Frontiers in Plant Science* **8**, 1932.
- Athanasίου K, Dyson BC, Webster RE, Johnson GN. 2010. Dynamic acclimation of photosynthesis increases plant fitness in changing environments. *Plant Physiology* **152**, 366–373.
- Avilan L, Lebreton S, Gontero B. 2000. Thioredoxin activation of phosphoribulokinase in a bi-enzyme complex from *Chlamydomonas reinhardtii* chloroplasts. *Journal of Biological Chemistry* **275**, 9447–9451.
- Baker NR. 2008. Chlorophyll fluorescence: a probe of photosynthesis *in vivo*. *Annual Review of Plant Biology* **59**, 89–113.
- Baker NR, Harbinson J, Kramer DM. 2007. Determining the limitations and regulation of photosynthetic energy transduction in leaves. *Plant, Cell & Environment* **30**, 1107–1125.
- Balsera M, Uberegui E, Schürmann P, Buchanan BB. 2014. Evolutionary development of redox regulation in chloroplasts. *Antioxidants & Redox Signaling* **21**, 1327–1355.
- Baniulis D, Yamashita E, Whitelegge JP, Zatsman AI, Hendrich MP, Hasan SS, Ryan CM, Cramer WA. 2009. Structure–function, stability, and chemical modification of the cyanobacterial cytochrome *b₆f* complex from *Nostoc* sp. PCC 7120. *Journal of Biological Chemistry* **284**, 9861–9869.
- Barkan A, Miles D, Taylor WC. 1986. Chloroplast gene expression in nuclear, photosynthetic mutants of maize. *The EMBO Journal* **5**, 1421–1427.
- Bauwe H, Hagemann M, Fernie AR. 2010. Photorespiration: players, partners and origin. *Trends in Plant Science* **15**, 330–336.
- Bauwe H, Kolukisaoglu U. 2003. Genetic manipulation of glycine decarboxylation. *Journal of Experimental Botany* **54**, 1523–1535.
- Bi H, Dong X, Wu G, Wang M, Ai X. 2015. Decreased TK activity alters growth, yield and tolerance to low temperature and low light intensity in transgenic cucumber plants. *Plant Cell Reports* **34**, 345–354.
- Boggetto N, Gontero B, Maberly SC. 2007. Regulation of phosphoribulokinase and glyceraldehyde 3-phosphate dehydrogenase in a freshwater diatom, *Asterionella formosa*. *Journal of Phycology* **43**, 1227–1235.
- Bonfil DJ, Ronen-Tarazi M, Sültemeyer D, Lieman-Hurwitz J, Schatz D, Kaplan A. 1998. A putative HCO₃[−] transporter in the cyanobacterium *Synechococcus* sp. strain PCC 7942. *FEBS Letters* **430**, 236–240.
- Bowes G, Ogren WL, Hageman RH. 1971. Phosphoglycolate production catalyzed by ribulose diphosphate carboxylase. *Biochemical and Biophysical Research Communications* **45**, 716–722.
- Bruce BD, Malkin R. 1991. Biosynthesis of the chloroplast cytochrome *b₆f* complex: studies in a photosynthetic mutant of *Lemna*. *The Plant Cell* **3**, 203–212.
- Buchanan BB. 1980. Role of light in the regulation of chloroplast enzymes. *Annual Review of Plant Physiology and Plant Molecular Biology* **31**, 341–374.
- Buchanan BB. 1991. Regulation of CO₂ assimilation in oxygenic photosynthesis: the ferredoxin/thioredoxin system. Perspective on its discovery, present status, and future development. *Archives of Biochemistry and Biophysics* **288**, 1–9.
- Buchanan BB, Balmer Y. 2005. Redox regulation: a broadening horizon. *Annual Review of Plant Biology* **56**, 187–220.
- Buchanan BB, Wolosiuk RA, Schurmann P. 1979. Thioredoxin and enzyme regulation. *Trends in Biochemical Sciences* **4**, 93–96.
- Burney JA, Davis SJ, Lobell DB. 2010. Greenhouse gas mitigation by agricultural intensification. *Proceedings of the National Academy of Sciences, USA* **107**, 12052–12057.
- Busch FA. 2013. Current methods for estimating the rate of photorespiration in leaves. *Plant Biology* **15**, 648–655.
- Busch FA. 2014. Opinion: the red-light response of stomatal movement is sensed by the redox state of the photosynthetic electron transport chain. *Photosynthesis Research* **119**, 131–140.

- Bykova NV, Keerberg O, Pärnik T, Bauwe H, Gardeström P. 2005. Interaction between photorespiration and respiration in transgenic potato plants with antisense reduction in glycine decarboxylase. *Planta* **222**, 130–140.
- Calfapietra C, Gielen B, Galema AN, Lukac M, De Angelis P, Moscatelli MC, Ceulemans R, Scarascia-Mugnozza G. 2003. Free-air CO₂ enrichment (FACE) enhances biomass production in a short-rotation poplar plantation. *Tree Physiology* **23**, 805–814.
- Campbell WJ, Ogren WL. 1990. Glyoxylate inhibition of ribulosebiphosphate carboxylase/oxygenase activation in intact, lysed, and reconstituted chloroplasts. *Photosynthesis Research* **23**, 257–268.
- Carmo-Silva AE, Marri L, Spalla F, Salvucci ME. 2011. Isolation and compositional analysis of a CP12-associated complex of Calvin cycle enzymes from *Nicotiana tabacum*. *Protein and Peptide Letters* **18**, 618–624.
- Carmo-Silva E, Scales JC, Madgwick PJ, Parry MA. 2015. Optimizing Rubisco and its regulation for greater resource use efficiency. *Plant, Cell & Environment* **38**, 1817–1832.
- Carvalho Jde F, Madgwick PJ, Powers SJ, Keys AJ, Lea PJ, Parry MA. 2011. An engineered pathway for glyoxylate metabolism in tobacco plants aimed to avoid the release of ammonia in photorespiration. *BMC Biotechnology* **11**, 111.
- Chang TG, Zhu XG, Raines C. 2017. Source–sink interaction: a century old concept under the light of modern molecular systems biology. *Journal of Experimental Botany* **68**, 4417–4431.
- Chastain CJ, Ogren WL. 1989. Glyoxylate inhibition of ribulosebiphosphate carboxylase/oxygenase activation state in vivo. *Plant and Cell Physiology* **30**, 937–944.
- Chazdon RL, Pearcy RW. 1986a. Photosynthetic responses to light variation in rainforest species: I. Induction under constant and fluctuating light conditions. *Oecologia* **69**, 517–523.
- Chazdon RL, Pearcy RW. 1986b. Photosynthetic responses to light variation in rainforest species: II. Carbon gain and photosynthetic efficiency during lightflecks. *Oecologia* **69**, 524–531.
- Chida H, Nakazawa A, Akazaki H, *et al.* 2007. Expression of the algal cytochrome *c6* gene in *Arabidopsis* enhances photosynthesis and growth. *Plant & Cell Physiology* **48**, 948–957.
- Cook CM, Mulligan RM, Tolbert NE. 1985. Inhibition and stimulation of ribulose-1,5-bisphosphate carboxylase/oxygenase by glyoxylate. *Archives of Biochemistry and Biophysics* **240**, 392–401.
- Cramer WA, Hasan SS, Yamashita E. 2011. The Q cycle of cytochrome *bc* complexes: a structure perspective. *Biochimica et Biophysica Acta* **1807**, 788–802.
- Cramer WA, Zhang H. 2006. Consequences of the structure of the cytochrome *b₆f* complex for its charge transfer pathways. *Biochimica et Biophysica Acta* **1757**, 339–345.
- Cramer WA, Zhang H, Yan J, Kurisu G, Smith JL. 2006. Transmembrane traffic in the cytochrome *b₆f* complex. *Annual Review of Biochemistry* **75**, 769–790.
- Crawford NA, Droux M, Kosower NS, Buchanan BB. 1989. Evidence for function of the ferredoxin/thioredoxin system in the reductive activation of target enzymes of isolated intact chloroplasts. *Archives of Biochemistry and Biophysics* **271**, 223–239.
- Dalal J, Lopez H, Vasani NB, *et al.* 2015. A photorespiratory bypass increases plant growth and seed yield in biofuel crop *Camelina sativa*. *Biotechnology for Biofuels* **8**, 175.
- Demmig-Adams B, Adams WW III. 1996. The role of xanthophyll cycle carotenoids in the protection of photosynthesis. *Trends in Plant Science* **1**, 21–26.
- Ding F, Wang M, Zhang S, Ai X. 2016. Changes in SBPase activity influence photosynthetic capacity, growth, and tolerance to chilling stress in transgenic tomato plants. *Scientific Reports* **6**, 32741.
- Dirzo R, Raven PH. 2003. Global state of biodiversity and loss. *Annual Review of Environment and Resources* **28**, 137–167.
- Douce R, Bourguignon J, Neuburger M, Rébeillé F. 2001. The glycine decarboxylase system: a fascinating complex. *Trends in Plant Science* **6**, 167–176.
- Drier SM, Simkin AJ, Alotaibi S, Fisk SJ, Madgwick PJ, Sparks CA, Jones HD, Lawson T, Parry MAJ, Raines CA. 2017. Increased SBPase activity improves photosynthesis and grain yield in wheat grown in greenhouse conditions. *Philosophical Transactions of the Royal Society B: Biological Sciences* **372**, 1730.
- Eisenhut M, Bauwe H, Hagemann M. 2007. Glycine accumulation is toxic for the cyanobacterium *Synechocystis* sp. strain PCC 6803, but can be compensated by supplementation with magnesium ions. *FEMS Microbiology Letters* **277**, 232–237.
- Eisenhut M, Ruth W, Haimovich M, Bauwe H, Kaplan A, Hagemann M. 2008. The photorespiratory glycolate metabolism is essential for cyanobacteria and might have been conveyed endosymbiotically to plants. *Proceedings of the National Academy of Sciences, USA* **105**, 17199–17204.
- Engel N, Eisenhut M, Qu N, Bauwe H. 2008. Arabidopsis mutants with strongly reduced levels of the T-protein subunit of glycine decarboxylase. In: Allen JF, Gantt E, Golbeck JH, Osmond CB, eds. *Photosynthesis. Energy from the sun*. Dordrecht: Springer, 819–822.
- Engel N, van den Daele K, Kolukisaoglu U, Morgenthal K, Weckwerth W, Pärnik T, Keerberg O, Bauwe H. 2007. Deletion of glycine decarboxylase in *Arabidopsis* is lethal under nonphotorespiratory conditions. *Plant Physiology* **144**, 1328–1335.
- Engler C, Gruetzner R, Kandzia R, Marillonnet S. 2009. Golden gate shuffling: a one-pot DNA shuffling method based on type IIs restriction enzymes. *PLoS One* **4**, e5553.
- Engler C, Kandzia R, Marillonnet S. 2008. A one pot, one step, precision cloning method with high throughput capability. *PLoS One* **3**, e3647.
- Engler C, Youlos M, Gruetzner R, Ehner TM, Werner S, Jones JD, Patron NJ, Marillonnet S. 2014. A golden gate modular cloning toolbox for plants. *ACS Synthetic Biology* **3**, 839–843.
- Erales J, Gontero B, Whitelegge J, Halgand F. 2009. Mapping of a copper-binding site on the small CP12 chloroplastic protein of *Chlamydomonas reinhardtii* using top-down mass spectrometry and site-directed mutagenesis. *Biochemical Journal* **419**, 75–82.
- Evans JR, Clarke VC. 2018. The nitrogen cost of photosynthesis. *Journal of Experimental Botany* (in press).
- Evans LT. 1993. *Crop evolution, adaptation, and yield*. Cambridge/New York: Cambridge University Press.
- Evans TL. 1998. Greater crop production: whence and whither? In: Waterlow JC, Armstrong DG, Fowdenand L, Riley R, eds. *Feeding a world population of more than eight billion people*. Cary, NC: Oxford University Press, 89–97.
- Evans TL, Fischer RA. 1999. Yield potential: its definition, measurement, and significance. *Crop Science* **39**, 1544–1551.
- Exposito-Rodriguez M, Laissue PP, Lopez-Calcagno PE, Mullineaux PM, Raines CA, Simkin AJ. 2017. Development of pGEMINI, a plant gateway destination vector allowing the simultaneous integration of two cDNA via a single LR-clonase reaction. *Plants* **6**, 55.
- FAO. 2017. *The future of food and agriculture—trends and challenges*. Rome: FAO.
- Farran I, Fernandez-San Millan A, Ancin M, Larraya L, Veramendi J. 2014. Increased bioethanol production from commercial tobacco cultivars overexpressing thioredoxin f grown under field conditions. *Molecular Breeding* **34**, 457–469.
- Faure M, Bourguignon J, Neuburger M, MacHerel D, Sieker L, Ober R, Kahn R, Cohen-Addad C, Douce R. 2000. Interaction between the lipoamide-containing H-protein and the lipoamide dehydrogenase (L-protein) of the glycine decarboxylase multienzyme system 2. Crystal structures of H- and L-proteins. *European Journal of Biochemistry* **267**, 2890–2898.
- Feng LL, Han YJ, Liu G, An BG, Yang J, Yang GH, Li YS, Zhu YG. 2007. Overexpression of sedoheptulose-1,7-bisphosphatase enhances photosynthesis and growth under salt stress in transgenic rice plants. *Functional Plant Biology* **34**, 822–834.
- Fischer RA, Rees D, Sayre KD, Lu ZM, Condon AG, Saavedra AL. 1998. Wheat yield progress associated with higher stomatal conductance and photosynthetic rate, and cooler canopies. *Crop Science* **38**, 1467–1475.
- Fischer RAT, Edmeades GO. 2010. Breeding and cereal yield progress. *Crop Science* **50**, S85–S98.
- Flügel F, Timm S, Arrivault S, Florian A, Stitt M, Fernie AR, Bauwe H. 2017. The photorespiratory metabolite 2-phosphoglycolate regulates photosynthesis and starch accumulation in *Arabidopsis*. *The Plant Cell* **29**, 2537–2551.

- Foyer CH, Bloom AJ, Queval G, Noctor G. 2009. Photorespiratory metabolism: genes, mutants, energetics, and redox signaling. *Annual Review of Plant Biology* **60**, 455–484.
- Fuentes SI, Allen DJ, Ortiz-Lopez A, Hernández G. 2001. Overexpression of cytosolic glutamine synthetase increases photosynthesis and growth at low nitrogen concentrations. *Journal of Experimental Botany* **52**, 1071–1081.
- Fukayama H, Ueguchi C, Nishikawa K, Katoh N, Ishikawa C, Masumoto C, Hatanaka T, Misoo S. 2012. Overexpression of Rubisco activase decreases the photosynthetic CO₂ assimilation rate by reducing Rubisco content in rice leaves. *Plant & Cell Physiology* **53**, 976–986.
- Geiger DR, Servaites JC. 1994. Diurnal regulation of photosynthetic carbon metabolism in C3 plants. *Annual Review of Plant Physiology and Plant Molecular Biology* **45**, 235–256.
- Genty B, Briantais JM, Baker NR. 1989. The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. *Biochimica et Biophysica Acta* **990**, 87–92.
- Genty B, Goulas Y, Dimon B, Peltier G, Briantais JM, Moya I. 1992. Modulation of efficiency of primary conversion in leaves. *Photosynthesis Research* **34**, 106.
- Georges F, Ray H. 2017. Genome editing of crops: a renewed opportunity for food security. *GM Crops & Food* **8**, 1–12.
- Gielen B, Calfapietra C, Lukac M, et al. 2005. Net carbon storage in a poplar plantation (POPFACE) after three years of free-air CO₂ enrichment. *Tree Physiology* **25**, 1399–1408.
- Głowacka K, Kromdijk J, Kucera K, Xie J, Cavanagh AP, Leonelli L, Leahey ADB, Ort DR, Niyogi KK, Long SP. 2018. Photosystem II subunit S overexpression increases the efficiency of water use in a field-grown crop. *Nature Communications* **9**, 868.
- Godfray HCJ. 2014. The challenge of feeding 9–10 billion people equitably and sustainably. *Journal of Agricultural Science* **152**, S2–S8.
- Godfray HC, Beddington JR, Crute IR, Haddad L, Lawrence D, Muir JF, Pretty J, Robinson S, Thomas SM, Toulmin C. 2010. Food security: the challenge of feeding 9 billion people. *Science* **327**, 812–818.
- GOFS. 2011. The future of food and farming. Final project report. London: The Government Office for Science.
- Gong HY, Li Y, Fang G, Hu DH, Jin WB, Wang ZH, Li YS. 2015. Transgenic rice expressing lctB and FBP/SBPase derived from cyanobacteria exhibits enhanced photosynthesis and mesophyll conductance to CO₂. *PLoS One* **10**, e0140928.
- Gontero B, Maberly SC. 2012. An intrinsically disordered protein, CP12: jack of all trades and master of the Calvin cycle. *Biochemical Society Transactions* **40**, 995–999.
- Graciet E, Gans P, Wedel N, Lebreton S, Camadro JM, Gontero B. 2003. The small protein CP12: a protein linker for supramolecular complex assembly. *Biochemistry* **42**, 8163–8170.
- Graciet E, Lebreton S, Gontero B. 2004. Emergence of new regulatory mechanisms in the Benson–Calvin pathway via protein–protein interactions: a glyceraldehyde-3-phosphate dehydrogenase/CP12/phosphoribulokinase complex. *Journal of Experimental Botany* **55**, 1245–1254.
- Grasses T, Pesaresi P, Schiavon F, Varotto C, Salamini F, Jahns P, Leister D. 2002. The role of Delta pH-dependent dissipation of excitation energy in protecting photosystem II against light-induced damage in *Arabidopsis thaliana*. *Plant Physiology and Biochemistry* **40**, 41–49.
- Haake V, Geiger M, Walch-Liu P, Engels C, Zrenner R, Stitt M. 1999. Changes in aldolase activity in wild-type potato plants are important for acclimation to growth irradiance and carbon dioxide concentration, because plastid aldolase exerts control over the ambient rate of photosynthesis across a range of growth conditions. *The Plant Journal* **17**, 479–489.
- Haake V, Zrenner R, Sonnewald U, Stitt M. 1998. A moderate decrease of plastid aldolase activity inhibits photosynthesis, alters the levels of sugars and starch, and inhibits growth of potato plants. *The Plant Journal* **14**, 147–157.
- Habash D, Massiah A, Rong H, Wallsgrove R, Leigh R. 2001. The role of cytosolic glutamine synthetase in wheat. *Annals of Applied Biology* **138**, 83–89.
- Hackenberg C, Kern R, Hüge J, Stal LJ, Tsuji Y, Kopka J, Shiraiwa Y, Bauwe H, Hagemann M. 2011. Cyanobacterial lactate oxidases serve as essential partners in N₂ fixation and evolved into photorespiratory glycolate oxidases in plants. *The Plant Cell* **23**, 2978–2990.
- Hager M, Biehler K, Illerhaus J, Ruf S, Bock R. 1999. Targeted inactivation of the smallest plastid genome-encoded open reading frame reveals a novel and essential subunit of the cytochrome *b₆f* complex. *The EMBO Journal* **18**, 5834–5842.
- Hammond ET, Andrews TJ, Mott KA, Woodrow IE. 1998. Regulation of Rubisco activation in antisense plants of tobacco containing reduced levels of Rubisco activase. *The Plant Journal* **14**, 101–110.
- Harrison EP, Olcer H, Lloyd JC, Long SP, Raines CA. 2001. Small decreases in SBPase cause a linear decline in the apparent RuBP regeneration rate, but do not affect Rubisco carboxylation capacity. *Journal of Experimental Botany* **52**, 1779–1784.
- Harrison EP, Willingham NM, Lloyd JC, Raines CA. 1998. Reduced sedoheptulose-1,7-bisphosphatase levels in transgenic tobacco lead to decreased photosynthetic capacity and altered carbohydrate accumulation. *Planta* **204**, 27–36.
- Hausler RE, Bailey KJ, Lea PJ, Leegood RC. 1996. Control of photosynthesis in barley mutants with reduced activities of glutamine synthetase and glutamate synthase. 3. Aspects of glyoxylate metabolism and effects of glyoxylate on the activation state of ribulose-1,5-bisphosphate carboxylase-oxygenase. *Planta* **200**, 388–396.
- Hay WT, Bihmidine S, Mutlu N, Hoang KL, Awada T, Weeks DP, Clemente TE, Long SP. 2017. Enhancing soybean photosynthetic CO₂ assimilation using a cyanobacterial membrane protein, lctB. *Journal of Plant Physiology* **212**, 58–68.
- Heineke D, Bykova N, Gardeström P, Bauwe H. 2001. Metabolic response of potato plants to an antisense reduction of the P-protein of glycine decarboxylase. *Planta* **212**, 880–887.
- Henkes S, Sonnewald U, Badur R, Flachmann R, Stitt M. 2001. A small decrease of plastid transketolase activity in antisense tobacco transformants has dramatic effects on photosynthesis and phenylpropanoid metabolism. *The Plant Cell* **13**, 535–551.
- Heyneke E, Fernie AR. 2018. Metabolic regulation of photosynthesis. *Biochemical Society Transactions* **46**, 321–328.
- Hojka M, Thiele W, Tóth SZ, Lein W, Bock R, Schöttler MA. 2014. Inducible repression of nuclear-encoded subunits of the cytochrome *b₆f* complex in tobacco reveals an extraordinarily long lifetime of the complex. *Plant Physiology* **165**, 1632–1646.
- Horton P, Ruban AV, Walters RG. 1996. Regulation of light harvesting in green plants. *Annual Review of Plant Physiology and Plant Molecular Biology* **47**, 655–684.
- Hoshida H, Tanaka Y, Hibino T, Hayashi Y, Tanaka A, Takabe T, Takabe T. 2000. Enhanced tolerance to salt stress in transgenic rice that overexpresses chloroplast glutamine synthetase. *Plant Molecular Biology* **43**, 103–111.
- Howard TP, Fryer MJ, Singh P, et al. 2011a. Antisense suppression of the small chloroplast protein CP12 in tobacco alters carbon partitioning and severely restricts growth. *Plant Physiology* **157**, 620–631.
- Howard TP, Lloyd JC, Raines CA. 2011b. Inter-species variation in the oligomeric states of the higher plant Calvin cycle enzymes glyceraldehyde-3-phosphate dehydrogenase and phosphoribulokinase. *Journal of Experimental Botany* **62**, 3799–3805.
- Howard TP, Metodiev M, Lloyd JC, Raines CA. 2008. Thioredoxin-mediated reversible dissociation of a stromal multiprotein complex in response to changes in light availability. *Proceedings of the National Academy of Sciences, USA* **105**, 4056–4061.
- Howard TP, Upton GJ, Lloyd JC, Raines CA. 2011c. Antisense suppression of the small chloroplast protein CP12 in tobacco: a transcriptional viewpoint. *Plant Signaling & Behavior* **6**, 2026–2030.
- Huma B, Kundu S, Poolman MG, Kruger NJ, Fell DA. 2018. Stoichiometric analysis of the energetics and metabolic impact of photorespiration in C3 plants. *The Plant Journal* **96**, 1228–1241.
- Hurry V, Anderson JM, Badger MR, Price GD. 1996. Reduced levels of cytochrome *b₆f* in transgenic tobacco increases the excitation pressure on Photosystem II without increasing sensitivity to photoinhibition in vivo. *Photosynthesis Research* **50**, 159–169.
- Hutchison RS, Groom Q, Ort DR. 2000. Differential effects of chilling-induced photooxidation on the redox regulation of photosynthetic enzymes. *Biochemistry* **39**, 6679–6688.

- Ichikawa Y, Tamoi M, Sakuyama H, Maruta T, Ashida H, Yokota A, Shigeoka S.** 2010. Generation of transplastomic lettuce with enhanced growth and high yield. *GM Crops* **1**, 322–326.
- Kaiser E, Matsubara S, Harbinson J, Heuvelink E, Marcelis LFM.** 2018a. Acclimation of photosynthesis to lightflecks in tomato leaves: interaction with progressive shading in a growing canopy. *Physiologia Plantarum* **162**, 506–517.
- Kaiser E, Morales A, Harbinson J.** 2018b. Fluctuating light takes crop photosynthesis on a rollercoaster ride. *Plant Physiology* **176**, 977–989.
- Kaiser E, Morales A, Harbinson J, Heuvelink E, Prinzenberg AE, Marcelis LF.** 2016. Metabolic and diffusional limitations of photosynthesis in fluctuating irradiance in *Arabidopsis thaliana*. *Scientific Reports* **6**, 31252.
- Kanazawa A, Kramer DM.** 2002. In vivo modulation of nonphotochemical exciton quenching (NPQ) by regulation of the chloroplast ATP synthase. *Proceedings of the National Academy of Sciences, USA* **99**, 12789–12794.
- Kaplan A, Lieman-Hurwitz J, Schatz D, Mittler R, Ronen-Tarazi M, Bonfil DJ.** 2001. Enhancing inorganic carbon fixation by photosynthetic organisms. US Patent 6,320,101,B1.
- Kaplan A, Reinhold L.** 1999. CO₂ concentrating mechanisms in photosynthetic microorganisms. *Annual Review of Plant Physiology and Plant Molecular Biology* **50**, 539–570.
- Kebeish R, Niessen M, Thiruveedhi K, Bari R, Hirsch HJ, Rosenkranz R, Stähler N, Schönfeld B, Kreuzaler F, Peterhänsel C.** 2007. Chloroplastic photorespiratory bypass increases photosynthesis and biomass production in *Arabidopsis thaliana*. *Nature Biotechnology* **25**, 593–599.
- Kelly GJ, Latzko E.** 1976. Inhibition of spinach-leaf phosphofructokinase by 2-phosphoglycollate. *FEBS Letters* **68**, 55–58.
- Keys AJ.** 2006. The re-assimilation of ammonia produced by photorespiration and the nitrogen economy of C3 higher plants. *Photosynthesis Research* **87**, 165–175.
- Khan MS.** 2007. Engineering photorespiration in chloroplasts: a novel strategy for increasing biomass production. *Trends in Biotechnology* **25**, 437–440.
- Khozaei M, Fisk S, Lawson T, Gibon Y, Sulpice R, Stitt M, Lefebvre SC, Raines CA.** 2015. Overexpression of plastid transketolase in tobacco results in a thiamine auxotrophic phenotype. *The Plant Cell* **27**, 432–447.
- Kikuchi G, Motokawa Y, Yoshida T, Hiraga K.** 2008. Glycine cleavage system: reaction mechanism, physiological significance, and hyperglycemia. *Proceedings of the Japan Academy. Series B, Physical and Biological Sciences* **84**, 246–263.
- Kim MR, Khaleda L, Jung IJ, Kim JY, Lee SY, Cha JY, Kim WY.** 2017. Overexpression of chloroplast-localized NADPH-dependent thioredoxin reductase C (NTRC) enhances tolerance to photo-oxidative and drought stresses in *Arabidopsis thaliana*. *Journal of Plant Biology* **60**, 175–180.
- Kirchhoff H, Horstmann S, Weis E.** 2000. Control of the photosynthetic electron transport by PQ diffusion microdomains in thylakoids of higher plants. *Biochimica et Biophysica Acta* **1459**, 148–168.
- Kisaki T, Tolbert NE.** 1970. Glycine as a substrate for photorespiration. *Plant and Cell Physiology* **11**, 247.
- Kisaki T, Yoshida N, Imai A.** 1971. Glycine decarboxylase and serine formation in spinach leaf mitochondrial preparation with reference to photorespiration. *Plant & Cell Physiology* **12**, 275.
- Knight JS, Duckett CM, Sullivan JA, Walker AR, Gray JC.** 2002. Tissue-specific, light-regulated and plastid-regulated expression of the single-copy nuclear gene encoding the chloroplast Rieske FeS protein of *Arabidopsis thaliana*. *Plant & Cell Physiology* **43**, 522–531.
- Knuesting J, Scheibe R.** 2018. Small molecules govern thiol redox switches. *Trends in Plant Science* **23**, 769–782.
- Köhler IH, Ruiz-Vera UM, VanLoocke A, Thomey ML, Clemente T, Long SP, Ort DR, Bernacchi CJ.** 2017. Expression of cyanobacterial FBP/SBPase in soybean prevents yield depression under future climate conditions. *Journal of Experimental Botany* **68**, 715–726.
- Kono M, Terashima I.** 2014. Long-term and short-term responses of the photosynthetic electron transport to fluctuating light. *Journal of Photochemistry and Photobiology. B, Biology* **137**, 89–99.
- Koßmann J, Müller-Röber B, Dyer TA, Raines CA, Sonnewald U, Willmitzer L.** 1992. Cloning and expression analysis of the plastidic fructose-1,6-bisphosphatase coding sequence from potato: circumstantial evidence for the import of hexoses into chloroplasts. *Planta* **188**, 7–12.
- Krall JP, Sheveleva EV, Pearcy RW.** 1995. Regulation of photosynthetic induction state in high- and low-light-grown soybean and *Alocasia macrorrhiza* (L.) G. Don. *Plant Physiology* **109**, 307–317.
- Kromdijk J, Glowacka K, Leonelli L, Gabilly ST, Iwai M, Niyogi KK, Long SP.** 2016. Improving photosynthesis and crop productivity by accelerating recovery from photoprotection. *Science* **354**, 857–861.
- Kruger EL, Volin JC.** 2006. Reexamining the empirical relation between plant growth and leaf photosynthesis. *Functional Plant Biology* **33**, 421–429.
- Külheim C, Agren J, Jansson S.** 2002. Rapid regulation of light harvesting and plant fitness in the field. *Science* **297**, 91–93.
- Kumar A, Li C, Portis AR Jr.** 2009. *Arabidopsis thaliana* expressing a thermostable chimeric Rubisco activase exhibits enhanced growth and higher rates of photosynthesis at moderately high temperatures. *Photosynthesis Research* **100**, 143–153.
- Kuras R, Wollman FA.** 1994. The assembly of cytochrome *b₆/f* complexes: an approach using genetic transformation of the green alga *Chlamydomonas reinhardtii*. *The EMBO Journal* **13**, 1019–1027.
- Kurek I, Chang TK, Bertain SM, Madrigal A, Liu L, Lassner MW, Zhu G.** 2007. Enhanced thermostability of *Arabidopsis* Rubisco activase improves photosynthesis and growth rates under moderate heat stress. *The Plant Cell* **19**, 3230–3241.
- Kurusu G, Zhang H, Smith JL, Cramer WA.** 2003. Structure of the cytochrome *b₆f* complex of oxygenic photosynthesis: tuning the cavity. *Science* **302**, 1009–1014.
- Laing WA, Stitt M, Heldt HW.** 1981. Control of CO₂ fixation—changes in the activity of ribulosephosphate kinase and fructose- and sedoheptulose-bisphosphatase in chloroplasts. *Biochimica et Biophysica Acta* **637**, 348–359.
- Laiss A, Oja V, Kiirats O, Raschke K, Heber U.** 1989. The state of the photosynthetic apparatus in leaves as analyzed by rapid gas exchange and optical methods: the pH of the chloroplast stroma and activation of enzymes *in vivo*. *Planta* **177**, 350–358.
- Lawson T, Bryant B, Lefebvre S, Lloyd JC, Raines CA.** 2006. Decreased SBPase activity alters growth and development in transgenic tobacco plants. *Plant, Cell & Environment* **29**, 48–58.
- Lawson T, Kramer DM, Raines CA.** 2012. Improving yield by exploiting mechanisms underlying natural variation of photosynthesis. *Current Opinion in Biotechnology* **23**, 215–220.
- Leakey AD, Ainsworth EA, Bernacchi CJ, Rogers A, Long SP, Ort DR.** 2009. Elevated CO₂ effects on plant carbon, nitrogen, and water relations: six important lessons from FACE. *Journal of Experimental Botany* **60**, 2859–2876.
- Lefebvre S, Lawson T, Zakhleniuk OV, Lloyd JC, Raines CA, Fryer M.** 2005. Increased sedoheptulose-1,7-bisphosphatase activity in transgenic tobacco plants stimulates photosynthesis and growth from an early stage in development. *Plant Physiology* **138**, 451–460.
- Lennartz K, Plücker H, Seidler A, Westhoff P, Bechtold N, Meierhoff K.** 2001. HCF164 encodes a thioredoxin-like protein involved in the biogenesis of the cytochrome *b₆f* complex in *Arabidopsis*. *The Plant Cell* **13**, 2539–2551.
- Le Quere C, Raupach MR, Canadell JG, et al.** 2009. Trends in the sources and sinks of carbon dioxide. *Nature Geoscience* **2**, 831–836.
- Li K, Qiu H, Zhou M, Lin Y, Guo Z, Lu S.** 2018. Chloroplast protein 12 expression alters growth and chilling tolerance in tropical forage *Stylosanthes guianensis* (Aublet) Sw. *Frontiers in Plant Science* **9**, 1319.
- Li XP, Gilmore AM, Caffarri S, Bassi R, Golan T, Kramer D, Niyogi KK.** 2004. Regulation of photosynthetic light harvesting involves intrathylakoid lumen pH sensing by the PsbS protein. *Journal of Biological Chemistry* **279**, 22866–22874.
- Li XP, Muller-Moule P, Gilmore AM, Niyogi KK.** 2002. PsbS-dependent enhancement of feedback de-excitation protects photosystem II from photoinhibition. *Proceedings of the National Academy of Sciences, USA* **99**, 15222–15227.
- Liang F, Lindblad P.** 2016. Effects of overexpressing photosynthetic carbon flux control enzymes in the cyanobacterium *Synechocystis* PCC 6803. *Metabolic Engineering* **38**, 56–64.
- Lieman-Hurwitz J, Asipov L, Rachmilevitch S, Marcus Y, Kaplan A.** 2005. Expression of cyanobacterial *ictB* in higher plants enhanced

photosynthesis and growth. In: Omasa K, Nouchi I, De Kok LJ, eds. Plant responses to air pollution and global change. Tokyo: Springer, 133–139.

Lieman-Hurwitz J, Rachmilevitch S, Mittler R, Marcus Y, Kaplan A. 2003. Enhanced photosynthesis and growth of transgenic plants that express *ictB*, a gene involved in HCO_3^- accumulation in cyanobacteria. *Plant Biotechnology Journal* **1**, 43–50.

Lilley JM, Bolger TP, Gifford RM. 2001. Productivity of *Trifolium subterraneum* and *Phalaris aquatica* under warmer, high CO_2 conditions. *New Phytologist* **150**, 371–383.

Lin H, Karki S, Coe RA, et al. 2016. Targeted knockdown of GDCH in rice leads to a photorespiratory-deficient phenotype useful as a building block for C_4 rice. *Plant & Cell Physiology* **57**, 919–932.

Long SP, Marshall-Colon A, Zhu XG. 2015. Meeting the global food demand of the future by engineering crop photosynthesis and yield potential. *Cell* **161**, 56–66.

Long SP, Zhu XG, Naidu SL, Ort DR. 2006. Can improvement in photosynthesis increase crop yields? *Plant, Cell & Environment* **29**, 315–330.

López-Calcano PE, Abuzaid AO, Lawson T, Raines CA. 2017. Arabidopsis CP12 mutants have reduced levels of phosphoribulokinase and impaired function of the Calvin–Benson cycle. *Journal of Experimental Botany* **68**, 2285–2298.

López-Calcano PE, Fisk SJ, Brown K, Bull SE, South PF, Raines CA. 2018. Overexpressing the H-protein of the glycine cleavage system increases biomass yield in glasshouse and field grown transgenic tobacco plants. *Plant Biotechnology Journal* (in press).

López-Calcano PE, Howard TP, Raines CA. 2014. The CP12 protein family: a thioredoxin-mediated metabolic switch? *Frontiers in Plant Science* **5**, 9.

Lu Y, Li Y, Yang Q, Zhang Z, Chen Y, Zhang S, Peng XX. 2014. Suppression of glycolate oxidase causes glyoxylate accumulation that inhibits photosynthesis through deactivating Rubisco in rice. *Physiologia Plantarum* **150**, 463–476.

Ludwig LJ, Canvin DT. 1971. The rate of photorespiration during photosynthesis and the relationship of the substrate of light respiration to the products of photosynthesis in sunflower leaves. *Plant Physiology* **48**, 712–719.

Maier A, Fahrenstich H, von Caemmerer S, Engqvist MK, Weber AP, Flügge UI, Maurino VG. 2012. Transgenic introduction of a glycolate oxidative cycle into *A. thaliana* chloroplasts leads to growth improvement. *Frontiers in Plant Science* **3**, 38.

Marillonnet S, Werner S. 2015. Assembly of multigene constructs using golden gate cloning. In: Castilho A, ed. *Glyco-engineering: methods and protocols*. New York: Springer New York, 269–284.

Marri L, Pesaresi A, Valerio C, Lamba D, Pupillo P, Trost P, Sparla F. 2010. In vitro characterization of Arabidopsis CP12 isoforms reveals common biochemical and molecular properties. *Journal of Plant Physiology* **167**, 939–950.

Marri L, Thieulin-Pardo G, Lebrun R, Puppo R, Zaffagnini M, Trost P, Gontero B, Sparla F. 2014. CP12-mediated protection of Calvin–Benson cycle enzymes from oxidative stress. *Biochimie* **97**, 228–237.

Marri L, Trost P, Pupillo P, Sparla F. 2005. Reconstitution and properties of the recombinant glyceraldehyde-3-phosphate dehydrogenase/CP12/phosphoribulokinase supramolecular complex of Arabidopsis. *Plant Physiology* **139**, 1433–1443.

Marri L, Zaffagnini M, Collin V, Issakidis-Bourguet E, Lemaire SD, Pupillo P, Sparla F, Miginiac-Maslow M, Trost P. 2009. Prompt and easy activation by specific thioredoxins of Calvin cycle enzymes of *Arabidopsis thaliana* associated in the GAPDH/CP12/PRK supramolecular complex. *Molecular Plant* **2**, 259–269.

Masclaux-Daubresse C, Daniel-Vedele F, Dechorgnat J, Chardon F, Gaufichon L, Suzuki A. 2010. Nitrogen uptake, assimilation and remobilization in plants: challenges for sustainable and productive agriculture. *Annals of Botany* **105**, 1141–1157.

Matthews JSA, Viallet-Chabrand S, Lawson T. 2018. Acclimation to fluctuating light impacts the rapidity of response and diurnal rhythm of stomatal conductance. *Plant Physiology* **176**, 1939–1951.

Merchant S, Bogorad L. 1987. The Cu(II)-repressible plastidic cytochrome c. Cloning and sequence of a complementary DNA for the pre-apoprotein. *Journal of Biological Chemistry* **262**, 9062–9067.

Metz JG, Miles D, Rutherford AW. 1983. Characterization of nuclear mutants of maize which lack the cytochrome *f/b*-563 complex. *Plant Physiology* **73**, 452–459.

Meyer Y, Siala W, Bashandy T, Riondet C, Vignols F, Reichheld JP. 2008. Glutaredoxins and thioredoxins in plants. *Biochimica et Biophysica Acta* **1783**, 589–600.

Michelet L, Zaffagnini M, Morisse S, et al. 2013. Redox regulation of the Calvin–Benson cycle: something old, something new. *Frontiers in Plant Science* **4**, 470.

Migge A, Carrayol E, Hirel B, Becker TW. 2000. Leaf-specific overexpression of plastidic glutamine synthetase stimulates the growth of transgenic tobacco seedlings. *Planta* **210**, 252–260.

Miglietta F, Peressotti A, Vaccari FP, Zaldei A, DeAngelis P, Scarascia-Mugnozza G. 2001. Free-air CO_2 enrichment (FACE) of a poplar plantation: the POPFACE fumigation system. *New Phytologist* **150**, 465–476.

Miles D. 1982. The use of mutations to probe photosynthesis in higher plants. In: Edelman E, Hallick RB, Chua NH, eds. *Methods in chloroplast molecular biology*. Amsterdam: Elsevier Biomedical Press, 75–107.

Miyagawa Y, Tamoi M, Shigeoka S. 2001. Overexpression of a cyanobacterial fructose-1,6-/sedoheptulose-1,7-bisphosphatase in tobacco enhances photosynthesis and growth. *Nature Biotechnology* **19**, 965–969.

Monde RA, Zito F, Olive J, Wollman FA, Stern DB. 2000. Post-transcriptional defects in tobacco chloroplast mutants lacking the cytochrome *b₆/f* complex. *The Plant Journal* **21**, 61–72.

Moroney JV, Jungnick N, Dimario RJ, Longstreth DJ. 2013. Photorespiration and carbon concentrating mechanisms: two adaptations to high O_2 , low CO_2 conditions. *Photosynthesis Research* **117**, 121–131.

Mukherjee S, Stasolla C, Brûlé-Babel A, Ayele BT. 2015. Isolation and characterization of rubisco small subunit gene promoter from common wheat (*Triticum aestivum* L.). *Plant Signaling & Behavior* **10**, e989033.

Müller P, Li XP, Niyogi KK. 2001. Non-photochemical quenching. A response to excess light energy. *Plant Physiology* **125**, 1558–1566.

Naranjo B, Diaz-Espejo A, Lindahl M, Cejudo FJ. 2016. Type-f thioredoxins have a role in the short-term activation of carbon metabolism and their loss affects growth under short-day conditions in *Arabidopsis thaliana*. *Journal of Experimental Botany* **67**, 1951–1964.

Nikkanen L, Rintamäki E. 2014. Thioredoxin-dependent regulatory networks in chloroplasts under fluctuating light conditions. *Philosophical Transactions of the Royal Society B: Biological Sciences* **369**, 20130224.

Nikkanen L, Toivola J, Diaz MG, Rintamäki E. 2017. Chloroplast thioredoxin systems: prospects for improving photosynthesis. *Philosophical Transactions of the Royal Society B: Biological Sciences* **372**, 20160474.

Nikkanen L, Toivola J, Rintamäki E. 2016. Crosstalk between chloroplast thioredoxin systems in regulation of photosynthesis. *Plant, Cell & Environment* **39**, 1691–1705.

Nölke G, Houdelet M, Kreuzaler F, Peterhansel C, Schillberg S. 2014. The expression of a recombinant glycolate dehydrogenase polypeptide in potato (*Solanum tuberosum*) plastids strongly enhances photosynthesis and tuber yield. *Plant Biotechnology Journal* **12**, 734–742.

Oliveira IC, Brears T, Knight TJ, Clark A, Coruzzi GM. 2002. Overexpression of cytosolic glutamine synthetase. Relation to nitrogen, light, and photorespiration. *Plant Physiology* **129**, 1170–1180.

Oliver DJ. 1994. The glycine decarboxylase complex from plant-mitochondria. *Annual Review of Plant Physiology and Plant Molecular Biology* **45**, 323–337.

Oliver DJ, Neuburger M, Bourguignon J, Douce R. 1990. Interaction between the component enzymes of the glycine decarboxylase multienzyme complex. *Plant Physiology* **94**, 833–839.

Ort DR, Merchant SS, Alric J, et al. 2015. Redesigning photosynthesis to sustainably meet global food and bioenergy demand. *Proceedings of the National Academy of Sciences, USA* **112**, 8529–8536.

Pérez-Bueno ML, Johnson MP, Zia A, Ruban AV, Horton P. 2008. The Lhcb protein and xanthophyll composition of the light harvesting antenna controls the DeltapH-dependency of non-photochemical quenching in *Arabidopsis thaliana*. *FEBS Letters* **582**, 1477–1482.

Pérez-Ruiz JM, Spínola MC, Kirchsteiger K, Moreno J, Sahrway M, Cejudo FJ. 2006. Rice NTRC is a high-efficiency redox system for chloroplast protection against oxidative damage. *The Plant Cell* **18**, 2356–2368.

Peterhansel C, Blume C, Offermann S. 2013a. Photorespiratory bypasses: how can they work? *Journal of Experimental Botany* **64**, 709–715.

- Peterhansel C, Horst I, Niessen M, Blume C, Kebeish R, Kürkcüoglu S, Kreuzaler F. 2010. Photorespiration. The Arabidopsis Book **8**, e0130.
- Peterhansel C, Krause K, Braun HP, Espie GS, Fernie AR, Hanson DT, Keech O, Maurino VG, Mielewicz M, Sage RF. 2013b. Engineering photorespiration: current state and future possibilities. Plant Biology **15**, 754–758.
- Pettersson G, Ryde-Pettersson U. 1988. A mathematical model of the Calvin photosynthesis cycle. European Journal of Biochemistry **175**, 661–672.
- Pohlmeier K, Paap BK, Soll J, Wedel N. 1996. CP12: a small nuclear-encoded chloroplast protein provides novel insights into higher-plant GAPDH evolution. Plant Molecular Biology **32**, 969–978.
- Poolman MG, Fell DA, Thomas S. 2000. Modelling photosynthesis and its control. Journal of Experimental Botany **51**, 319–328.
- Portis AR Jr, Li C, Wang D, Salvucci ME. 2008. Regulation of Rubisco activase and its interaction with Rubisco. Journal of Experimental Botany **59**, 1597–1604.
- Portis AR Jr, Parry MA. 2007. Discoveries in Rubisco (Ribulose 1,5-bisphosphate carboxylase/oxygenase): a historical perspective. Photosynthesis Research **94**, 121–143.
- Price GD, Pengelly JJ, Forster B, Du J, Whitney SM, von Caemmerer S, Badger MR, Howitt SM, Evans JR. 2013. The cyanobacterial CCM as a source of genes for improving photosynthetic CO₂ fixation in crop species. Journal of Experimental Botany **64**, 753–768.
- Price GD, von Caemmerer S, Evans JR, Siebke K, Anderson JM, Badger MR. 1998. Photosynthesis is strongly reduced by antisense suppression of chloroplastic cytochrome *b_f* complex in transgenic tobacco. Australian Journal of Plant Physiology **25**, 445–452.
- Price GD, Yu JW, Voncaemmerer S, Evans JR, Chow WS, Anderson JM, Hurry V, Badger MR. 1995. Chloroplast cytochrome *b_{6/f}* and ATP synthase complexes in tobacco—transformation with antisense RNA against nuclear-encoded transcripts for the Rieske FeS and Atp-Delta polypeptides. Australian Journal of Plant Physiology **22**, 285–297.
- Rachmilevitch S, Cousins AB, Bloom AJ. 2004. Nitrate assimilation in plant shoots depends on photorespiration. Proceedings of the National Academy of Sciences, USA **101**, 11506–11510.
- Raines CA. 2003. The Calvin cycle revisited. Photosynthesis Research **75**, 1–10.
- Raines CA, Paul MJ. 2006. Products of leaf primary carbon metabolism modulate the developmental programme determining plant morphology. Journal of Experimental Botany **57**, 1857–1862.
- Ray DK, Mueller ND, West PC, Foley JA. 2013. Yield trends are insufficient to double global crop production by 2050. PLoS One **8**, e66428.
- Rojas CM, Senthil-Kumar M, Wang K, Ryu CM, Kaundal A, Mysore KS. 2012. Glycolate oxidase modulates reactive oxygen species-mediated signal transduction during nonhost resistance in *Nicotiana benthamiana* and Arabidopsis. The Plant Cell **24**, 336–352.
- Rojas-González JA, Soto-Suárez M, García-Díaz Á, Romero-Puertas MC, Sandalio LM, Mérida Á, Thormählen I, Geigenberger P, Serrato AJ, Sahrawy M. 2015. Disruption of both chloroplastic and cytosolic FBPase genes results in a dwarf phenotype and important starch and metabolite changes in *Arabidopsis thaliana*. Journal of Experimental Botany **66**, 2673–2689.
- Rosenthal DM, Locke AM, Khozaei M, Raines CA, Long SP, Ort DR. 2011. Over-expressing the C₃ photosynthesis cycle enzyme sedoheptulose-1,7-bisphosphatase improves photosynthetic carbon gain and yield under fully open air CO₂ fumigation (FACE). BMC Plant Biology **11**, 123.
- Rouhier N, Cerveau D, Couturier J, Reichheld JP, Rey P. 2015. Involvement of thiol-based mechanisms in plant development. Biochimica et Biophysica Acta **1850**, 1479–1496.
- RSOL. 2009. Reaping the benefits: science and the sustainable intensification of global agriculture. London: Royal Society.
- Ruuska SA, Andrews TJ, Badger MR, Price GD, von Caemmerer S. 2000. The role of chloroplast electron transport and metabolites in modulating Rubisco activity in tobacco. Insights from transgenic plants with reduced amounts of cytochrome *b_f* complex or glyceraldehyde 3-phosphate dehydrogenase. Plant Physiology **122**, 491–504.
- Sage RF, Seemann JR, Sharkey TD. 1987. The time course for deactivation and reactivation of ribulose-1,5-bisphosphate carboxylase following changes in CO₂ and O₂. In: Biggins J, ed. Progress in photosynthesis research. Dordrecht: Springer Netherlands, 285–288.
- Sagers RD, Gunsalus IC. 1961. Intermediary metabolism of *Diplococcus glycinophilus*. I. Glycine cleavage and one-carbon interconversions. Journal of Bacteriology **81**, 541–549.
- Sahrawy M, Avila C, Chueca A, Cánovas FM, López-Gorgé J. 2004. Increased sucrose level and altered nitrogen metabolism in *Arabidopsis thaliana* transgenic plants expressing antisense chloroplastic fructose-1,6-bisphosphatase. Journal of Experimental Botany **55**, 2495–2503.
- Sanz-Barrio R, Corral-Martinez P, Ancin M, Segui-Simarro JM, Farran I. 2013. Overexpression of plastidial thioredoxin f leads to enhanced starch accumulation in tobacco leaves. Plant Biotechnology Journal **11**, 618–627.
- Scheibe R. 1991. Redox-modulation of chloroplast enzymes: a common principle for individual control. Plant Physiology **96**, 1–3.
- Scheibe R, Wedel N, Vetter S, Emmerlich V, Sauermann SM. 2002. Co-existence of two regulatory NADP-glyceraldehyde 3-P dehydrogenase complexes in higher plant chloroplasts. European Journal of Biochemistry **269**, 5617–5624.
- Schöttler MA, Flügel C, Thiele W, Bock R. 2007. Knock-out of the plastid-encoded PetL subunit results in reduced stability and accelerated leaf age-dependent loss of the cytochrome *b_{6/f}* complex. Journal of Biological Chemistry **282**, 976–985.
- Schöttler MA, Tóth SZ, Boulouis A, Kahlau S. 2015. Photosynthetic complex stoichiometry dynamics in higher plants: biogenesis, function, and turnover of ATP synthase and the cytochrome *b_{6/f}* complex. Journal of Experimental Botany **66**, 2373–2400.
- Schürmann P. 2003. Redox signaling in the chloroplast: the ferredoxin/thioredoxin system. Antioxidants & Redox Signaling **5**, 69–78.
- Schürmann P, Buchanan BB. 2008. The ferredoxin/thioredoxin system of oxygenic photosynthesis. Antioxidants & Redox Signaling **10**, 1235–1274.
- Schürmann P, Jacquot JP. 2000. Plant thioredoxin systems revisited. Annual Review of Plant Physiology and Plant Molecular Biology **51**, 371–400.
- Schwenkert S, Legen J, Takami T, Shikanai T, Herrmann RG, Meurer J. 2007. Role of the low-molecular-weight subunits PetL, PetG, and PetN in assembly, stability, and dimerization of the cytochrome *b_{6/f}* complex in tobacco. Plant Physiology **144**, 1924–1935.
- Serrato AJ, Pérez-Ruiz JM, Spínola MC, Cejudo FJ. 2004. A novel NADPH thioredoxin reductase, localized in the chloroplast, which deficiency causes hypersensitivity to abiotic stress in *Arabidopsis thaliana*. Journal of Biological Chemistry **279**, 43821–43827.
- Sharkey TD. 1988. Estimating the rate of photorespiration in leaves. Physiologia Plantarum **73**, 147–152.
- Shimada Y, Tsuchiya T, Akimoto S, Tomo T, Fukuya M, Tanaka K, Mimuro M. 2008. Spectral properties of the CP43-deletion mutant of *Synechocystis* sp. PCC 6803. Photosynthesis Research **98**, 303–314.
- Simkin AJ, Lopez-Calcano PE, Davey PA, Headland LR, Lawson T, Timm S, Bauwe H, Raines CA. 2017a. Simultaneous stimulation of sedoheptulose 1,7-bisphosphatase, fructose 1,6-bisphosphate aldolase and the photorespiratory glycine decarboxylase-H protein increases CO₂ assimilation, vegetative biomass and seed yield in Arabidopsis. Plant Biotechnology Journal **15**, 805–816.
- Simkin AJ, McAusland L, Headland LR, Lawson T, Raines CA. 2015. Multigene manipulation of photosynthetic carbon assimilation increases CO₂ fixation and biomass yield in tobacco. Journal of Experimental Botany **66**, 4075–4090.
- Simkin AJ, McAusland L, Lawson T, Raines CA. 2017b. Overexpression of the RieskeFeS protein increases electron transport rates and biomass yield. Plant Physiology **175**, 134–145.
- Slattery RA, Walker BJ, Weber APM, Ort DR. 2018. The impacts of fluctuating light on crop performance. Plant Physiology **176**, 990–1003.
- Soleh MA, Tanaka Y, Nomoto Y, Iwahashi Y, Nakashima K, Fukuda Y, Long SP, Shiraiwa T. 2016. Factors underlying genotypic differences in the induction of photosynthesis in soybean [*Glycine max* (L.) Merr.]. Plant, Cell & Environment **39**, 685–693.
- Solomon S. 2007. Climate change 2007. The physical science basis: Working Group I contribution to the Fourth Assessment Report of the IPCC. Cambridge: Cambridge University Press.

- Sonneuwald U, Fernie AR.** 2018. Next-generation strategies for understanding and influencing source–sink relations in crop plants. *Current Opinion in Plant Biology* **43**, 63–70.
- South P, Ort DR.** 2017. Engineering biochemical bypass to photorespiration to improve photosynthesis and crop production. *FASEB Journal* **31** (Suppl), 628.3.
- South PF, Cavanagh AP, Lopez-Calcano PE, Raines CA, Ort DR.** 2018. Optimizing photorespiration for improved crop productivity. *Journal of Integrative Plant Biology* **60**, 1217–1230.
- Stitt M, Schulze D.** 1994. Does Rubisco control the rate of photosynthesis and plant-growth—an exercise in molecular ecophysiology. *Plant, Cell & Environment* **17**, 465–487.
- Suzuki Y, Kondo E, Makino A.** 2017. Effects of co-overexpression of the genes of Rubisco and transketolase on photosynthesis in rice. *Photosynthesis Research* **131**, 281–289.
- Takizawa K, Kanazawa A, Kramer DM.** 2008. Depletion of stromal P(i) induces high ‘energy-dependent’ antenna exciton quenching (q(E)) by decreasing proton conductivity at CF(O)–CF(1) ATP synthase. *Plant, Cell & Environment* **31**, 235–243.
- Taler D, Galperin M, Benjamin I, Cohen Y, Kenigsbuch D.** 2004. Plant eR genes that encode photorespiratory enzymes confer resistance against disease. *The Plant Cell* **16**, 172–184.
- Tamoi M, Nagaoka M, Miyagawa Y, Shigeoka S.** 2006. Contribution of fructose-1,6-bisphosphatase and sedoheptulose-1,7-bisphosphatase to the photosynthetic rate and carbon flow in the Calvin cycle in transgenic plants. *Plant & Cell Physiology* **47**, 380–390.
- Taylor SH, Long SP.** 2017. Slow induction of photosynthesis on shade to sun transitions in wheat may cost at least 21% of productivity. *Philosophical Transactions of the Royal Society B: Biological Sciences* **372**, 20160543.
- Thompson LR, Zeng Q, Kelly L, Huang KH, Singer AU, Stubbe J, Chisholm SW.** 2011. Phage auxiliary metabolic genes and the redirection of cyanobacterial host carbon metabolism. *Proceedings of the National Academy of Sciences, USA* **108**, E757–E764.
- Thormählen I, Meitzel T, Groysman J, Öchsner AB, von Roepenack-Lahaye E, Naranjo B, Cejudo FJ, Geigenberger P.** 2015. Thioredoxin f1 and NADPH-dependent thioredoxin reductase C have overlapping functions in regulating photosynthetic metabolism and plant growth in response to varying light conditions. *Plant Physiology* **169**, 1766–1786.
- Tikhonov AN.** 2014. The cytochrome *b₆f* complex at the crossroad of photosynthetic electron transport pathways. *Plant Physiology and Biochemistry* **81**, 163–183.
- Tilman D, Balzer C, Hill J, Befort BL.** 2011. Global food demand and the sustainable intensification of agriculture. *Proceedings of the National Academy of Sciences, USA* **108**, 20260–20264.
- Tilman D, Clark M.** 2015. Food, agriculture and the environment: can we feed the world and save the Earth? *Daedalus* **144**, 8–23.
- Timm S, Florian A, Arrivault S, Stitt M, Fernie AR, Bauwe H.** 2012. Glycine decarboxylase controls photosynthesis and plant growth. *FEBS Letters* **586**, 3692–3697.
- Timm S, Florian A, Fernie AR, Bauwe H.** 2016. The regulatory interplay between photorespiration and photosynthesis. *Journal of Experimental Botany* **67**, 2923–2929.
- Timm S, Giese J, Engel N, Wittmiß M, Florian A, Fernie AR, Bauwe H.** 2018. T-protein is present in large excess over the other proteins of the glycine cleavage system in leaves of *Arabidopsis*. *Planta* **247**, 41–51.
- Timm S, Wittmiß M, Gamlien S, Ewald R, Florian A, Frank M, Wirtz M, Hell R, Fernie AR, Bauwe H.** 2015. Mitochondrial dihydrolipoyl dehydrogenase activity shapes photosynthesis and photorespiration of *Arabidopsis thaliana*. *The Plant Cell* **27**, 1968–1984.
- Tinocoanguren C, Percy RW.** 1995. A comparison of light quality and quantity effects on the growth and steady-state and dynamic photosynthetic characteristics of three tropical tree species. *Functional Ecology* **9**, 222–230.
- Toivola J, Nikkanen L, Dahlström KM, Salminen TA, Lepistö A, Vignols HF, Rintamäki E.** 2013. Overexpression of chloroplast NADPH-dependent thioredoxin reductase in *Arabidopsis* enhances leaf growth and elucidates in vivo function of reductase and thioredoxin domains. *Frontiers in Plant Science* **4**, 389.
- Tolbert NE.** 1979. Glycolate metabolism by higher plants and algae. In: Gibbs M, Latzko E, eds. *Photosynthesis II. Encyclopedia of plant physiology (New Series)*, Vol. **6**. Berlin, Heidelberg: Springer, 338–352.
- Tolbert NE.** 1997. The C2 oxidative photosynthetic carbon cycle. *Annual Review of Plant Physiology and Plant Molecular Biology* **48**, 1–25.
- Trost P, Fermani S, Marri L, Zaffagnini M, Falini G, Scagliarini S, Pupillo P, Sparla F.** 2006. Thioredoxin-dependent regulation of photosynthetic glyceraldehyde-3-phosphate dehydrogenase: autonomous vs. CP12-dependent mechanisms. *Photosynthesis Research* **89**, 263–275.
- Uematsu K, Suzuki N, Iwamae T, Inui M, Yukawa H.** 2012. Increased fructose 1,6-bisphosphate aldolase in plastids enhances growth and photo-synthesis of tobacco plants. *Journal of Experimental Botany* **63**, 3001–3009.
- Violet-Chabrand S, Matthews JS, Simkin AJ, Raines CA, Lawson T.** 2017. Importance of fluctuations in light on plant photosynthetic acclimation. *Plant Physiology* **173**, 2163–2179.
- Vitousek PM, Aber JD, Howarth RW, Likens GE, Matson PA, Schindler DW, Schlesinger WH, Tilman D.** 1997. Human alteration of the global nitrogen cycle: sources and consequences. *Ecological Applications* **7**, 737–750.
- Walker BJ, South PF, Ort DR.** 2016a. Physiological evidence for plasticity in glycolate/glycerate transport during photorespiration. *Photosynthesis Research* **129**, 93–103.
- Walker BJ, VanLoocke A, Bernacchi CJ, Ort DR.** 2016b. The costs of photorespiration to food production now and in the future. *Annual Review of Plant Biology* **67**, 107–129.
- Wallsgrave RM, Keys AJ, Bird IF, Cornelius MJ, Lea PJ, Mifflin BJ.** 1980. The location of glutamine synthetase in leaf cells and its role in the re-assimilation of ammonia released in photorespiration. *Journal of Experimental Botany* **31**, 1005–1017.
- Wedel N, Soll J, Paap BK.** 1997. CP12 provides a new mode of light regulation of Calvin cycle activity in higher plants. *Proceedings of the National Academy of Sciences, USA* **94**, 10479–10484.
- Weigel H, Manderscheid R.** 2012. Crop growth responses to free air CO₂ enrichment and nitrogen fertilization: rotating barley, ryegrass, sugar beet and wheat. *European Journal of Agronomy* **43**, 97–107.
- Willey DL, Gray JC.** 1988. Synthesis and assembly of the cytochrome b₆-f complex in higher plants. *Photosynthesis Research* **17**, 125–144.
- Wilson F, Harrison K, Armitage AD, Simkin AJ, Harrison RJ.** 2019. CRISPR/Cas9-mediated mutagenesis of phytoene desaturase in diploid and octoploid strawberry. *BioRxiv* doi: 10.1101/471680. [Preprint]
- Wingler A, Lea PJ, Leegood RC.** 1997. Control of photosynthesis in barley plants with reduced activities of glycine decarboxylase. *Planta* **202**, 171–178.
- Wirtz W, Stitt M, Heldt HW.** 1982. Light activation of Calvin cycle enzymes as measured in pea leaves. *FEBS Letters* **142**, 223–226.
- Wolosiuk RA, Buchanan BB.** 1977. Thioredoxin and glutathione regulate photosynthesis in chloroplasts. *Nature* **266**, 565–567.
- Wolosiuk RA, Crawford NA, Yee BC, Buchanan BB.** 1979. Isolation of three thioredoxins from spinach leaves. *Journal of Biological Chemistry* **254**, 1627–1632.
- WorldBank.** 2008. World development report 2008. Washington, DC: Agriculture for Development, World Bank.
- Xin CP, Tholen D, Devloo V, Zhu XG.** 2015. The benefits of photorespiratory bypasses: how can they work? *Plant Physiology* **167**, 574–585.
- Xu M, Bernát G, Singh A, Mi H, Rögner M, Pakrasi HB, Ogawa T.** 2008. Properties of mutants of *Synechocystis* sp. strain PCC 6803 lacking inorganic carbon sequestration systems. *Plant & Cell Physiology* **49**, 1672–1677.
- Yadav SK, Khatri K, Rathore MS, Jha B.** 2018. Introgression of UfCyt c6, a thylakoid lumen protein from a green seaweed *Ulva fasciata* Delile enhanced photosynthesis and growth in tobacco. *Molecular Biology Reports* **45**, 1745–1758.
- Yamori W.** 2016. Photosynthetic response to fluctuating environments and photoprotective strategies under abiotic stress. *Journal of Plant Research* **129**, 379–395.
- Yamori W, Kondo E, Sugiura D, Terashima I, Suzuki Y, Makino A.** 2016. Enhanced leaf photosynthesis as a target to increase grain yield:

insights from transgenic rice lines with variable Rieske FeS protein content in the cytochrome b6/f complex. *Plant, Cell & Environment* **39**, 80–87.

Yamori W, Masumoto C, Fukayama H, Makino A. 2012. Rubisco activase is a key regulator of non-steady-state photosynthesis at any leaf temperature and, to a lesser extent, of steady-state photosynthesis at high temperature. *The Plant Journal* **71**, 871–880.

Yamori W, Sakata N, Suzuki Y, Shikanai T, Makino A. 2011a. Cyclic electron flow around photosystem I via chloroplast NAD(P)H dehydrogenase (NDH) complex performs a significant physiological role during photosynthesis and plant growth at low temperature in rice. *The Plant Journal* **68**, 966–976.

Yamori W, Takahashi S, Makino A, Price GD, Badger MR, von Caemmerer S. 2011b. The roles of ATP synthase and the cytochrome b₆/f complexes in limiting chloroplast electron transport and determining photosynthetic capacity. *Plant Physiology* **155**, 956–962.

Yang XF, Wang YT, Chen ST, Li JK, Shen HT, Guo FQ. 2016. PBR1 selectively controls biogenesis of photosynthetic complexes by modulating translation of the large chloroplast gene Ycf1 in Arabidopsis. *Cell Discovery* **2**, 16003.

Yoshida K, Hara A, Sugiura K, Fukaya Y, Hisabori T. 2018. Thioredoxin-like2/2-Cys peroxiredoxin redox cascade supports oxidative thiol modulation

in chloroplasts. *Proceedings of the National Academy of Sciences, USA* **115**, E8296–E8304.

Yoshida K, Hisabori T. 2017. Distinct electron transfer from ferredoxin-thioredoxin reductase to multiple thioredoxin isoforms in chloroplasts. *The Biochemical Journal* **474**, 1347–1360.

Zaffagnini M, Bedhomme M, Groni H, Marchand CH, Puppo C, Gontero B, Cassier-Chauvat C, Decottignies P, Lemaire SD. 2012. Glutathionylation in the photosynthetic model organism *Chlamydomonas reinhardtii*: a proteomic survey. *Molecular & Cellular Proteomics* **11**, M111.014142.

Zelitch I, Schultes NP, Peterson RB, Brown P, Brutnell TP. 2009. High glycolate oxidase activity is required for survival of maize in normal air. *Plant Physiology* **149**, 195–204.

Zhou Q, Yu Q, Wang Z, Pan Y, Lv W, Zhu L, Chen R, He G. 2013. Knockdown of GDCH gene reveals reactive oxygen species-induced leaf senescence in rice. *Plant, Cell & Environment* **36**, 1476–1489.

Zhu XG, de Sturler E, Long SP. 2007. Optimizing the distribution of resources between enzymes of carbon metabolism can dramatically increase photosynthetic rate: a numerical simulation using an evolutionary algorithm. *Plant Physiology* **145**, 513–526.

Zhu XG, Long SP, Ort DR. 2010. Improving photosynthetic efficiency for greater yield. *Annual Review of Plant Biology* **61**, 235–261.