Feeding the world: improving photosynthetic efficiency for sustainable crop production

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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 cultivable 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; Califapietra 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; Kolßmann 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 developmental 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.
Evidence that transgenic manipulation of photosynthesis could increase yield

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.

Fig. 1. Schematic representation of the Calvin–Benson cycle. Sedoheptulose-1,7-bisphosphatase (SBPase: EC 3.1.3.37), fructose-1,6-bisphosphatases (FBPase; EC 3.1.3.11), transketolase (TK; EC 2.2.1.1), phosphoribulokinase (PRK; EC 2.7.1.19), ribulose-phosphate 3-epimerase (RPE; EC 5.1.3.1), triosephosphate isomerase (TPI; EC 5.3.1.1), glyceraldehyde 3-phosphate dehydrogenase (GAPDH; EC 1.2.1.12), phosphoglycerate kinase (PGK; EC 2.7.2.3), ribose 5-phosphate isomerase A (RPI; EC.5.3.1.6), Rubisco (EC 4.1.1.39).
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

### 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 CO₂ assimilation | 42% increase in dry weight and a 53% increase in seed yield | Simkin et al. (2017a)* |
| 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 et al. (2005); Simkin et al. (2015c) |
| Tomato                           | Constitutive expression. 55–139% increase in SBPase activity, ~25% increase in CO₂ 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 et al. (2016)c |
| Wheat                            | Constitutive expression. Up to 90% increase in SBPase activities in some lines, increase in CO₂ assimilation | Up to 40% increase in grain yield | Driever et al. (2017)c |
| Rice                             | Constitutive expression. Up to 200% increase in SBPase activities in some lines, increased CO₂ assimilation rates under elevated temperature | Higher growth rates under elevated temperature | Feng et al. (2007)c |
| Cyanobacterial SBPase Tobacco     | Tissue-specific expression. More than 20% increase in the rate of photosynthetic CO₂ fixation | 50% increase in final dry weight | Tamoi et al. (2006)a |
| Cyanobacterial FBPase Tobacco     | Tissue-specific expression. 15% increase in CO₂ fixation rates in some lines | 30% increase in dry weight | Tamoi et al. (2006)a |
| FBPaldolase                      | Arabidopsis | Tissue specific expression. 46–80% increase in FBPaldolase activity, 31% increase in CO₂ assimilation | 32% increase in dry weight, 35% increase in seed yield | Simkin et al. (2017a)a |
| Tobacco                          | Tissue-specific expression. 40–90% increase in FBPaldolase activities, 19% increase in photosynthetic CO₂ fixation | 10–30% increase in dry weight at ambient CO₂ with a 70–120% increase in high CO₂ | Uematsu et al. (2012)f |
| Transketolase                    | Tobacco | Constitutive expression. 76–150% increase in transketolase activity, no increase in photosynthesis | Negative effect on plant growth resulting in leaf chlorosis | Khozaei et al. (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 et al. (2017)a |
| Cyanobacterial SBP/ FBPase Tobacco | Tissue-specific expression. 70% increase in FBPase activity, 130% increase in SBPase activity, 20% increase in photosynthetic CO₂ fixation | Increase in biomass of 40–50% | Miyagawa et al. (2001)a |
| Lettuce                          | Tissue-specific expression. Photosynthetic capacity was increased by 30–60% | 60% increase in fresh weight | Ichikawa et al. (2010)a |
| Cyanobacterial SBP/ FBPase Soybean | Constitutive expression. 4–14% increase in CO₂ fixation rates in some lines | Under ambient CO₂, elevated temperature led to reductions in seed yield. Under elevated CO₂ and elevated temperature, seed yield was maintained while the WT showed 11% and 22% reductions | Köhler et al. (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.
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/SBP) 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 an increase in biomass of 70–120%. An increase in aldolase activities, a 1.5-fold elevation of photosynthetic activity (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 reassimilation of NH3 via glutamine synthetase and glutamine 2-oxoglutarate aminotransferase also adds to the energetic costs (Wallsgrove et al., 1980; Keys, 2006; Maclusky-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.

**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).
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 CO₂ 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 CO₂, 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

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).
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 Wingler 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 glycolate content and had lower CO₂ assimilation rates under drought stress (Wingler 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., 2014a) (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-Calcagno 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 photosynthetic 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-Calcagno 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, triose-phosphate 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; Hauser 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) c₆ 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 c₆ 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 c₆ can transfer electrons from the Cyt b₆ 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 c₆ 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 b₆f complex

The Cyt b₆f 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 PSI and PSI, providing ATP and NADPH for photosynthetic carbon fixation by oxidizing PQH₂ and reducing plastocyanin (Kurisu 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 fj), PetB (Cyt bh), 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
functions as a dimer, enhancing its complexity. The transmembrane domains of the cyt $b_6$ 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 $b_6f$ 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 $b_6f$ complex (Price et al., 1998; Yamori et al., 2011b). First, Cyt $b_6f$ inhibitors were used (Kirchhoff et al., 2000), and then antisense studies suppressing the Rieske FeS protein (PetC) have shown that the Cyt $b_6f$ 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

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### 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 | 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), Timm et al. (2012) |
| | H-protein | | | | |
| | 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-Calcagno et al. (2018) |
| | 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-Calcagno et al. (2018) |
| | Glycine decarboxylase | 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) |
| | L-protein | | | | |
| | Glycine decarboxylase | Arabidopsis | No alterations in photosynthetic CO$_2$ uptake | No increase in plant growth | Timm et al. (2018) |
| | T-protein | | | | |
| 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) |
| | 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) |
| 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) |
| 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) |
| | Tobacco | Constitutive expression. 20–28% increase in CO$_2$ assimilation rates | 71% increase in biomass | Simkin et al. (2015) |
| | Rice | Constitutive expression. 18% increase in CO$_2$ assimilation | 17.9% increase in biomass and increased plant height | Gong et al. (2015) |
| | 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) |

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.
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 qL and a lower 1–qP (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 PSII/PSII proteins LhcaI, PsaA, PsaB, PsbD, and AtpD (Vialet-Chabrand et al., 2017). Furthermore, the hsf 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 b,f, 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 over-expression 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 C3 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 C3 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 HCO₃⁻ accumulation; however, subsequent work demonstrated that ictB is not a HCO₃⁻ 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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ assimilation, Rubisco carboxylation ($V_{\text{max}}$), electron transport ($J_{\text{max}}$), 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 Khoozei 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-Calcagno et al., 2018). However, López-Calcagno 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; Kühler 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 (Athanasius et al., 2010; Alter et al., 2012; Kono and Terashima, 2014; Kaiser et al., 2016, 2018a; Yamori, 2016; Vialet-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; Vialet-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; Kühlheim 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 bisphosphate regeneration capacity (J_m), 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; Knuesting and Scheibe, 2018; Nikkanen and Rintamaki, 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. Trx f 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 described as an important player in stress and oxidative damage responses (Serrato et al., 2004; Pérez-Ruiz et al., 2006). Like Trx s, 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; Tinocojjanguren 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; Carmona-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 duration and magnitude 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
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 maintained under high CO 2 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 \( J_{\text{max}} \) 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.

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

| Manipulation | Gene targeted | Plant | Manipulation detail | Phenotype | References |
|--------------|---------------|-------|---------------------|-----------|------------|
| Regulatory proteins | Rca | Rice | Tissue-specific expression of the barley Rca | Reduction in Rubisco amount | Fukayama et al. (2012) |
| | | | | Reduction in CO2 assimilation | | |
| | | | | Increased rate of photosynthetic induction by light | | |
| | Rice | Rice | Tissue-specific expression of the maize Rca | Increased rate of photosynthetic induction by light | Yamori et al. (2012) |
| | | | | Increased rate of Rubisco activation at high temperature (40 °C) | | |
| | Arabidopsis | Arabidopsis | Constitutive expression of a thermostable Rca isoform | Increased rate of Rubisco activation | Kurek et al. (2007) |
| | | | | Increased CO2 assimilation, biomass, and seed yield at high temperature | | |
| | Arabidopsis | Arabidopsis | Tissue-specific expression of chimeric Rca | Increased rate of Rubisco activation | Kumar (2009) |
| | | | | Increased CO2 assimilation, biomass, and seed yield at high temperature | | |
| CP12 | Tobacco | Tobacco | Antisense down-regulation of CP12 gene family | Reductions in PRK and GAPDH activity | Howard et al., 2011a, 2011c |
| | | | | Reduced photosynthetic CO2 assimilation | | |
| | | | | Reductions in biomass | | |
| | Arabidopsis | Arabidopsis | KO of cp12-1 and cp12-3 plus reductions of expression of cp12-2 below 20% of WT levels | 80% reductions in PRK levels | Lopez-Calcagno et al. (2017) |
| | | | | Reduced photosynthetic CO2 assimilation | | |
| | Aublet | Aublet | Constitutive expression of CP12 | Over 50% reductions in biomass | Li et al. (2018) |
| | | | | Increased biomass, photosynthetic rates, GAPDH, and PRK activities | | |
| | | | | Increased survival, and reduced ion leakage after chilling treatment | | |
| | Aublet | Aublet | Reduced CP12 expression | Reduced biomass, photosynthetic rates, GAPDH, and PRK activities | Li et al. (2018) |
| | | | | Reduced survival, and increased ion leakage after chilling treatment | | |
| | Trx f | Tobacco | Plastidial expression of Trx f | Up to 21% increase in specific leaf weight | Sanz-Barrio et al. (2013); Farran et al. (2014); Aranjuelo et al. (2015) |
| | | | | Up to 5.5-fold increase in fermentable carbohydrates per unit dry weight | | |
| | | | | Lower photospirosis rate | | |
| NTRC | Arabidopsis | Arabidopsis | Constitutive expression of NTRC | 42–263% increase in dry weight | Toivola et al. (2013); Nikkanen et al. (2016); Kim et al. (2017) |
| | | | | Increased starch | | |
| | | | | Increased photosynthesis | | |
| | | | | Enhanced tolerance to photo-oxidative and drought stresses | | |
| | Null mutant | Null mutant | | 90% reductions in growth | Toivola et al. (2013) |

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).
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 μmol m⁻² s⁻¹ light (no significant difference in biomass was observed when plants were grown at 130 μmol m⁻² 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., 2007; Carmo-Silva et al., 2011; Howard et al., 2011b). This complex has been studied extensively in vitro (Avilán 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-Calcagno 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-Calcagno 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-Calcagno 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; Rouhi 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 QA (Glowacka et al., 2018). Changes in the oxidation state of the plastocyanin-pool have been proposed to be able to control stomatal movement (Busch, 2014), and the PsbS transgensics experiments showed a linear relationship between stomatal conductance and QA 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 (Wallskgrove et al., 1980; Hoshida et al., 2000; Migge et al., 2000; Fuentes et al., 2001; Habash et al.,
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.

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Author contributions

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

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